

Tracking marine megafauna for conservation and marine spatial planning

Edited by

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Tracking marine megafauna for conservation and marine spatial planning

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Editorial: Tracking marine megafauna for conservation and marine spatial planning

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Editorial on the Research Topic

Tracking marine megafauna for conservation and marine spatial planning

1 Introduction

Marine megafauna are an important component of marine ecosystems providing a range of cultural, regulating and provisioning ecosystem services to humans (Dunn et al., 2019; Hammerschlag et al., 2019). They transport energy, nutrients, and other materials vertically and horizontally through the oceans (Roman et al., 2014; Kiszka et al., 2015; Estes et al., 2016; Hammerschlag et al., 2019), and through their large size and often high mobility, influence other species through consumption and risk avoidance behaviour. Marine megafauna also include important focal species (Zacharias and Roff, 2001) in marine conservation and management, given their role as sentinel species or ecological indicators (Hazen et al., 2019).

Despite their important role in ecosystems, the widespread and increasing threats faced by many marine megafauna taxa has led to a poor conservation status of many species (e.g., Rees et al., 2016; Dias et al., 2019; Nelms et al., 2021; Jorgensen et al., 2022). Understanding and mitigating the threats faced by marine megafauna is challenging (Lascelles et al., 2014; Reisinger et al., 2022) because both the threats and the marine environment are highly dynamic in space and time, and animals' occurrences vary with shifts in environmental and oceanographic conditions at different scales. Additionally, these animals are often highly mobile, making it difficult to pinpoint the occurrences of different individuals in specific locations.

There are several definitions for the term 'marine megafauna'. For example, Estes et al. (2016) define marine megafauna as species with maximum reported mass >45 kg,

including 338 extant species of cetaceans, pinnipeds, sirenians, the sea otter (*Enhydra lutris*), the polar bear (*Ursus maritimus*), the emperor penguin (*Aptenodytes forsteri*), marine reptiles, bony and cartilaginous fishes, cephalopods, and the giant clam (*Tridacna gigas*). Here, we take the view of Authier et al. (2017), who do not impose a strict body mass threshold, but consider marine megafauna to be a coherent group based on their ecological similarities (at or near the top of food webs, with no or few predators) and that share conservation issues.

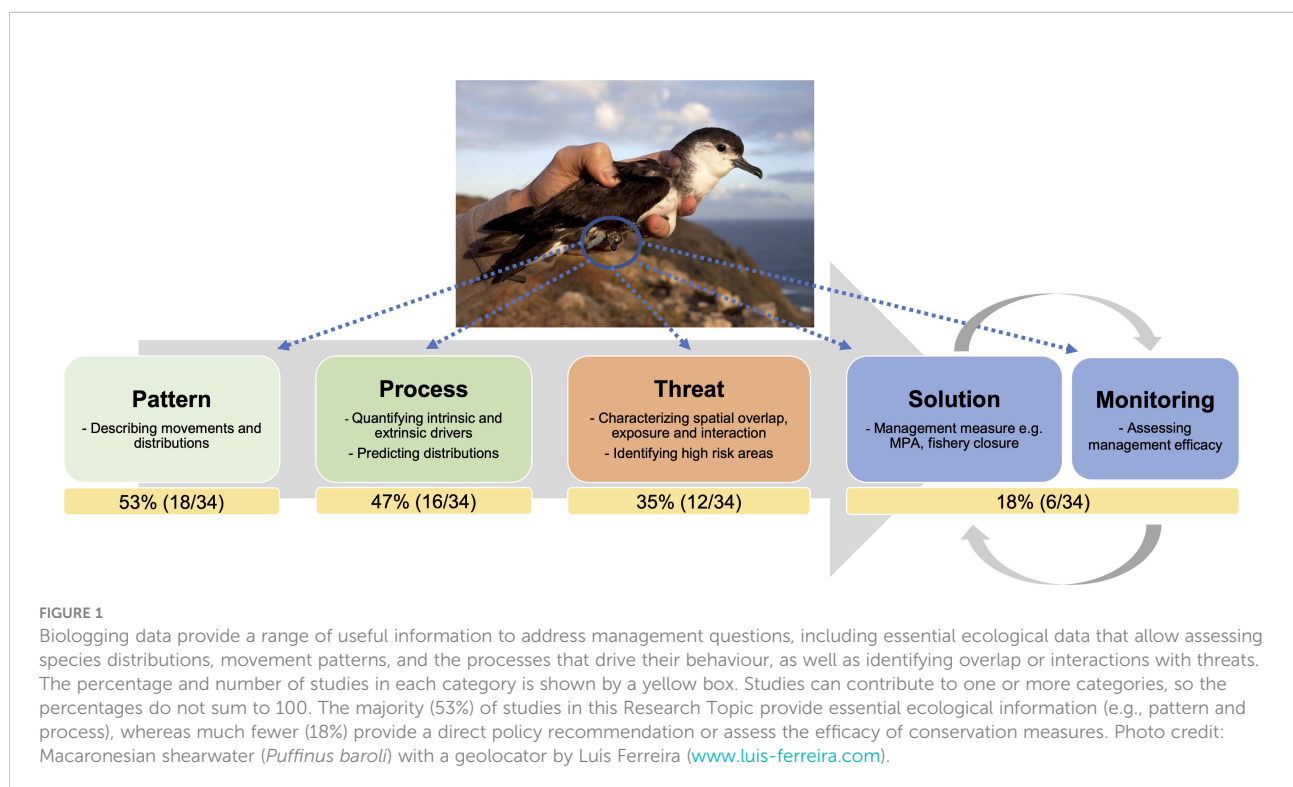
This Research Topic covers a broad taxonomic representation, spanning seabirds, cetaceans, sea turtles, pinnipeds, elasmobranchs, teleosts, a sirenian, the polar bear, and a large crustacean, the red king crab (*Paralithodes camtschaticus*). Articles submitted address how biologging is being used to understand the movement behaviour and distribution of marine megafauna, and how this information can play a key role to prioritise conservation goals. The resulting 34 articles illustrate how biologging is informing conservation of marine megafauna, and in light of these studies, we discuss challenges, methodological implications and future directions for biologging in conservation.

2 Patterns and processes

A massive increase in the use of biologging, including miniaturised animal-attached tags for logging or relaying data about animal movements, behaviour, physiology, or environment (Rutz and Hays, 2009; Williams et al., 2020), has been instrumental

in providing this otherwise hard to come by information (Hussey et al., 2015). Due to technological limitations (e.g., tag weight), funding or other resource limitations, remoteness, difficulty of capture, and handling or tagging, the movements and distributions of many species, populations or life stages remain poorly understood (Pereira et al., 2022). Many studies in this Research Topic provide baseline information important for conservation (e.g., Laidre et al., Schorr et al., Figure 1). For example, Setyawan et al. used a combination of methods to document the movements of juvenile reef manta rays (*Mobula alfredi*) in Indonesia and found that individuals are largely resident within the Wayag lagoon, emphasising the need for area-based protection. Biologging studies also enable an understanding of the patterns and processes driving range shifts (Cloyed et al.). For instance, Aune et al. tagged invasive red king crabs to better understand their habitat requirements and environmental conditions facilitating their invasion into new fjords in Norway.

Biologging also provides the opportunity to explore habitat requirements and quantify the environmental drivers of species distribution. Studies in this Research Topic demonstrate that bottom depth (Dehnhard et al.), topography (Wyles et al.), marine productivity (Thiebot et al.) and sea ice cover (Harcourt et al., Fortune et al.), among other factors, influence the movement and foraging decisions of marine megafauna (Figure 1). However, their importance differs between populations or species, highlighting the need for species- and population-specific studies (Carter et al., O'Hanlon et al.). Moreover, some studies have failed to find effects of environmental features on foraging decisions,



likely because wide-ranging species (such as seabirds) may have weak or broad preferences for available habitats (Halpin et al., Morten et al.). Biologging studies also enable an understanding of individual-level patterns and processes driving movement or foraging strategies. For example, foraging strategies of individuals can vary according to sub-colony (Morinay et al.) and be related to colony size (Rebstock et al.) and individual-level specialisation independent of these factors (Descamps et al.). In most habitat modelling studies, environmental variables are commonly assumed to be surrogates of the distribution and abundance of lower trophic level prey, but very few incorporate data on prey abundance (Chambault et al.). Proud et al. showed that incorporating 3-dimensional prey distributions from active acoustics can improve predictions of the foraging distributions of king penguins (*Aptenodytes patagonicus*).

3 Overlap and interaction with anthropogenic stressors

By pinpointing where, why and how marine megafauna overlap, interact and respond to anthropogenic activities, biologging can highlight areas for protection and contribute to a more sustainable exploitation of marine resources (Hays et al., 2019; Grémillet et al., 2022). In this Research Topic, we focus on the ways in which biologging has extended our ability to measure the exposure of marine megafauna to anthropogenic threats (Figure 1) such as fisheries, shipping, and offshore platforms and seismic surveys.

3.1 Fisheries

Fisheries have impacted marine megafauna worldwide, either directly as target catch, bycatch (Lewison et al., 2004), or through indirect interactions such as competition for food resources (Grémillet et al., 2018). Biologging has provided crucial information on the extent to which species overlap with and are exposed to fishing activity (e.g. Clay et al., 2019; Queiroz et al., 2019). For example, by comparing the distributions of satellite-tagged white sharks (*Carcharodon carcharias*) and fishing effort, Kock et al. showed that sharks overlapped with longline and gillnet fisheries within 25% of South Africa's Exclusive Economic Zone (EEZ). High-precision tracking of individual animals and fishing vessels can also reveal the extent to which marine taxa interact with fishing vessels (Weimerskirch et al., 2020; Morten et al., Reisinger et al.).

3.2 Shipping

Shipping is increasing globally, presenting a growing threat to marine megafauna (Pirodda et al., 2019) and biologging may provide valuable information regarding where and when marine

species are exposed to vessel strikes, which are often undetected and unreported (Womersley et al., 2022). Pasanisi et al. mapped for the first time the oceanic areas of high exposure between loggerhead turtles (*Caretta caretta*) and shipping traffic in the western Mediterranean, while Thiebot et al. showed that key habitats of four Arctic seabirds are not fully covered by a designated shipping avoidance area, recommending a northward extension that better affords protection. By incorporating high-resolution data on vertical movements, both Fonseca et al. and Oliveira et al. show that fin (*Balaenoptera physalus*) and sperm whales (*Physeter macrocephalus*) may be more vulnerable to collision on the sea surface at night, or when conducting fast dive ascents, respectively.

3.3 Offshore platforms and seismic surveys

Increasing global energy demands have led to the expansion of both petrochemical and renewable platforms, which may pose significant threats to marine biodiversity (Venegas-Li et al., 2019; Harwood and King, 2022). Yet, few studies have attempted to quantify the extent to which animals interact with these structures. Collins et al. showed that foraging Leach's Storm-Petrels (*Hydrobates leucorhous*) flew within the surroundings of an oil platform in 17.5% of the trips, though birds rarely approached them at night. Rebstock et al. also showed that Magellanic penguins (*Spheniscus magellanicus*) from multiple colonies off the east coast of Argentina extensively overlapped with a large area permitted for hydrocarbon exploration and where seismic surveys are regularly carried out.

4 Establishment and monitoring of area-based conservation measures

There is an increasing global push towards setting aside large swathes of the ocean as marine protected areas (MPA), however, their efficacy in protecting marine megafauna habitats remains unclear, particularly for species with vast home ranges. Biologging data play an increasingly important role in MPA design, implementation and management (Hays et al., 2019) and multispecies studies have shed light into the degree to which wide-ranging species are protected by MPAs throughout key life-history stages (Handley et al., 2020; Hindell et al., 2020; Baylis et al., 2021).

Several studies showed that MPAs in their current form allow some protection (Harcourt et al., Kock et al., Patrício et al.); for instance, the Ross Sea MPA off Antarctica encompassed all Weddell seal (*Leptonychotes weddellii*) habitat given their largely coastal distribution (Harcourt et al.), while green turtles (*Chelonia mydas*) in West Africa spent 78% of their time within five sites in a

regional MPA network, which are mostly no-take zones (Patricio et al.). In contrast, other studies found that current MPA boundaries present gaps in protection (Carter et al., Conners et al.). In the United Kingdom, the distribution of grey seals (*Halichoerus grypus*) does not match the distribution of Special Areas for Conservation (SACs), which were legally designated for their protection (Carter et al.). Conners et al. compiled biologging data from 36 species to compare space use in relation to the size and location of global MPAs, and found them too small to encompass the complete home ranges of most species (MPAs covered <5% of core areas). It is suggested that MPAs focus on targeting seasonal aggregations and critical life history stages, and be enacted alongside other management measures such as bycatch mitigation.

5 Megafauna as ecosystem indicators

While this Research Topic has largely focused on how biologging can inform the conservation of studied species, it is widely recognised that marine megafauna can act as sentinels indicating the state of ecosystems, habitats or other species (e.g., prey distributions) that are more challenging to monitor directly (Hazen et al., 2019; Jelich et al., 2022). Two complementary studies present the use of seabirds as indicators of humpback whale (*Megaptera novaeangliae*) abundance in US waters; Cimino et al. tracked western gulls (*Larus occidentalis*) in the California Current over a 7-year period and found that gulls often feed in association with whales, while Silva et al. found tagged great shearwaters (*Ardenna gravis*) in the Stellwagen Bank National Marine Sanctuary overlapped with whale distributions. Both studies suggest that seabirds could be used as indicators of whales and their prey (e.g., krill), given the relative ease and low cost of tagging seabirds relative to other species.

6 Methodological implications and the future of biologging for conservation

While biologging has provided a wealth of knowledge on the distribution and behaviour of megafauna, it should be viewed as a complement to other methods, providing information where traditional tools cannot. In this Research Topic, we also included several studies that examine species distributions through alternative means. For example, passive acoustic monitoring of humpback whales, which have characteristic calls, established their occurrence between the coast of South Africa and the Antarctic shelf across a multi-year period (Shabangu and Kowarski). Bottom-mounted acoustic hydrophones revealed

social interactions of North Pacific minke whales (*Balaenoptera acutorostrata*) (Martin et al.). Active acoustic tracking combines concepts of acoustic monitoring (networks of receivers) and biologging (animal-mounted acoustic devices emitting data) to assess key aspects of the movement ecology of marine megafauna (Alexandri and Diamant). Besides acoustic technologies, the combination of animal-mounted biologging data with - non exhaustively - data from autonomous underwater vehicles, buoys, or ship-based observations (Cimino et al., Silva et al.) could be used to improve the conservation of marine megafauna, especially those species which inhabit cryptic ecosystems, such as underneath the sea ice.

Studies based on a single colony or year often may not be representative of the space use of a population or species across time (e.g., Dehnhard et al., Morinay et al.). This highlights the need for large datasets to improve our ability to provide useful information to policy makers and conservation bodies. A recent example is MegaMove (www.megamove.org), a global consortium endorsed by the UN Ocean Decade (<https://www.oceandecade.org/>), of hundreds of researchers from around the world focused on advancing conservation of marine megafauna through strategic mitigation of threats guided by an innovative global science effort. Refinements of habitat modelling approaches to better predict the foraging distributions of animals from untracked populations (Ronconi et al.) is another way to address fundamental questions at large scale. Improving the performance of species distribution models (Goetz et al.) is, however, of the utmost importance, as low performance models make real-time management challenging (Halpin et al.).

There is no doubt that technological advances will continue to bring progress to the biologging field and enhance our knowledge of the ecology of marine megafauna. In parallel with the improvement in the miniaturisation of devices, their autonomy and hydrodynamic design¹, the use of new sensors and biologging approaches will help tackle conservation issues. This is already illustrated by seabird-borne devices that monitor the Automated Identification Systems (AIS) of fishing vessels (Weimerskirch et al., 2020). Animal-borne oceanographic devices may include new biochemical and physical sensors, increasing our ability to monitor the oceans and understand the interactions between marine megafauna and their environment.

The increasing availability of biologging data with new levels of complexity also brings a new challenge associated with the efficient and effective analyses of those datasets. Analyses of large and complex datasets require substantial computational capacity and a high degree of analytical proficiency (Joo et al., 2020; Grémillet et al., 2022). Multidisciplinary collaborations will be key to develop new ways to analyse data and investigate the new

¹ Note the recent emergence of non-rigid biologgers, like the pliable "Marine Skin" logger, represents a huge improvement in respecting the hydrodynamics of marine organisms (Shaikh et al., 2019).

complexities that arise from merging multiple datasets. Making the resources available online in the form of open data and codes, which has facilitated the reproducibility of results among the scientific community (Sequeira et al., 2019; Williams et al., 2020) has been encouraged. Yet, practical examples where these studies have led to clearly identifiable real-world changes in conservation or marine spatial planning efforts are scarce. This is demonstrated in this Research Topic whereby the majority ($n = 18$, 53%) of studies were largely focused on describing spatial and behavioural patterns of marine megafauna populations, with few ($n = 6$, 18%) directly assessing the efficacy of management measures (Figure 1). Future studies should therefore be designed to address specific conservation goals and promote early engagement among scientists and stakeholders in the decision-making processes, in order to maximise the use of ecological information into effective conservation measures (Hays et al., 2019).

Author contributions

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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Conflict of interest

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Regional Variation in Winter Foraging Strategies by Weddell Seals in Eastern Antarctica and the Ross Sea

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The relative importance of intrinsic and extrinsic determinants of animal foraging is often difficult to quantify. The most southerly breeding mammal, the Weddell seal, remains in the Antarctic pack-ice year-round. We compared Weddell seals tagged at three geographically and hydrographically distinct locations in East Antarctica (Prydz Bay, *Terre Adélie*, and the Ross Sea) to quantify the role of individual variability and habitat structure in winter foraging behaviour. Most Weddell seals remained in relatively small areas close to the coast throughout the winter, but some dispersed widely. Individual utilisation distributions (UD_i , a measure of the total area used by an individual seal) ranged from 125 to 20,825 km². This variability was not due to size or sex but may be due to other intrinsic states for example reproductive condition or personality. The type of foraging (benthic vs. pelagic) varied from $56.6 \pm 14.9\%$ benthic dives in Prydz Bay through $42.1 \pm 9.4\%$ *Terre Adélie* to only $25.1 \pm 8.7\%$ in the Ross Sea reflecting regional hydrographic structure. The probability of benthic diving was less likely the deeper the ocean. Ocean topography was also influential at the population level; seals from *Terre Adélie*, with its relatively narrow continental shelf, had a core (50%) UD of only 200 km², considerably smaller than the Ross Sea (1650 km²) and Prydz Bay (1700 km²). Sea ice concentration had little influence on the time the seals spent in shallow coastal waters, but in deeper offshore water they used areas of higher ice concentration. Marine Protected Areas (MPAs) in the Ross Sea encompass all the observed Weddell seal habitat, and future MPAs that include the Antarctic continental shelf are likely to effectively protect key Weddell seal habitat.

Keywords: marine protected areas, Antarctica, marine ecosystems, bathymetry, ecosystem monitoring, Weddell seals

INTRODUCTION

Where and how animals forage is fundamental to almost all aspects of their biology. Animal foraging strategies are determined by a complex mix of intrinsic (e.g., personality, sex, age, and reproductive status) and extrinsic (e.g., topography/bathymetry, resource availability, habitat) factors which shape the distribution and availability of prey and presence of predators (McNamara and Houston, 1986; Stephens and Krebs, 1986; Daunt et al., 2005; Stephens, 2008; Russell et al., 2015). The relative importance of these factors varies within and among species, but how a population or species responds to change, whether short- or long-term, will depend on a complex interplay of the relative importance of these factors and the advantages that they confer. Quantifying the role of intrinsic and extrinsic factors in determining foraging strategies can be difficult due to the dynamic nature of individual behaviour and environmental conditions (Humphreys et al., 2006). One way to disentangle competing factors is to apply a comparative approach wherein different demographic classes or geographic regions are compared (Catry et al., 2009). For example, regional comparisons of foraging behaviour in Northern fur seals, *Callorhinus ursinus*, (Nordstrom et al., 2013), and southern elephant seals, *Mirounga leonina*, (Hindell et al., 2016) have revealed habitat partitioning and distinct individual foraging strategies that differ by sex and/or location.

In the marine environment, megafauna often exhibit different foraging behaviours over continental shelves compared to open ocean environments, with more directed movement in the latter, presumably a function of its less complex, if not more dynamic, features (Sequeira et al., 2018). The Southern Ocean is one of Earth's most extreme marine environments, and its physical structure is highly variable seasonally and spatially (Constable et al., 2003). Coastal bathymetry in the Southern Ocean is complex, with shallow banks and deep canyons compounding dynamic and static aspects of the shelf environment, as illustrated by the inflow of Modified Circumpolar Deep water (mCDW) onto the shelf and the outflow of Antarctic Bottom water to the abyssal ocean (Williams et al., 2016). This is further confounded by the formation and movement of ice (Cavalieri et al., 1999) which influences primary production and food web dynamics (Nicol et al., 2000). At the same time, the Southern Ocean is a highly productive environment that attracts multiple predator species including migratory (e.g., southern elephant seals, killer whales, *Orcinus orca*) and resident species such as Weddell seals (*Leptonychotes weddellii*), Adélie (*Pygoscelis adeliae*), and emperor (*Aptenodytes forsteri*) penguins (Hindell et al., 2020). Although migratory species forage voraciously during spring and summer, they are excluded from the continental shelf regions around the Antarctic continent as the winter ice expands by up to 300% (Cavalieri et al., 1999; Brierley and Thomas, 2002). Of the resident species, only Weddell seals and Emperor penguins appear capable of surviving *in situ* year-round without obligative dispersal (Burns and Kooyman, 2001). Emperor penguins winter-over with males fasting while incubating their single egg, and females dispersing to forage (Kirkwood and Robertson, 1997), but Weddell seals continue to forage under the sea ice

and actively maintain breathing holes throughout the winter (Kooyman et al., 1981).

There is limited understanding of the extrinsic factors influencing Weddell seal distribution and foraging behaviour during winter. Pioneering investigations showed that an isolated colony at White Island, Ross Archipelago (78°8'S 167°24'E) foraged by diving to the sea floor, primarily feeding upon benthic prey (Castellini et al., 1984). Similarly, free-ranging Weddell seals off *Terre Adélie* and in Prydz Bay, stayed within 5 km of breathing holes, moving only as local food became depleted (Heerah et al., 2016). Heerah et al. (2016) also reported regional differences, with seals in Prydz Bay travelling up to three times the distance and spending half the time in hunting mode than seals off *Terre Adélie*. Hunting dives at both locations were pelagic, concentrated in areas of high ice concentration, over areas of relatively complex bathymetry and favouring water masses such as Antarctic Surface Water and mCDW (Heerah et al., 2013, 2016). However, other studies from the Ross Sea (Testa, 1994) and the Weddell Sea (Nachtsheim et al., 2019; Photopoulou et al., 2020; Labrousse et al., 2021) reported dispersal of several hundred kilometres, albeit for the most part staying close to or over the continental shelf.

Intrinsic factors that influence foraging strategies of marine predators include age, sex, body-size, condition, reproductive status (Weise et al., 2010; Votier et al., 2017; Salton et al., 2019), intra-specific competition (Kuhn et al., 2014), and individual personality traits. Within a dynamic environment, distinct foraging strategies (e.g., epipelagic, mesopelagic or benthic) may coexist in a population (Cherel and Hobson, 2007); or be state-dependent with animals in poorer condition adopting riskier foraging behaviours (Beltran et al., 2021). Diverse foraging strategies are likely to arise because within a diverse prey field, different individuals will have greater foraging success depending on local conditions, and no single individual strategy will dominate under all conditions.

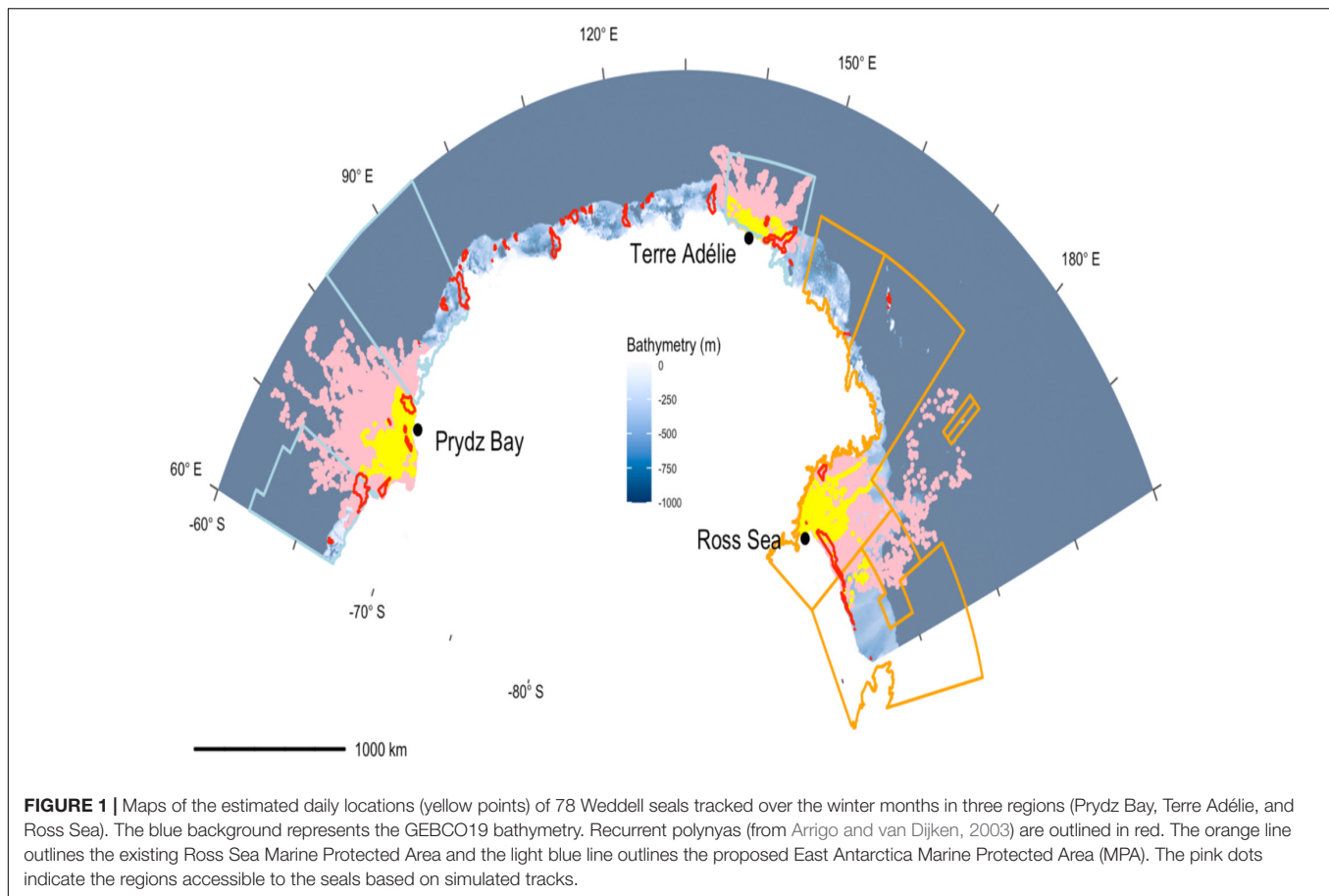
Weddell seal movements are constrained during winter by heavy pack-ice and access to open water to breathe. This study quantifies factors influencing the distribution and foraging behaviour of Weddell seals, by for the first time comparing three geographically discrete locations in Antarctica during the austral winter. We consider three aspects of Weddell seal foraging ecology: (i) individual differences in benthic vs. pelagic foraging and foraging trip characteristics; (ii) the relationship between winter distribution of individual seals and bathymetry and sea ice concentration; and (iii) comparing these physical characteristics with the overall utilisation distributions for each deployment location.

MATERIALS AND METHODS

Deployment Locations (Refer to Figures 1, 3)

Prydz Bay (Davis Station)

Prydz Bay is the third largest embayment on the Antarctic coast and is located in the southern Indian Ocean sector. Prydz Bay is



broadly similar to its larger counterparts in the Weddell and Ross Seas. The bay is generally 500–600 m deep, but there are areas that are over 1000 m in depth (1085 m) adjacent to the Amery Ice Shelf. The bathymetry within Prydz Bay is complex and there are numerous shallow banks rising to 200 m depth e.g., Fram Bank and Four Ladies Bank (Nunes Vaz and Lennon, 1996).

Terre Adélie (Dumont d'Urville Station, DDU)

Our study site in *Terre Adélie* was the only one not situated in major embayment resulting in a relatively narrow shelf, 120–130 km wide. There is a complex network of submarine canyons with the Jussieu and Cuvier canyons connecting the shelf break and inner-shelf depressions. Within the canyons, there is a steep corrugated slope with deep-sea channels between 2000 and 3000 m in depth. At the base of the slope is a gentler lower rise that in areas exceeds 3000 m deep. Over the shelf, shallow banks of 200 m (Adélie and Mertz Banks) alternate with deep inner-shelf depressions, some of which are large e.g., the D'Urville Trough, the George V and Adélie Basins (Koubbi et al., 2010).

Ross Sea (Scott Base)

The Ross Sea continental shelf is extensive, unusually deep (mean depth 600 m) with a complex bathymetry which includes numerous deep troughs (up to 1200 m deep) and shallow banks (less than 200 m). Where the seals were tagged in the south, the region is dominated by the deep McMurdo Sound (up to

700 m). An important feature of the Ross Sea is the high rates of tidal current flow that occurs across the region which results in the resuspension of phytodetritus, in turn providing benthic suspension feeders with enhanced concentrations of food and transporting organic matter over large distances. This enhanced benthic productivity plays an important role in structuring the ecosystem, including the distribution of larger predator species such as Weddell seals (Smith et al., 2007).

Tag Deployment and Data Processing

Weddell seals were equipped with either Satellite-Relayed Data Loggers (SRDLs) or Conductivity-Temperature-Depth SRDLs (CTD-SRDLs) manufactured by the Sea Mammal Research Unit, University of St Andrews (Boehme et al., 2009). Deployments took place at two sites in East Antarctica: in Prydz Bay near Davis Station (-68.58° , 77.97° , $n = 27$, years: 2006, 2007, and 2011) and *Terre Adélie* near Dumont d'Urville Station, (DDU) (-66.66° , 140.00° , $n = 22$, years: 2006, 2007, 2008, 2009, and 2019) and one site in the Ross Sea near Scott Base (-77.85° , 166.76° , $n = 29$, years: 2014, 2016, and 2019). Note that the Prydz Bay and the *Terre Adélie* data sets (excluding 2019) formed the basis of Heerah et al. (2016). Only females were tagged in Prydz Bay and the Ross Sea, in *Terre Adélie* both sexes were tagged. The tags were all deployed following the annual moult in February. The capture, sedation and tagging procedures followed those described in

detail elsewhere (Mellish et al., 2010; Heerah et al., 2013; Shero et al., 2018), with the tags glued directly on the head of the seal. The tags recorded data on a seal's diving behaviour as well as *in situ* hydrographic conditions. Summaries of these data were transmitted via the polar-orbiting Argos satellite constellation whenever seals surfaced to breathe (Harcourt et al., 2019). Only seals for which the tag transmitted for longer than 50 days were included in the analyses.

Diving Behaviour and Bathymetry

The dive data underwent an initial quality control to remove anomalously deep dives. This was done by calculating a lower edge for the *dive duration* vs. *dive depth* scatter plot (using a quantile regression set at 0.05). Dives that fell below this edge were deemed to be too deep for that duration (thereby requiring unrealistic rates of travel) and were flagged for removal. We also removed dives of less than 5 min duration as these were regarded as unlikely to be foraging, and dives deeper than -1000 m as these were deeper than the Antarctic continental shelf (Padman et al., 2010). A location was recorded for each remaining dive by using a state-space-model with a 2 h time step and interpolating from the start time of each dive (Jonsen et al., 2020). Each dive was then allocated a bathymetric depth using GEBCO19 [GEBCO Compilation Group (GEBCO), 2021].

A scatter plot of bathymetric depth against the maximum dive depth of each dive indicated that 23.6% of the total 171,201 dives were more than 20 m deeper than the GEBCO19 bathymetry at that point (**Supplementary Figure 1**). The three sources of error that contribute to this mismatch are (1) errors in dive location estimates, (2) errors in the tag's depth sensors and (3) errors in the bathymetry. These uncertainties were problematic for allocating individual dives to a behavioural type (e.g., hunting "benthic" vs. "pelagic" prey). Therefore, we calculated the difference in depth between the GEBCO19 bathymetry for those dives that exceeded the bathymetry. We then calculated the 30 percentile of these differences, as this approximates 1 Standard Error of a distribution centred on the red line representing equivalence of a dives depth and estimated bathymetry at that point. This value was ~ 100 m. Assuming that these mismatches were symmetrical about the 1:1 line in **Supplementary Figure 1**, we then categorised any dives that were within 100 m of the GEBCO bathymetry as "benthic" dives and those that were >100 m from the bottom as "pelagic" dives. Dives more than 100 m deeper than the bottom was classified as "unknown" (**Supplementary Figure 1**).

We compared simple metrics of diving behaviours (maximum depth and dive duration) for benthic and pelagic dives between the three study sites using generalised linear mixed models (GLMMs) with individual seal as a random term and deployment location as the main effect. We also modelled the probability of making a benthic dive relative to the bathymetry at the location of that dive using a logistic GLMM, again with individual seal as a random term. We then used this model to make spatial predictions of where seals were likely to make benthic dives through the entire domain (defined by the extent of seal tracks) at each deployment location.

Calculation of Utilisation Distributions

Utilisation Distributions are a common way of quantifying spatial use by individuals and populations (Laver and Kelly, 2008). We used a raster-based approach to calculate the utilisation distributions (*UD*), in which we recognised two types of Utilisation Distributions: (i) Individual utilisation distributions (*UDi*), that is the total area used by an individual seal and (ii) Sample utilisation distributions (*UDs*) representing the spatial use by the population of seals tagged at each deployment location. We used a raster with a 5×5 km grid cell. This resolution corresponds to the estimated accuracy (± 5 km) of state-space-model modelled ARGOS-based elephant seal locations using the same trackers (Jonsen et al., 2020). The *UDs* analysis required three rasters (**Supplementary Figure 2**); (i) the density (number) of seals that visited each 5×5 km cell, (ii) the mean time spent by each seal in each cell (i.e., the overall mean of the individual *UDi* raster stack) (iii) the product of these two rasters provides a measure of overall habitat utilisation in terms of *seal days per cell*. This value is a close analogue of kernel density analysis but has the advantage of not imposing a smoother over the data. With sufficient data this smoothing is unnecessary as we have an empirical, quantitatively assessed, measure of the degree of use *per cell*. To estimate the degree of representativeness of the sample of seals compared to the actual population of seals at each location, we calculated the cumulative area occupied by increasing numbers of seals (**Supplementary Figure 3**) (Hindell et al., 2003). Finally, we calculated the percent usage contours by sorting the *UDs* values in each cell, taking the cumulative sum, and using that to identify user defined contours. While there are many methods for summarising utilisation distributions there is broad agreement on the use of 50% contours (i.e., enclosing 50% of locations) to define the *core* usage areas and 90% to indicate *overall* usage (Laver and Kelly, 2008).

Individual Utilisation Distributions Statistics

First, we calculated the area (km^2) of each *UDi* by counting the number of 5×5 km cells visited by each seal and compared these among the three deployment locations using a GLMM which included deployment duration as a random term to account for animals with longer durations potentially having larger *UD* areas. Seal standard length (m) was included in the model to account for animal size potentially being an important source of individual variation in space use (Hindell et al., 2021). We used length as it was the only morphometric measure common to all studies. We also compared *UDi* areas between sexes at DDU, the only site where males were also instrumented, to ascertain if there were differences in habitat use and foraging by sex (Photopoulou et al., 2020).

The Role of Bathymetry and Sea-Ice Concentration on the Winter Distribution of Individual Seals

We fit GLMMs relating the number of days that an individual spent in a 5×5 km cell to the bathymetry and ice concentration in that cell. Ice concentration in a cell varied little over the winter

months, so we took the mean of the ice concentrations over the study period in each cell. While this may lose some fine-scale detail, the Antarctic continental shelf is fully covered by sea-ice by April (Eayrs et al., 2019) and so inconsequential (study lasts March–October). Prior to analysis, outliers (1 and 99% percentiles) for both the response and predictor variables were trimmed from the data set. Predictor variables were also centred and scaled to unit variance to facilitate efficient optimisation of the GLMMs. The distributions of each variable were checked for normality and the response variable (seal days per cell) was subsequently log-transformed. Inter-correlation between the predictor variables were checked with cross-correlation analyses, comparing Pearson Correlation coefficients. The full model GLMMs (with individual seal as a random term) were initially run with and without a spatial autocorrelation term to test its effect on model performance. We found that the spatial autocorrelation term did not affect model performance and so all subsequent analyses were run excluding it. Comparison of log-likelihoods and corrected Akaike Information Criterion (AICc) indicated that the model performed best without spatial autocorrelation, so this was not used in the final model assessment. Overall model fit was assessed with the conditional r-squared which provides the variance explained by the entire model, i.e., both fixed effects and random effects. Finally, we ranked the full suite of 19 models by AICc to identify the best performing model (Burnham and Anderson, 2002, 2004).

The Role of Bathymetry and Sea-Ice Concentration on the Winter Distribution of the Populations of Weddell Seals

We assessed qualitatively the physical characteristics of the seals' habitats at the population level by contrasting the distribution of bathymetry and sea-ice concentrations within three locations, (i) the core UD_s (50%) the overall UD_s (90%) and the regions potentially available to the seals. The UD_s derived from observed locations only provide information about where animals occur, not about where they could have gone. To estimate potentially available geographic space, we simulated sets of tracks for each observed track using the *availability* R package¹ simulating 10 tracks *per* seal. This yielded simulated tracks with movement characteristics (distributions of step length and turning angle) similar to observed tracks, but tracks were random and independent of environmental effects. These simulated tracks provide an estimate of the geographic space that each animal could have occupied (given its movement characteristics and track length) if it had no habitat preferences (Raymond et al., 2014; Hindell et al., 2020). We compared the ice concentration on July 30 (averaged for all years of the study) as this was the time when ice extent was nearing its maximum, and when most tags were still transmitting.

Analyses were conducted in R 4.0.2 (R Core Team, 2021). *FoieGras* was used to filter the seal tracks (Jonsen et al., 2020). Descriptive statistics presented as mean (X) and standard deviation (\pm s.d) unless indicated. All models were Generalised

Linear Mixed Effects Models in the R package LME4. The models were assessed by ranking candidate models using AICc, and evidence ratios calculated for each model comparison to provide a2n indication of the importance relative to the top model (Burnham and Anderson, 2004).

RESULTS

Overview of Seal Distributions

Tags transmitted for 150.1 ± 72 days (mean \pm s.d. **Table 1** and **Supplementary Figure 3**) and this did not vary between sites (**Supplementary Table 1a**). Seals from all three *deployment locations* occurred almost exclusively on the Antarctic continental shelf (seafloor > -1000 m) with seals staying within 200 km of the *central point* of their distribution (**Figure 1**). This central point was not where they were tagged, because they were tagged when aggregated to moult. Post-moult, the animals moved to other areas as the sea-ice grew. The seals then remained relatively local with individuals moving on average 138.2 ± 117.8 km from that central point. This differed among the three *deployment locations*; seals tagged in the Ross Sea travelled further than seals in Prydz Bay (mean maximum distance = 178.0 ± 147.3 km compared to Prydz Bay mean max = 151.0 ± 89.1 km) and *Terre Adélie* (mean max = 70.5 ± 70.4 km) (**Table 1**).

Diving Behaviour

All seals made at least some benthic dives. Nearly 50% of dives were pelagic, 40% benthic and 12% unknown. Seals apportioned dives differently between deployment locations, with 60% benthic dives in Prydz Bay, 42% in *Terre Adélie* and 25% in the Ross Sea (**Table 2**).

Benthic dives were deeper than pelagic dives (**Table 2**). The mean \pm s.e. depth of a benthic dive was deepest in the Ross Sea (216 ± 40.0 m), followed by Prydz Bay at 205 ± 67.9 m and *Terre Adélie* at 122 ± 36.6 m (**Table 2**). For pelagic dives, the deepest were in the Ross Sea (148 ± 27.4 m) followed by Prydz Bay

TABLE 1 | Summary statistics (mean \pm s.d.) of tracking data from Weddell seals and three deployment locations during the winter months.

	Deployment Location			
	Prydz Bay ($n = 27$)	Terre Adélie ($n = 22$)	Ross Sea ($n = 29$)	Overall (all sites) ($n = 78$)
Mean deployment duration (days)	152 ± 14.1	142 ± 13.8	154 ± 14.4	150.1 ± 8.2
Maximum duration (days)	267	261	261	267
Mean maximum distance (km)	151.0 ± 16.6	70.5 ± 15.0	178.0 ± 27.4	138.2 ± 13.3
Maximum distance (km)	354.4	272.6	586.0	586.0

Maximum distance is the maximum distance from the central point of their distribution (see section "Materials and Methods" for full description).

¹<https://github.com/AustralianAntarcticDivision/availability>

(86.9 ± 23.7 m) and the shallowest in *Terre Adélie* (64.9 ± 18.9 m) (Table 2). The proportion of dives classified as unknown varied with Prydz Bay and *Terre Adélie* low (7.2 and 8.5%, respectively), but in the Ross Sea 18.1% were classified as unknown, reflecting the poorer understanding of its bathymetry.

The probability of a seal making a benthic dive decreased with increasing ocean depth (Supplementary Table 1g), but varied among the regions (Figure 2A and Supplementary Table 1g). In Prydz Bay and the Ross Sea, benthic dives were highly likely (probability = 0.75) at ocean depths of around -250 m, while the 0.75 likelihood was approximately -125 m in *Terre Adélie*.

Utilisation Distributions

Individual Utilisation Distributions

Individual Utilisation Distributions (UD_i s) varied among individuals and locations (Figure 2B), but individual size (seal length) was not influential (Supplementary Table 1e). The median area of the UD_i for seals in *Terre Adélie* was 825 km^2 , less than 1/3 of the 3150 km^2 in Prydz Bay and 3625 km^2 in the Ross Sea. There were no differences in the size of the UD_i s for male and female seals in *Terre Adélie* (Supplementary Table 1d). Consequently, we did not discriminate male and female seals in subsequent analyses.

TABLE 2 | Benthic Habitat: the role of benthic habitat on Weddell seal distribution and behaviour.

		Deployment Location		
		Prydz Bay	Terre Adélie	Ross Sea
Dive Depths (m)	Mean depth-pelagic \pm s.e.	86.9 \pm 23.7	64.9 \pm 18.9	148 \pm 27.4
	Mean depth-benthic \pm s.e.	205 \pm 67.9	122 \pm 35.2	216 \pm 40.0
	Mean percentage benthic dives	56.6 \pm 14.9	42.1 \pm 9.44	25.1 \pm 8.7
Percentage time in Benthic Habitat (≥ -250 m)	Mean \pm se	51.3 \pm 19.3	75 \pm 12.7	21.4 \pm 10.7
Core Utilisation Distribution	Maximum	100	99.9	75.9
	Minimum	5.22	18.8	0.596
	<i>n</i>	27	22	29
	Total area of core UD (km ²)	1600	200	1475
	Area of core UD benthic habitat (km ²)	1200	175	525
	% of core UD benthic habitat	75	85	36

(a) Dive depths of benthic and pelagic dives. Dive depth data are the fitted values from the GLMMs comparing dive depth (benthic) and dive depth (pelagic) among the three locations. (b) Percentage time that individuals spent in likely benthic habitat (defined as waters less than -250 m) illustrated with; mean, maximum and minimum. (c) Summary of the relative importance of benthic habitat in the core utilisation distribution (50% UD) including; total area of the core UD, total area of benthic habitat within the core, and percentage of the core UD that is benthic habitat.

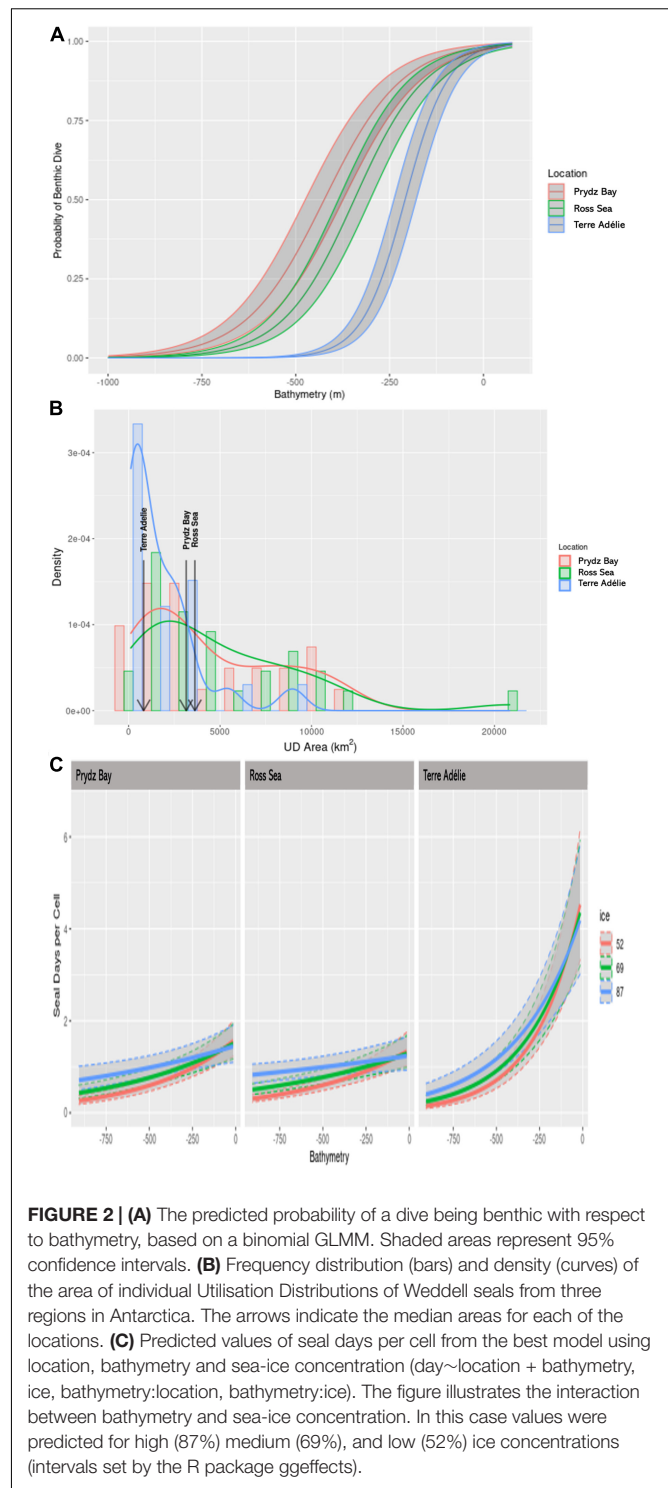


FIGURE 2 | (A) The predicted probability of a dive being benthic with respect to bathymetry, based on a binomial GLMM. Shaded areas represent 95% confidence intervals. (B) Frequency distribution (bars) and density (curves) of the area of individual Utilisation Distributions of Weddell seals from three regions in Antarctica. The arrows indicate the median areas for each of the locations. (C) Predicted values of seal days per cell from the best model using location, bathymetry and sea-ice concentration (day~location + bathymetry, ice, bathymetry:location, bathymetry:ice). The figure illustrates the interaction between bathymetry and sea-ice concentration. In this case values were predicted for high (87%) medium (69%), and low (52%) ice concentrations (intervals set by the R package ggeffects).

The Role of Bathymetry and Sea-Ice Concentration on the Winter Distribution of Individual Seals

The best model relating the number of seal days per $5 \times 5 \text{ km}$ pixel included location, bathymetry, ice concentration and the interactions of deployment location with bathymetry and

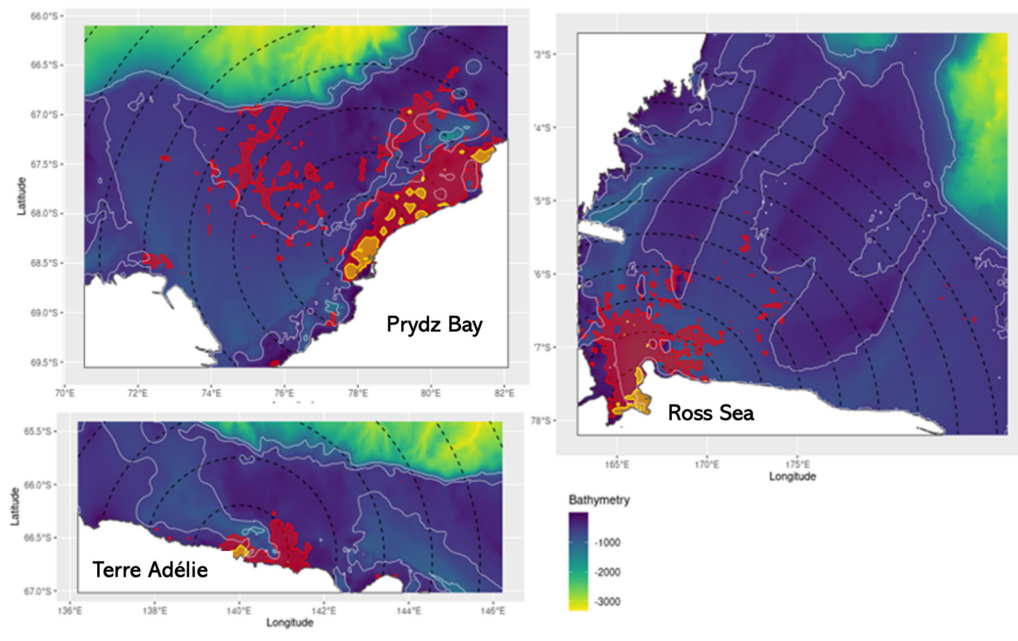


FIGURE 3 | The sample Utilisation Distributions for Weddell seals at each location. These represent the number seal days per 5×5 km pixel and were calculated as the product of the mean of the individual UD_s (mean days per pixel) and the total number of seals that used each pixel. The yellow areas enclose the cells in which 50% of all seal days occurred (which we regard as the core UD for each population) and the red polygons enclose the cells in which 90% of all seal days occurred. The black dotted lines indicate 50 km bands from the centre of the overall distribution (defined as the most commonly used 5×5 km pixel). The white contours represent the -1000 and -500 m bathymetric contours.

bathymetry with ice concentration, an AICc value of 12538.1 and an AICc weight of 0.996 (Supplementary Table 1f). When considering main effects, bathymetry was best of the single term models with an AICc of 12670.7, followed by ice concentration (12776.0) and then location (12784.3). The null model had an AICc of 12794.9. Intensity of use of a cell was negatively related to bathymetry with the areas of most intensive use in shallowest waters, and this was most pronounced in *Terre Adélie* (Figure 2C). However, when considering the interaction terms, the intensity of use was slightly higher in high ice concentration over deep water (Figure 2C).

The Role of Bathymetry and Sea-Ice Concentration on the Winter Distribution of the Populations of Weddell Seals

Our sample sizes, while not large enough to capture the estimated maximum area used by a theoretical population of seals (Supplementary Figure 4), did cover more than 85% of the estimated asymptote. In Prydz Bay, the Gompertz model fitted to the saturation curve had an asymptote of 58335 km², of which our 26 seals occupied (91.8%). In *Terre Adélie* the 22 seals occupied 86.7% of the estimated 21185 km², and in the Ross Sea the 28 seals occupied 91.0% of the estimated 66724 km².

The core (50%) population UD_s were in shallow waters within 200 km of the central pixel (Figure 3) at all locations. In Prydz Bay, the core UD_s extended northward along the coast, largely contained within the -500 m bathymetric contour. The seals in

Terre Adélie had the smallest core UD_s mostly within 50 km of the central point and also within the -500 m bathymetric contour. The core UD_s for seals in the Ross Sea was concentrated on the western edge of McMurdo Sound extending 50 km north of Ross Island. In Prydz Bay the core 50% UD_s with an area of 1700 km² occupied 12.6% of the overall 90% UD_s of the sample of seals at that site. In *Terre Adélie* the core UD (200 km²) occupied 10% of the overall 90% UD_s, and in the Ross Sea (core = 1650 km²) 11.1% of the 90% UD_s.

The bathymetry available to the seals differed from those in the overall and core UD_s, indicating a strong preference for shelf waters, with randomised tracks venturing off continental shelf break, with mean values deeper than -1000 m for seals from Prydz Bay and *Terre Adélie* (Figure 4 and Supplementary Table 2). Seals from the Ross Sea showed a different pattern, with available habitat almost exclusively contained to shelf. The bathymetry within the core UD_s also differed from the overall (90%) UD_s (Figure 4 and Supplementary Table 2). At all three locations, the core areas were in considerably shallower water than the overall area (Supplementary Table 2), reflecting the coastal positions of the core UD_s. In the Ross Sea overall UD_s had the deepest bathymetry (mean = -608 ± 147 m) followed by Prydz Bay (-370 ± 112 m) and then *Terre Adélie* (-262 ± 118 m) reflecting the topographic characteristics of the locations. Ice characteristics varied between available, core and overall areas (Figure 4 and Supplementary Table 2). Ice concentrations were consistently higher within regions available to the seals (Figure 4) compared to regions they actually used. Further, ice

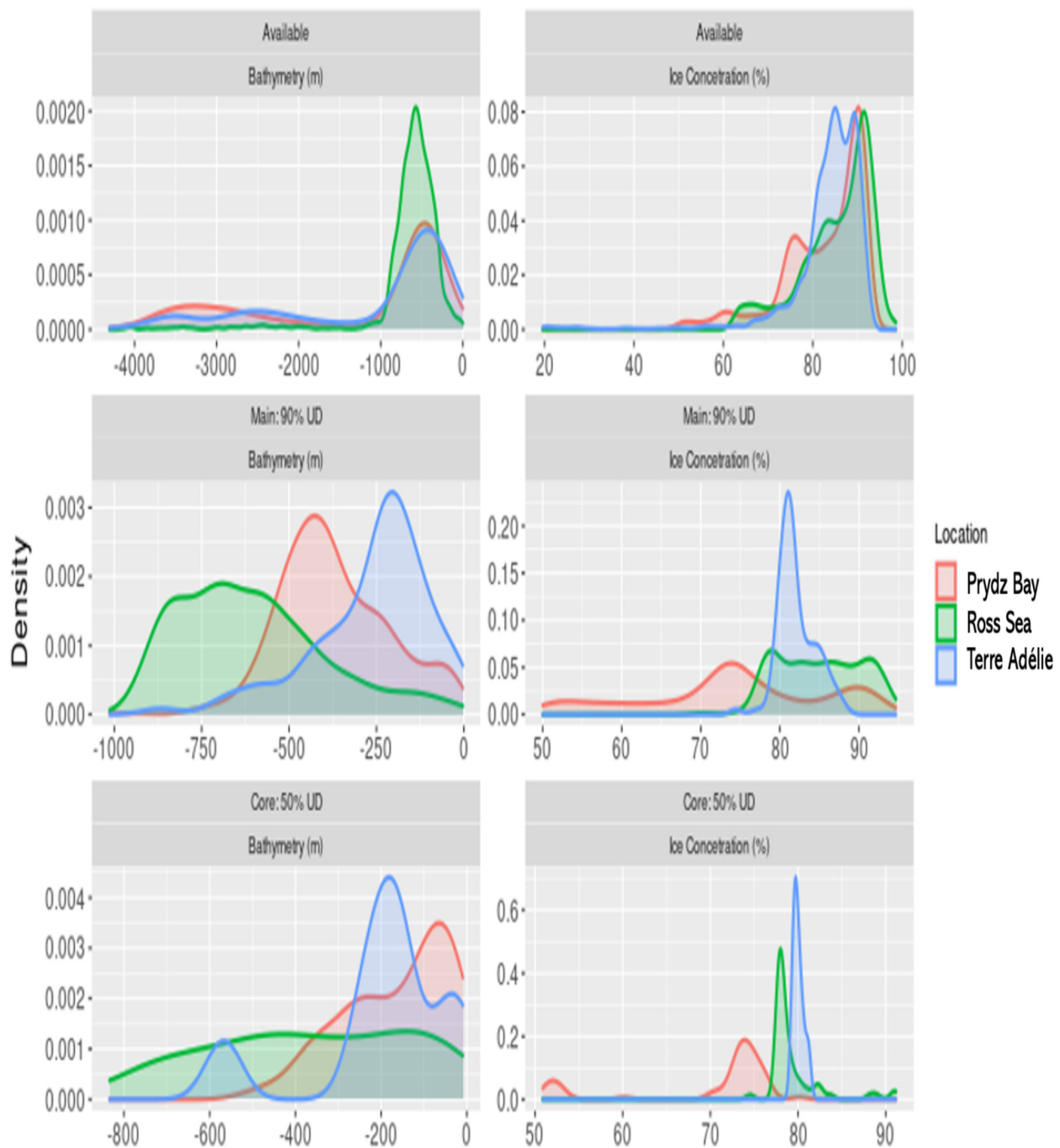


FIGURE 4 | Frequency distributions (expressed as densities) of the bathymetry (m) and ice concentrations (%) on July 30 comparing (i) the region potentially available to the seals (see Methods), (ii) the full sample Utilisation Distributions (UD_s) and (iii) the core UD_s .

concentration was slightly lower in core UD_s than overall UD_s , although the differences were relatively minor, being largest in the Ross Sea (85.0 ± 3.7 [90%] compared to 79.4 ± 2.2 [50%]).

The area of shallow water where benthic foraging was most likely [i.e., ≥ -250 m (**Figure 2A**)] constituted 85% of the core UD in Terre Adélie, 85% in Prydz Bay and only 36% in the Ross Sea (**Table 2**).

DISCUSSION

By comparing data from three different regions, we found that Weddell seal foraging behaviour during the winter months is strongly influenced by extrinsic factors, but individual variability still plays a key role. Of the extrinsic factors, bathymetry played the most important role in determining the distribution and

foraging behaviour of Weddell seals. The seals made on average more pelagic dives than benthic dives, and benthic foraging behaviour was more likely in shallower waters less than -250 m. Off *Terre Adélie* and in Prydz Bay individual seals spent 60% of their time in waters less than -250 m, making predominantly benthic dives. By contrast, seals in the Ross Sea spent less time in benthic habitats, and we attribute this to the relatively small area of benthic habitat within their core area dominated by the deep McMurdo Sound. However, individual variation in foraging behaviour persisted at each site, reflecting differences in intrinsic factors. Some individuals remained very local, foraging predominantly on the benthos throughout the winter, while others moved further afield, foraging more pelagically.

A potential limitation in this study is that bathymetry is poorly known in remote regions like the Southern Ocean (Millan et al., 2020). The Weddell seal dive data reflects this inaccuracy with 24% of the dives recorded being deeper than the ocean floor provided by GEBCO19. To account for this potential source of error, we designated foraging behaviours conservatively. Many studies have reported that seal dive depths recorded by SRDLs and CTD-SRDLs are accurate (Boehme et al., 2009; Costa et al., 2010; Padman et al., 2010; Roquet et al., 2014) and the locations of diving seals have at least a relatively well-derived error component (Jonsen et al., 2020). Given the paucity of direct ship-borne measurement for many of these areas of the Southern Ocean, integrating seal dive depths with those collected by more traditional means may help to constrain and therefore improve the confidence of many bathymetry models (Padman et al., 2010).

Foraging Behaviour

Weddell seal foraging occurs in a mix of habitat types (benthic, epipelagic, and mesopelagic) and they have a catholic diet taking benthic fish, crustaceans and cephalopods as well as mesopelagic prey such as *Pleurogramma* spp. (Supplementary Table 3). The likelihood of benthic foraging increased in shallower water. To reach the benthos in these areas, seals traverse the entire water column rather than stopping to feed in the pelagic zone, either because the mesopelagic prey are not there or because the seals get a greater energetic return from benthic prey. Harcourt et al. (2007) found that males that dived deeply during the breeding season in McMurdo Sound lost weight at a slower rate than those remaining shallow. This suggests that deeper prey resources are especially profitable or at least predictable (Photopoulou et al., 2020). Making diet inference based simply on predator dive behaviour is potentially confounded by the knowledge that some key prey species such as silverfish and toothfish can occupy multiple habitats (O'Driscoll et al., 2011). Feeding studies and acoustic observations of silverfish are consistent with a predominantly pelagic niche (Pinkerton, 2017; O'Driscoll et al., 2018), but adult silverfish are sometimes found close to the bottom over the Ross Sea shelf (O'Driscoll et al., 2011). In contrast, toothfish over the Ross Sea shelf are likely to be predominantly demersal (Pinkerton et al., 2016), but pelagically feeding in McMurdo Sound (Ainley et al., 2013).

As seals venture into deeper water, the benefits of benthic foraging are likely to decline due to the energetic trade-offs. These

are associated with deeper diving, such as reduced time available in the foraging zone, greater cost of transport to and from deeper depths (Thompson and Fedak, 2001; Williams et al., 2004), physiologic costs associated with exceeding the aerobic dive limit or even potentially cardiac anomalies (Williams et al., 2015). This may explain why the seals in all three regions used predominantly shallower habitats in accordance with their relative availability.

Regional Variation in Habitat Use Is Explained by Site Variability Not Inherent Population Level Behavioural Differences

Across the three sites dive behaviour differed due to regional differences in bathymetry. For example, off *Terre Adélie* there was more shallow benthic diving than in Prydz Bay or the Ross Sea. In the Ross Sea Weddell seals foraged more pelagically, presumably because water is deeper in McMurdo Sound. Overall, the seals in all three regions remained close to the continental land mass in areas of heavy ice concentration (75–85% in core areas) over relatively shallow waters (<200 m). This corroborates previous observations of Weddell seal distributions and their preference for relatively shallow water areas (Stirling, 1969) in areas of dense ice (Lake et al., 2005; Boehme et al., 2016; Heerah et al., 2016; Nachtsheim et al., 2019). We observed differences between sites in the areas used by the seals, most likely due to the differences in physical habitats. Prydz Bay and *Terre Adélie* seals were close to regions where productive circumpolar deep water may reduce their need to forage further afield. In the Ross Sea, the seals were further from areas of influx of circumpolar deep water, with bathymetry influencing the advection of circumpolar deep water (Williams et al., 2016).

A recent study in the Weddell Sea observed differences in diving behaviour between males and females (Photopoulou et al., 2020), but we did not, which is possibly due to the similar body size of the males and females we studied. Photopoulou et al. (2020) reported that male Weddell seals spent more time in high-salinity shelf water masses at depth, benthically diving, while females ventured off the continental shelf and visited warmer, shallower water masses while undertaking a mix of benthic and pelagic dives. Our sample did not include sub-adults or juveniles, age classes which have very different distributions in other Southern Ocean pinnipeds (e.g., elephant seals, Hindell et al., 2021). Burns et al. (1999) reported that some weaned Weddell seal pups from McMurdo Sound in the southern Ross Sea dispersed widely, others did not, but all stayed relatively close to the Antarctic coastline.

Individual Variability

In this study there was a high degree of inter-individual variation in winter foraging behaviour. Some individuals were notably sedentary, did not move far from tagging location and had small home ranges. Others had large home ranges, travelled several hundred kilometres, and made more pelagic dives. These differences may be due to divergent behavioural traits among individual seals (Toscano et al., 2016; Troxell-Smith and Mella, 2017). Individual behavioural traits under-pins differences in foraging behaviour in other species (Patrick et al., 2014; Toscano et al., 2016; Krüger et al., 2019; DiNuzzo and Griffen, 2020;

Steinhoff et al., 2020), and distinct, stable foraging strategies have been identified in many pinnipeds [e.g., Australian sea lions, *Neophoca cinerea* (Lowther et al., 2011); Galapagos sea lions, *Zalophus wollebaeki* (Villegas-Amtmann et al., 2008)], consistent with individual traits (Schwarz et al., 2021). In dynamic environments, multiple foraging strategies within a population may reduce resource competition (Lewis et al., 2006; Baylis et al., 2015). We found no relationship between home range area and seal size. In northern elephant seals, *Mirounga angustirostris*, body condition influences foraging behaviour, with animals in poor condition adopting riskier foraging strategies (Beltran et al., 2021) but, post-tagging we have no information on individual condition on our animals. Development of *in situ* proxies of condition (e.g., buoyancy) in Weddell seals similar to those well established in elephant seals (Biuw et al., 2003) could help to resolve whether these differences result from intrinsic strategies or arise from variance in foraging success. Finally, pre- and post-tagging reproductive status may both be important. The majority of these animals were females and at the time of tagging some would have just weaned their pup from the preceding breeding season, while others were not reproductive that season. Animals that skip breeding have different energetic demands as they have avoided the high cost incurred by birthing and lactation, where females lose about 30% of their body mass (Wheatley et al., 2006; Shero et al., 2015). Females that skipped breeding are in much better condition and so may have the luxury of adopting a safer foraging strategy as with fat northern elephant seals (Beltran et al., 2021). Conversely, not all females are pregnant each year. Pregnancy incurs increased energetic demands which translates to increased winter foraging effort (Shero et al., 2018), and this may well influence space use.

Our results differ from studies of Weddell seal distributions in the Weddell Sea (Boehme et al., 2016; Nachtsheim et al., 2019; Photopoulou et al., 2020; Labrousse et al., 2021), where tracked individuals showed diverse and wide-ranging movements including moving off the Antarctic continental shelf. In those studies, seals were often captured from ships some distance from the coast and later in the winter. In our study, all seals were captured just after their annual moult (~2–3 months after the breeding season) at or near their breeding sites on coastal fast ice. We hypothesise that the seals tagged offshore in the Weddell Sea may contain a higher proportion of those individuals that are predisposed to make longer excursions, and so represent a different sample from those tagged near their breeding areas. Supportive evidence arises from Nachtsheim et al. (2019) who were forced to tag four of their six animals in a sheltered inlet due to bad weather. They found that the four Weddell seals they tagged on the fast ice stayed close to their colony, while the two tagged on the pack ice ventured further afield.

Bathymetry and ice concentration were important determinants of Weddell seal distribution. Sea-ice concentration on the continental shelf in east Antarctica is dynamic both within and among years (Massom et al., 2013), but in most years ice concentration reaches a maximum in late winter, around August (Eayrs et al., 2019), while still exhibiting considerable spatial variation due to recurrent coastal polynyas (Arrigo et al., 2015). These seals did not concentrate in polynyas, but instead

those individuals that made excursions beyond the core areas moved into areas of relatively high ice concentrations (80% plus). Inhabiting high sea-ice concentration areas may improve access to prey or reduce the risk of attack by predators such as killer whales (Lauriano et al., 2020). Similarly, sedentary individuals remaining in the fast ice may reduce predation risk.

Implications

Antarctica and the surrounding Southern Ocean, like many regions across the globe, are changing in response to changes in climate (Rogers et al., 2020) and anthropogenic activities such as increased exploitation (e.g., fisheries), and these can profoundly affect endemic biota (Bestley et al., 2020). To quantify how these broad scale changes affect individuals and animal populations requires information on animal distribution and behaviour, and the structure and dynamics of the physical environment (Hindell et al., 2020). Quantifying movement and habitat use by predators for conservation and management strategies is particularly pertinent given the recent designation of the Ross Sea region Marine Protected Area (MPA), and the ongoing debate for new MPAs in east Antarctica and elsewhere in the Southern Ocean (Hays et al., 2019; Hindell et al., 2020). It is especially important in the management context to develop policies that protect the endemic biota over the long-term while regulating the human behaviours like fishing within the broader framework of a changing climate, over which it is much harder to effect change (Hays et al., 2019; Hindell et al., 2020). In the Southern Ocean, animal conservation and fisheries regulation is generally managed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) under an ecosystem-based management approach which includes establishing a network of MPAs in the Southern Ocean. Information on where, when and how animals use their habitats is critical for the design and evaluation of these MPAs.

CONCLUSION

We found that Weddell seals in the Eastern Antarctic are relatively sedentary, preferring to forage in shallow water on the continental shelf. We detected regional differences in the proportion of benthic and foraging dives that accord with the available habitat. Within populations, we identified significant individual variability, ranging from little dispersal, and foraging within a relatively small core area, to individuals that ventured further afield, diving pelagically when in deeper waters but keeping to areas of high ice concentration. All the animals tagged in the Ross Sea remained within the boundaries of the Ross Sea MPA. The proposed MPAs in East Antarctica, Weddell Sea and Western Antarctic Peninsula also encompass potential core Weddell seal habitat (LaRue et al., 2019; Teschke et al., 2020). However, none of the areas used by seals in Prydz Bay are inside any current or proposed MPAs and this is obviously an important region to consider. This study suggests that protecting shelf areas will protect Weddell seals within that prescribed area, but local populations outside MPAs will only indirectly benefit.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: <https://portal.aodn.org.au/>.

ETHICS STATEMENT

The animal study was reviewed and approved by Macquarie University ARA 2014_057.

AUTHOR CONTRIBUTIONS

RH, MH, and CM lead the writing. MH, CM, and IJ conducted the analysis. RH, CM, MH, KG, J-BC, and MP organised the funding. RH, MH, CM, KG, KH, RHo, XH, MS, RF, BL, and ET conducted field work. All contributed writing and final edits.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2021.720335/full#supplementary-material>

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West Indian Manatees Use Partial Migration to Expand Their Geographic Range Into the Northern Gulf of Mexico

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Partial migration provides a mechanism for species to shift their geographic ranges into new, environmentally favorable regions but has been poorly studied as a means to alleviate effects of climate change. Populations at the edge of their geographic range are ideal to investigate how migratory behaviors may enable range expansion as adjacent areas become more climatically favorable. We determined the contribution of partial migration to the range expansion of West Indian manatees (*Trichechus manatus*) using GPS data from tagged individuals that migrated between the northern Gulf of Mexico (nGoM) and primary habitat in peninsular Florida. Most of these manatees migrated to the nGoM annually and exhibited high site fidelity among years. Many individuals spent cumulatively more time in the nGoM than in peninsular Florida, indicating the nGoM is a regular part of their geographic range, and they returned to peninsular Florida to meet temperature-related physiological needs for survival. Autumn migrations most frequently terminated at Crystal River, Florida, and manatees that commenced migration late in the season stopped less frequently and had more directed movements. Spring migrations most frequently terminated at Mobile Bay, Alabama, and several manatees quickly and directly migrated from Florida to nGoM stopover sites. Migrations ranged from 10 to 133 days in length, and variation in duration was primarily driven by use of stopover sites and directedness of travel. These data confirm partial migration as an important component of manatee migratory behavior that has already enabled range shifts for manatees on the U.S.A. Gulf of Mexico coast and has potential to facilitate future responses to climate change. As the most common type of migration across the animal kingdom, partial migration may provide a global mechanism for a diverse variety of species to resist the range limiting effects of climate change.

Keywords: climate change, ecosystem change, migration duration, step length, site fidelity, *Trichechus manatus*

INTRODUCTION

Migration is the directed, often seasonal movement of individuals among locations that provide important resources or refuges (Dingle and Drake, 2007; Shaw and Couzin, 2013; Cagnacci et al., 2016). Migration is often essential to species that must relocate because environmental conditions are not conducive to the species's survival year-round (Dingle and Drake, 2007;

Mysterud et al., 2011; Bischof et al., 2012). Partial migration, where only part of the population migrates and individuals can switch between resident and migratory tactics, is the most common type of migration among animals (Dingle and Drake, 2007; Chapman et al., 2011, 2012; Shaw and Couzin, 2013). Motivation to migrate, or to switch between migratory and residency tactics, is driven by interacting environmental factors, such as temperature, resource quality and availability, intra- and interspecific competition, and predation (Brodersen et al., 2011; Chapman et al., 2011; Mysterud et al., 2011; Eggeman et al., 2016). Many of these factors and their interactive effects are altered by anthropogenic disturbances and climate change (Winder and Schindler, 2004; Hoegh-Guldberg and Bruno, 2010). As a result, migration patterns in many species are changing or are likely to change in the coming decades (Cotton, 2003; Saino et al., 2011; Nelson et al., 2012). These changes will have negative and positive species-specific effects (Van Buskirk et al., 2009; Saino et al., 2011; Ruiz-Cooley et al., 2013), but most research has focused on how climate change may disrupt migratory patterns and phenological relationships (Van Buskirk et al., 2009; Visser et al., 2009; Saino et al., 2011; Batalden et al., 2014). Much less work has focused on how migration strategies such as partial migration may provide a mechanism for species to expand or shift their range as climate changes (but see Ruiz-Cooley et al., 2013; Hovick et al., 2016).

Partial migration may benefit populations under climate change scenarios because these migrations allow species to flexibly track favorable conditions through space and time (Naidoo et al., 2012; Hovick et al., 2016; Acker et al., 2021; Bright Ross et al., 2021). Through partial migration, species may be able to exploit new areas as they become available, residing in new areas while conditions are favorable, and retreating, often seasonally, when conditions become unfavorable (Naidoo et al., 2012; Bright Ross et al., 2021). If conditions in the areas of expansion remain favorable for longer periods throughout the year, individuals may be able to stay longer and eventually transition from migrants to residents (Bright Ross et al., 2021). Populations that are living at or near their geographic range limit will likely be the first to experience conditions that allow them to move into new areas (Perry et al., 2005; Parmesan, 2006), and it is likely easier to detect these movements in these areas. Populations that already exhibit migratory plasticity may be better able to respond to changing environmental conditions (Martin et al., 2018; Bright Ross et al., 2021), making them ideal study populations to examine the role of partial migration in facilitating climate driven range expansions.

West Indian manatees (*Trichechus manatus*; hereafter referred to as manatees) are a threatened and protected sirenian with the northern most populations occurring in the southeastern United States of America (U.S.A.). Some of these populations are potentially expanding into estuarine and tidal riverine habitats outside the known habitats of highest density on the southeastern U.S.A. coastline (Gannon et al., 2007; Marsh et al., 2011; Cummings et al., 2014). During winter, manatees in the U.S.A. depend on warm water refugia, such as natural warm springs or power plant effluents, primarily in peninsular Florida (Irvine, 1983; Deutsch et al., 2003; Laist and Reynolds, 2005). Manatee densities can be extremely high at refugia during cold periods when water temperatures are below 20°C

(Laist et al., 2013), and most manatees leave refuge sites when water temperatures rise above this thermal threshold (Deutsch et al., 2003; Cummings et al., 2014; Hieb et al., 2017). Tagging and photo-identification studies provide evidence of partial migration, with most manatees migrating at least locally. One study of 48 satellite telemetry tagged manatees found 87% of manatees migrated short (50–150 km), medium (150–400 km), or long (>400 km) distances from refuge sites, with some manatees migrating to habitats outside of Florida (Deutsch et al., 2003). More recent studies indicate an increasing number of manatees make regular, seasonal migrations that span hundreds of kilometers (Cummings et al., 2014; Hieb et al., 2017; Cloyed et al., 2019; Rood et al., 2020). Habitat use by manatees that migrate, even short distances, can be defined in terms of the duration of time spent at specific locations (Deutsch et al., 2003). The resulting mosaic of partial migrations helps define manatee distributions and range through time and may confer resiliency to environmental variation (Mysterud et al., 2011; Martin et al., 2018; Purdon et al., 2018; Picardi et al., 2020). Furthermore, increased occurrence of manatees outside of Florida is likely driven by a combination of population growth, favorable temperatures, and potential changes in dietary resources associated with ecological and climatic changes (Marsh et al., 2011, 2017; DaCosta et al. Unpublished). These factors make manatees useful sentinels to test how partial migration may facilitate range shifts or expansion due to climate change.

While increasing geographical range can be encouraging for a threatened species (Neel et al., 2012), development of new patterns of movement across greater distances presents challenges for effective conservation and management (e.g., Neel et al., 2012; Cloyed et al., 2019). In the northern Gulf of Mexico (nGoM), manatee sightings have been documented since the early 1900s, but sightings have increased exponentially during the past several decades (Gunter, 1941; Powell and Rathbun, 1984; Fertl et al., 2005; Hieb et al., 2017). Similarly, manatee strandings and mortalities have recently increased in this region as manatees face diverse threats, such as cold stress during winter months and vessel collision throughout their range (Hieb et al., 2017; Cloyed et al., 2019). Manatees are also likely harbingers of climate driven, ecological changes in places like the nGoM, as other tropical associated species are becoming increasingly common (Fodrie et al., 2010; Heck et al., 2015; Scheffell et al., 2018). Understanding the ecologically meaningful components of manatee migrations will support ongoing range-wide management, conservation, and species recovery actions, as well as provide evidence for how other species that exhibit partial migration may be affected under future climate scenarios (Martin et al., 2018; Bright Ross et al., 2021).

Here, we expand on a previous study of satellite telemetry tagged manatees (Aven et al., 2016) using Global Positioning System (GPS) data from manatees that migrated between the nGoM and peninsular Florida to determine whether partial migration contributed to the expanding range of manatees. We defined spatial and temporal patterns of migration for manatees along the nGoM coast by identifying terminal (most easterly or westerly) and stopover locations, the latter based on duration of use by manatees. We defined movements among individuals with the net-squared displacement (NSD) method (Bunnfeld et al., 2011) and determined how factors such as number of

stopovers, directedness of travel, season, and migration distance affected the duration of migrations among individuals. These data provide the most detailed information to-date on manatee movements in the U.S.A. outside of Florida to support ongoing assessments of manatee abundance, distribution, and habitat use across the species range. These data emphasize the ecological importance of partial migration and other flexible migration strategies to facilitate movements at the edge of a geographic range and the potential for these strategies to enable responses to climate change.

MATERIALS AND METHODS

Study Area

We tracked manatee movements across the northern and eastern Gulf of Mexico, from Lake Pontchartrain, Louisiana, a brackish lake that is connected to Mississippi Sound (longitude $\sim 90.00^\circ$ W), to Tampa Bay, Florida, a highly urbanized estuary (-82.45° W) (**Figure 1**). Seasonal variation in water temperatures during the time of study ranged from a daily average of $\sim 32^\circ\text{C}$ in the summer (June - August) to $\sim 16^\circ\text{C}$ in the winter (December - February) in the northern Gulf of Mexico (nGoM) and from a daily average of $\sim 32^\circ\text{C}$ in the summer to $\sim 21^\circ\text{C}$ in winter in the eastern Gulf of Mexico (Buckingham et al., 1999; Cloyed et al., 2019). Within the study area, natural, thermal springs at the Wakulla, Homosassa, and Crystal Rivers, Florida and power plant discharge sites in Crystal River, Big Bend, and Tampa Bay, Florida provided warm-water refuge sites used by manatees (Laist and Reynolds, 2005; Laist et al., 2013). The study area includes extensive tidal river and open water systems with highly diverse habitats, such as seagrass beds in St. George Sound, Apalachicola/St. Joseph Bay, and St. Andrew Bay, Florida, marshes, barrier islands, and active and remnant oyster reefs (*Crassostrea virginica*) (Livingston, 1984; Stout, 1984; Lewis, 1987). Several large rivers provide freshwater habitats and dietary resources preferred by manatees, including (west-to-east) the Mississippi, Pearl, Pascagoula, Mobile-Tensaw, Apalachicola, Ochlockonee, Wakulla, Suwannee, and Crystal Rivers. The Intracoastal Waterway runs the length of the study area and is used by manatees traveling along the nGoM coast (Aven et al., 2015; Cloyed et al., 2019).

Data Collection

Manatee movement data were collected via GPS satellite telemetry from manatees between September 2009 and January 2015. Manatees were captured and tagged using established methods for manatee health assessments, and one manatee, TCR026, was tagged following rescue and rehabilitation (**Supplementary Table 1**; Bonde et al., 2012). Health assessments were part of an ongoing, multi-agency effort in which biologists and veterinarians determine the health and wellbeing of wild manatees by measuring morphometrics (i.e., straight-length), temperature, heart rate, and respiration rate and collecting blood samples for later analyses (Bonde et al., 2012). Individual manatees were located via an aerial observer and were targeted for capture in a net deployed from a specialized capture

boat. Captured manatees were brought aboard the boat and underwent a veterinary evaluation prior to outfitting with a belt and floating, tow-behind tagging platform (Telonics Inc., Mesa, AZ, United States) (Deutsch et al., 2003; Aven et al., 2015). Each belt was outfitted with a Sonotronics CHP-87-L acoustic transmitter (Sonotronics, Inc., Tucson, AZ, United States) detectable by passive acoustic monitors (PAMs; Lotek WHS2000; Lotek Wireless Inc., Newmarket, ON, Canada). Tags were programmed to record GPS locations every 15 or 30 min, and locations were downloaded following tag recovery. Captures and releases occurred at the same location, and manatees were usually released within an hour. For TCR026, rescue capture occurred in Magnolia Springs, Alabama during January 2015 and release was in Crystal River, Florida during March 2015. Tags were exchanged near the end of their battery life or recovered after a designed breakaway released the tracking gear from the manatee to protect against entanglement. New tags or tag and tether combinations were attached by snorkeling or during a subsequent capture event (**Supplementary Table 1**). Tag recovery was 98% because lost tags were easily located in the shallow, coastal systems where tags were lost.

Manatee locations were monitored using Service ARGOS satellite system and by obtaining periodic visual observations (Aven et al., 2015). Data were directly downloaded from tagging platforms and included standard GPS locations or quick-fix pseudorange (QFP) positions accurate within 10 or 75 m, respectively. All locations that had successful GPS fixes or resolved QFP positions were included in the dataset. GPS data were plotted in ArcMap 10.3 to verify accuracy of locations, and all locations on land were removed (0.00006%). To fill data gaps for manatee locations when satellite GPS data were unavailable, additional location data were provided from PAMs and photo-identification methods. PAMs were deployed at strategic locations in Mobile Bay, Alabama and Apalachicola, Florida (as described in Aven et al., 2015, in which a portion of these data were previously reported). Photo-identification data were obtained during field observations and from opportunistic, publicly reported manatee sightings to the Dauphin Island Sea Lab's Manatee Sighting Network (DISL/MSN; Pabody et al., 2009; Hieb et al., 2017). Photos of individual manatees were submitted to the Manatee Individual Photo-identification System (Beck and Reid, 1995) to define and document the regional sighting history of each animal in collaboration with the U.S. Geological Survey Sirenia Project, Florida Fish and Wildlife Conservation Commission, Mote Marine Laboratory, and other researchers and managers who contributed to the database. All work on manatees was performed under U.S. Fish and Wildlife Service Research Permits MA107933-1 and MA37808A-0, Alabama Department of Conservation and Natural Resources Division of Wildlife and Freshwater Fisheries annual permits, and University of South Alabama (581568, 1038636) and Sea to Shore Alliance (S2S201003) IACUC protocols.

Movement Analysis

To determine the terminal and stopover locations of migrations and the duration manatees spent at each location, we calculated the mean daily locations of manatees from all recorded latitudes

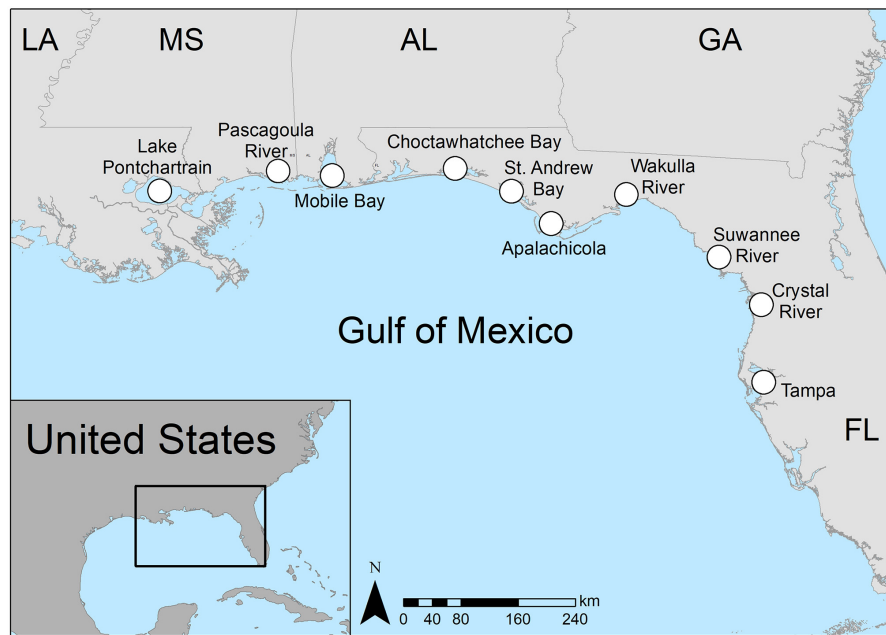


FIGURE 1 | Major stopover sites and terminal locations used by manatees migrating in the study area, along the northern Gulf of Mexico and peninsular Florida coasts.

and longitudes per day for each manatee during each seasonal migration. Autumn migrations were eastward in direction and occurred August–December, while spring migrations were westward and occurred February–August. During the study period, we calculated the number of times sites were used as terminal locations (i.e., the most westerly or easterly site used), and the number of manatees that visited each terminal location. We did not count any terminal locations in cases where tags detached during migration unless there were PAM or photo-identification records at a site after the tag detached. We considered locations to be stopovers when manatees spent more than 7 consecutive days at that location (Deutsch et al., 2003). If manatees spent more than 7 days at a terminal location it was also considered a stopover. We examined the daily locations of manatees within stopover locations to delineate boundaries for each site. To be consistent with previous work, when location data were not available (i.e., non-continuous tagging duration due to tag loss, malfunction, etc.) for fewer than 25 days, and the animal was in the same location before and after the data-gap period, the animal was considered to occupy the same stopover location throughout that time (Deutsch et al., 2003). When location data were unavailable for more than 25 days, we considered the manatee's location before and after the data-gap period to be separate stopover occurrences regardless of location (Deutsch et al., 2003).

To better understand manatee movement patterns during migration, we calculated total distance, duration and step lengths of migration segments during each migration season. We calculated total migration distance as the distance between two terminal sites using Geographic Information System (GIS) tools to delineate a continuous aquatic path following the contour

of the nGoM coast and the most direct migratory travel routes used by most manatees. To estimate the total duration of migration, we considered migrations to have commenced when a manatee moved in a consistent direction, with differences between daily mean longitudes of $> 0.02^\circ$, until the manatee reached its terminal location. Step lengths are segments of an animal's trajectory that all occur in a similar direction (Edelhoff et al., 2016) and were calculated to better understand fine scale movements and directedness of travel during migration among terminal and stopover locations. We defined step length as the distance (calculated as the sum of distances between GPS locations) a manatee moved in a certain direction before making a turn $\geq 45^\circ$ (Turchin, 1998). To obtain a measurement of overall directedness of travel during migration, we averaged step lengths for the total duration of each migration. Additionally, we determined the locations of long steps (i.e., step lengths > 20 km).

Migration Models

We used net-squared displacement (NSD) models to evaluate migration patterns among individuals (Bunnefeld et al., 2011), where NSD is defined as the linear distance between two points in space. We calculated NSD as the shortest distance between the location of a manatee and a defined point within Mobile Bay (30.6284° N, -88.0318° W) using the haversine formula in the *geosphere* package in R (Hijmans et al., 2019). Mobile Bay was chosen as the starting point because it was a primary terminal and stopover location in the nGoM outside of peninsular Florida, and it was the general region where manatees were captured and outfitted with tags. NSD models use a collection of single- and double-logistic and linear equations to differentiate between fixed and mixed migration, dispersal, nomadism, and residency as

originally developed by Bunnefeld et al. (2011). Fixed migration occurs when individuals return to the same location where migration commenced and is fit with a double-logistic equation

$$NSD = \frac{\delta}{1 + e^{\frac{\theta_a - t}{\varphi_a}}} - \frac{-\delta}{1 + e^{\frac{\theta_s - t}{\varphi_s}}} \quad (1)$$

where δ is the asymptotic height (i.e., maximum NSD), θ_a and θ_s are the times, in days, that migration is half completed for the autumn and spring migrations, respectively (Bunnefeld et al., 2011). φ_a and φ_s are the times that between half and $\sim 3/4$ of the migration is completed for the autumn and spring migrations, respectively, and t is time since 1 August, because most manatees were tagged in August or early September. Mixed migration occurs when individuals return to the same region but not the exact location where migration had commenced and is also modeled with a double-logistic equation

$$NSD = \frac{\delta_a}{1 + e^{\frac{\theta_a - t}{\varphi_a}}} - \frac{-\delta_s}{1 + e^{\frac{\theta_s - t}{\varphi_s}}} \quad (2)$$

where the asymptotes δ can vary between the autumn (δ_a) and spring (δ_s) (Bunnefeld et al., 2011). Dispersal occurs when individuals permanently relocate to a new location and is modeled with a single-logistic equation

$$NSD = \frac{\delta}{1 + e^{\frac{\theta - t}{\varphi}}} \quad (3)$$

(Bunnefeld et al., 2011). Nomadism occurs when individuals disperse from their initial location and move continually to new locations but never settle permanently

$$NSD = \beta t \quad (4)$$

where β is a constant (Bunnefeld et al., 2011). Finally, residency occurs when individuals never leave their initial location and is modeled with a linear equation that only has an intercept

$$NSD = c \quad (5)$$

where c is a constant (Bunnefeld et al., 2011).

We fit each equation to movement of individuals for whom we had reliable satellite telemetry data during both autumn and spring migrations. We estimated NSD model parameters using the *nls()* function of the *nls2* package in R (Grothendieck, 2013). We used Akaike Information Criterion (AIC) to determine the best fitting model for each individual (Bunnefeld et al., 2011; Burnham et al., 2011), where the model with the lowest AIC value was considered the best-fitting model (Burnham et al., 2011). To measure the relative strength of each model, we calculated normalized Akaike weights, w_i , for each model i , where $w_i = \frac{e^{-0.5 \Delta AIC_i}}{\sum_j e^{-0.5 \Delta AIC_j}}$, which provides a probability that the given model is the best-fitting model: $w > 0.9$ indicate strong model support over others, and $w > 0.1$ indicate some model support and should be considered in the analysis (Burnham et al., 2011).

Statistical Analyses

To determine factors that mediated the duration of manatee migrations, we used generalized linear mixed effects models with an identity link (Zuur, 2009). The response variable of these models was the duration, in days, of manatee migrations. Fixed effects included average step length, season (autumn, spring), migration distance, and number of stopovers. Interactive terms included season*step length and season*migration distance. We also ran a null model and included manatee individual as a random effect in all models (Zuur, 2009), and all models were run with the *lme()* function in the R package *lme4* using a maximum likelihood method (Bates et al., 2015). We performed a model selection analysis to determine which model best explained variation in the duration of migrations and used AIC values corrected for small sample sizes (AICc) to determine the best-fitting models. We calculated normalized Akaike weights, w_i , for each model i and used those weights to calculate weighted parameter averages (Burnham et al., 2011). All statistical analyses were performed in R (R Core Team, 2013).

RESULTS

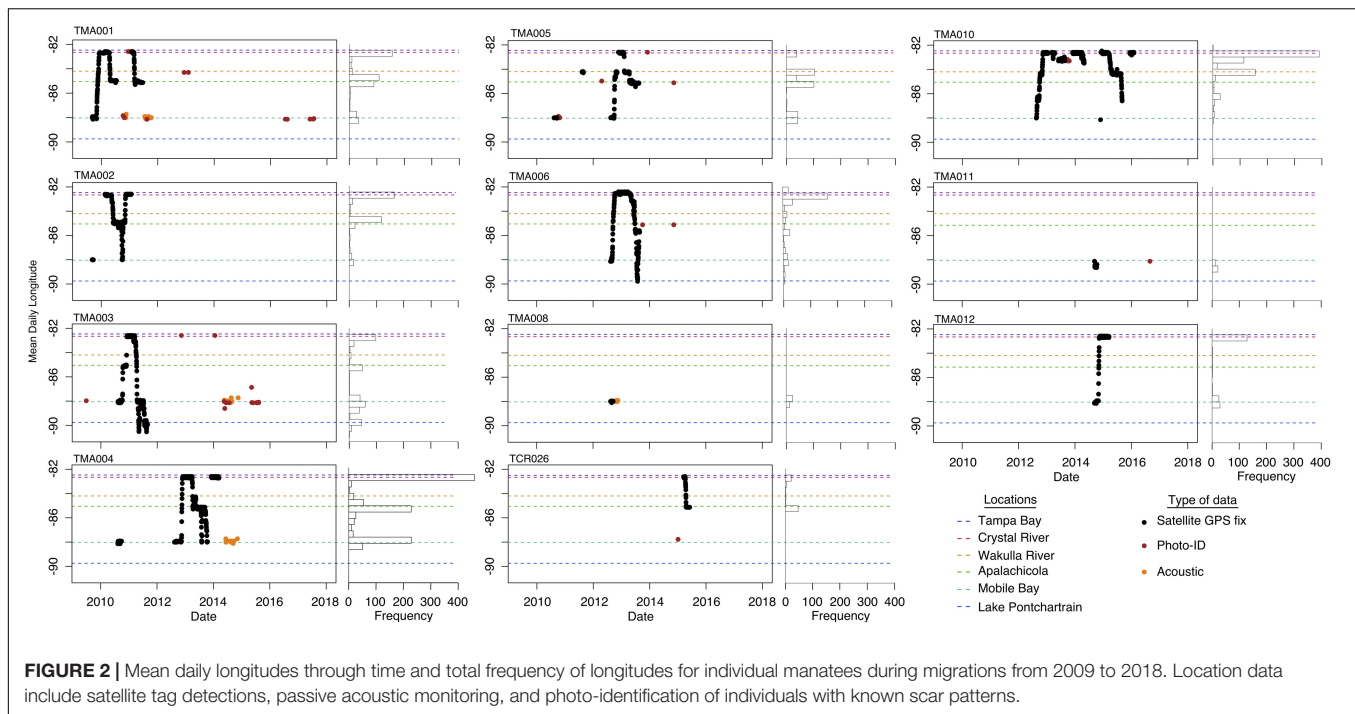
Manatee Tagging

We tagged 11 manatees between September 2009 and March 2015. Eight of those tagged manatees were adult males and the remaining three were adult females (Supplementary Table 1). Continuous tagging duration ranged from 0.5 to 13 months, and non-continuous tagging duration (i.e., an individual tagged more than once) ranged from 4 to 22 months. Collection of GPS location data for tagged manatees ended in February 2016 (Figure 2).

Daily Mean Locations, Terminal Locations, and Stopover Locations

Daily mean locations revealed predictable, seasonal movements in which manatees migrated from the nGoM to peninsular Florida during autumn (eastward) and returned to the nGoM during spring (westward; Figure 2). Some manatees migrated directly back to peninsular Florida during autumn migrations and usually overwintered in Crystal River but also Suwannee River and Tampa Bay (Figure 2). Other manatees stopped at one or more stopover sites during migration between terminal locations (Figure 2). All manatees except one, TMA010, returned to the nGoM after overwintering in peninsular Florida (Figure 2).

Crystal River and Mobile Bay were the two most frequently used terminal locations for autumn/eastward and spring/westward migrations, respectively (Figures 2, 3A,B). Eight manatees used Crystal River, and ten manatees used Mobile Bay as a terminal location (Figures 2, 3A). Crystal River was used as a terminal location 14 times and Mobile Bay was used 16 times (Figures 2, 3B). Three individuals, TMA003, TMA006, and TMA010, were tracked over multiple years and possibly had different terminal locations among years (Figure 2). Suwannee River and Tampa Bay were each used once as terminal sites by two different manatees during autumn



migration (**Figures 2, 3A,B**). These eastern terminal locations were overwintering sites (**Figure 2**). Apalachicola and Lake Pontchartrain were each used twice as terminal locations by two different manatees during spring migrations (**Figures 2, 3A,B**).

We identified 10 stopover locations between, and including, Lake Pontchartrain and Tampa Bay. The stopover locations most used by tagged manatees were (west-east) Mobile Bay, Apalachicola/St. Joseph Bay, and Wakulla, Ochlocknee, and Crystal Rivers (**Figure 2**). Mobile Bay and Apalachicola were the most frequently used stopover locations along the nGoM coast (**Figure 2**). Additionally, manatees used Lake Pontchartrain, Pascagoula River, Choctawhatchee Bay, St. Andrews Bay, and Suwannee River as stopover locations (**Figure 2**). During autumn migrations, manatees stopped most frequently at sites farther east along the Florida panhandle (**Figures 2, 3C**) and made fewer, shorter stops at more westerly sites in Alabama and Mississippi. Manatees frequently stopped at Apalachicola for 30–60 days before continuing east (**Figures 2, 3C**). Manatees also frequently stopped at Wakulla River for 14–30 days, and one manatee stopped at Suwannee River for ~30 days during autumn migration (**Figure 3C**). During spring/westward migrations, manatees stopped most frequently and for the longest periods of time in Apalachicola and Mobile Bay, where manatees spent 30–110 days (**Figures 2, 3D**). Some manatees ($n = 3$) also frequently used Suwannee and Wakulla Rivers for 30–60 days on their way west (**Figure 2**). Manatees ($n = 2$) that migrated west of Mobile Bay during spring/westward migrations most frequently used Pascagoula River and Lake Pontchartrain for 40–45 days each (**Figures 2, 3D**). Although manatees spent more time at Crystal River and Tampa Bay than other sites, most manatees ($n = 8$) spent more time cumulatively in the nGoM, between Wakulla River and Lake Pontchartrain than at any sites

in peninsular Florida (Suwannee River, Crystal River, Tampa Bay; **Figure 2**). Cumulatively, manatees spent 200–250 days of the year in the nGoM and 100–150 days of the year in peninsular Florida.

Migration Models

We were able to fit all five net-squared displacement (NSD) models to satellite telemetry data for seven round-trip migrations by seven manatees (**Figures 2, 4; Supplementary Tables 2–8**). For five of those seven round trip migrations, mixed migration was the best-fitting model (**Table 1; Figure 4**), where manatees departed Mobile Bay, overwintered in Crystal River or Tampa Bay, and returned to the nGoM but not necessarily to Mobile Bay. TMA006 was best fit with a fixed model because TMA006 returned relatively close to Mobile Bay (**Figure 4**), but the mixed migration model also had a high AIC weight (**Supplementary Table 6**). The one manatee migration trip that was not best fit by the mixed or fixed migration model, TMA010, was best fit by a dispersal model. TMA010 did not return to the nGoM during 2013 but summered in Suwannee River in northern peninsular Florida (**Table 1; Figure 4**).

Overall Migration Patterns and Durations

We documented eight autumn and eight spring migrations (**Table 2**). Autumn migrations commenced between August and November, ended between October and December, and ranged in length from 10 to 79 days (**Table 2**). In general, manatees that commenced autumn migrations earlier had longer migration durations and used more stopovers (**Table 2; Figure 4**). Spring migrations commenced as early as February and as late as May, ended between February and September, and ranged in length from 10 to 133 days (**Table 2**). For manatees that made the spring

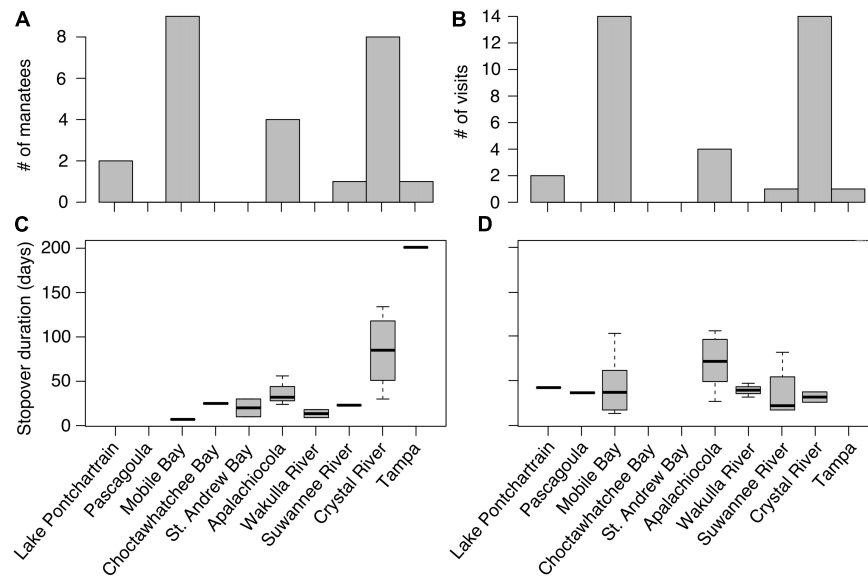


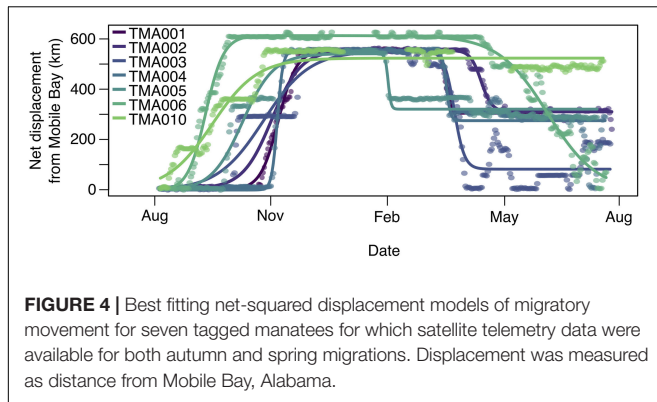
FIGURE 3 | The number of satellite telemetry tagged manatees (A) and visits (B) at terminal locations along manatee migration routes in the northern Gulf of Mexico and peninsular Florida. Stopover duration (days) for satellite tagged manatees at each site during autumn (C) and spring (D) migrations. Tampa was used once as a terminal location and stopover.

TABLE 1 | Best-fitting net-squared displacement models for each manatee where satellite telemetry data were available for both autumn and spring migrations.

Animal ID	Year	Best-fitting model	Equation	AIC weight
TMA001	2009–2010	Mixed migration	$NSD = \frac{553.68}{1 + e^{\frac{73.14 - t}{7.70}}} + \frac{-244.54}{1 + e^{\frac{217.60 - t}{2.13}}}$	1
TMA002	2009–2010	Mixed migration	$NSD = \frac{550.79}{1 + e^{\frac{68.72 - t}{13.07}}} + \frac{-244.82}{1 + e^{\frac{256.61 - t}{4.84}}}$	1
TMA003	2010–2011	Mixed migration	$NSD = \frac{554.72}{1 + e^{\frac{84.46 - t}{18.71}}} + \frac{-470.40}{1 + e^{\frac{238.84 - t}{4.10}}}$	1
TMA004	2012–2013	Mixed migration	$NSD = \frac{554.52}{1 + e^{\frac{97.35 - t}{2.27}}} + \frac{-278.57}{1 + e^{\frac{235.3 - t}{1.69}}}$	1
TMA005	2012–2013	Mixed migration	$NSD = \frac{544.95}{1 + e^{\frac{61.50 - t}{12.41}}} + \frac{-220.49}{1 + e^{\frac{177.56 - t}{1.13}}}$	1
TMA006	2012–2013	Fixed migration	$NSD = \frac{617.85}{1 + e^{\frac{38.06 - t}{7.34}}} + \frac{-617.85}{1 + e^{\frac{317.83 - t}{20.54}}}$	0.71
TMA010	2012–2013	Dispersal	$NSD = \frac{526.04}{1 + e^{\frac{43.63 - t}{18.63}}}$	1

journey to the nGoM, those that went directly to Apalachicola made quick, direct migrations, and those that continued past Apalachicola had much longer migrations durations with more stopovers (Figures 2, 4). The duration of migrations was most affected by the number of stopovers and the directedness of travel, with a lesser effect of season; migrations with longer durations

included more stopovers, had less direct travel (i.e., shorter average step lengths), and tended to occur in the spring (Table 3; Figure 5). The model that best fit the variation in the data supported these movement patterns and included the number of stopovers and average step lengths (Table 4). However, the model that included only the number of stopovers had a low AIC value



and high weight (Table 4). The strength of the effects of these factors and the ordering of the models suggest that the number of stopovers had the greatest effect on migration duration, followed by average step length and season (Tables 3, 4; Figure 5). Migration distance had little effect on duration (Tables 3, 4).

Collectively, manatees made 179 steps that were longer than 20 km (i.e., long step lengths). The longest step lengths occurred between Mobile Bay and Apalachicola (Figure 6), and the longest single step (142 km) also occurred in this region (Figure 6). The next longest step lengths occurred between Wakulla and Crystal Rivers, with the longest steps in this region occurring just east of the Wakulla River (Figure 6). Some long steps also occurred between Apalachicola and Wakulla River as well as between Lake Pontchartrain and Mobile Bay, but step lengths in these areas were generally shorter (Figure 6).

DISCUSSION

We found that West Indian manatees in the southeastern U.S.A. expanded their geographic range poleward through partial migrations. Tagged manatees made repeated, seasonal movements between the nGoM and peninsular Florida, extensively using and exhibiting high fidelity to multiple sites in the nGoM. Manatees are becoming increasingly common in the

TABLE 3 | Weighted estimates of parameter values from the selection analysis on modeling the duration of migrations.

Parameter	Model-averaged estimates (SE)	<i>t</i>	<i>p</i>
Intercept	35.747 (134.97)	0.26	0.79
Number of stopovers	27.444 (8.424)	4.74	< 0.01
Step lengths	−3.459 (6.808)	−0.51	0.62
Season	−0.609 (7.1601)	−0.08	0.93
Spring: step length	−3.454 (0.011)	0.40	0.70
Distance	~0.000 (~0.000)	−0.99	0.55
Spring: distance	~0.000 (~0.000)	0.99	0.66

nGoM (Hieb et al., 2017), and the migratory patterns we found are supported by the timing and number of opportunistic manatee sightings in the nGoM (Pabody et al., 2009; Hieb et al., 2017), and similar in timing to migrations along the southeastern Atlantic coast (Deutsch et al., 2003; Cummings et al., 2014). These migrations enable manatees to track favorable environmental conditions as they expand poleward and into regions outside manatees' more modern range (Moore, 1951a,b). Similar migratory patterns are driving range shifts in other species (McKilligan et al., 1993; Ruiz-Cooley et al., 2013; Hovick et al., 2016). The poleward range expansion of jumbo squid, *Dosidicus gigas*, into warming waters of the eastern Pacific is at least in part facilitated by migratory flexibility (Ruiz-Cooley et al., 2013). The cattle egret, *Bubulcus ibis*, a species that has experienced rapid global range expansion in the last century, performs migrations that exploit seasonal resources and likely contribute to their range expansion at least in southern Australia (McKilligan et al., 1993). Among North American terrestrial birds, those with partial and intra-continental migrations had greater latitudinal range shifts compared to residents and neotropical migrants, likely because the former can more easily track conditions in migratory regions (Hovick et al., 2016). Similar to poleward range shifts, altitudinal migration has enabled roe deer in central Europe to exploit decreased winter snowpack and shift the altitudinal limit of their winter range (Bright Ross et al., 2021). Partial migration may, therefore, be

TABLE 2 | Start and end dates and duration (days) of manatee seasonal migrations between the northern Gulf of Mexico and peninsular Florida.

Manatee	Year	Autumn			Spring		
		Start	End	Duration	Start	End	Duration
TMA001	2009–2010	11/01/09	12/02/09	31	04/15/10	04/26/10	11
TMA001	2010–2011	NA	NA	NA	02/28/11	03/09/11	10
TMA002	2009–2010	NA	NA	NA	05/17/10	09/27/10	133
TMA002	2010–2011	09/28/10	11/12/10	46	NA	NA	NA
TMA003	2010–2011	10/10/10	12/09/10	60	03/14/11	07/21/11	129
TMA004	2012–2013	11/14/12	11/25/12	11	03/31/13	07/31/13	123
TMA005	2012–2013	09/28/12	11/22/12	56	02/06/13	04/17/13	70
TMA006	2012–2013	09/07/12	10/08/12	31	04/28/13	07/30/13	94
TMA010	2012–2013	08/22/12	11/09/12	79	NA	NA	NA
TMA012	2014–2015	11/02/14	11/12/14	10	NA	NA	NA
TCR026	2014–2015	NA	NA	NA	04/07/15	04/19/15	12

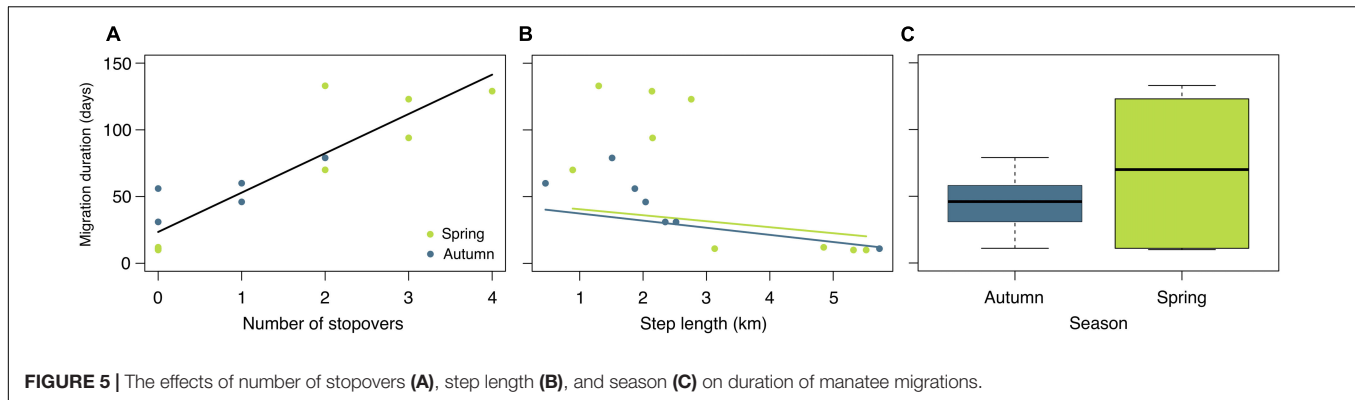


FIGURE 5 | The effects of number of stopovers (A), step length (B), and season (C) on duration of manatee migrations.

TABLE 4 | Ranking of the selection analysis for modeling migration durations.

Model	AIC _c	ΔAIC _c	w _i	Deviance Explained
Stopovers + Step length	149.80	0.00	0.49	0.19
Stopovers	150.18	0.38	0.40	0.16
Stopovers + Season	153.63	3.83	0.07	0.17
Stopovers + Step length + Season	155.11	5.31	0.03	0.19
Stopovers + Step length + Season + Distance	161.22	11.42	< 0.01	0.20
Stopovers + Step length + Season + Step*Season	161.42	11.62	< 0.01	0.20
Step length + Season	168.15	18.35	< 0.01	0.08
Step length	169.10	19.30	< 0.01	0.05
Stopovers + Step length + Season + Distance + Season*Step length	169.31	19.51	< 0.01	0.20
Step length + Season + Step length*Season	171.42	21.62	< 0.01	0.09
1	173.72	23.92	< 0.01	0.00
Season	175.88	26.08	< 0.01	0.01
Distance	176.54	26.74	< 0.01	0.00
Stopovers + Step length + Season + Distance + Season*Step length + Season*Distance	181.78	31.49	< 0.01	0.19

Models with lower AIC values better fit the data, and models with Akaike weight, w_i , > 0.10 are supported by the data.

a general mechanism for climate driven range shifts among a diverse range of species as it is the most common type of migration and occurs in most animal phyla (Dingle and Drake, 2007; Chapman et al., 2011, 2012; Shaw and Couzin, 2013).

Although manatees observed in the nGoM and other areas outside peninsular Florida have long been assumed to be temporary or accidental visitors (Gunter, 1941; Fertl et al., 2005), our results indicate that the nGoM is part of their geographic range, and this region will likely become increasingly important under future climate projections. Most of the tagged manatees we studied spent cumulatively more time in the nGoM, between Wakulla River and Lake Pontchartrain, than in peninsular Florida. This novel finding suggests that some manatees use peninsular Florida primarily when they need to seasonally seek thermal refuge and reside in the nGoM for the remainder of the year. For example, of the 11 tagged manatees, nine showed repeated migration to many of the same locations annually, and TMA001 has been documented in the nGoM outside of Florida in nine of the past 12 years (Carmichael et al., 2021). As climate changes and sea temperatures warm in coming years, the need to return to refugia in Florida may diminish and manatees may spend more time in and ultimately transition residency from peninsular Florida to areas like the nGoM. Timing and

locations of manatee sightings in the nGoM during recent cold seasons provides evidence that a few manatees have possibly stayed in the region into or through the cold season instead of promptly returning to refuge sites in peninsular Florida (Carmichael et al., 2021); from 2018 to 2021 live manatees were confirmed in waters along the Mississippi-Alabama coast from mid-November to March, and manatees have been sighted during March and April with symptoms of mild cold stress sustained at an unknown location during the cold season (Carmichael et al., 2021). The movement patterns of our tagged manatees along with these observations may therefore provide early evidence that some sites in the nGoM may become warm water, overwintering sites and that long-term changes in migratory tactics could include transitioning to periodic overwintering or residency.

Manatees use habitats at stopover sites within the nGoM for extended periods, making their motivation for stopovers different from other species. Manatees in this study often spent longer periods of time at stopovers than at terminal locations, sometimes staying only a few days at westernmost sites before returning eastward. For most other species, migration includes highly directed movements (Sheppard et al., 2006; Michelot et al., 2017), and the use of stopovers is often limited to replenishing

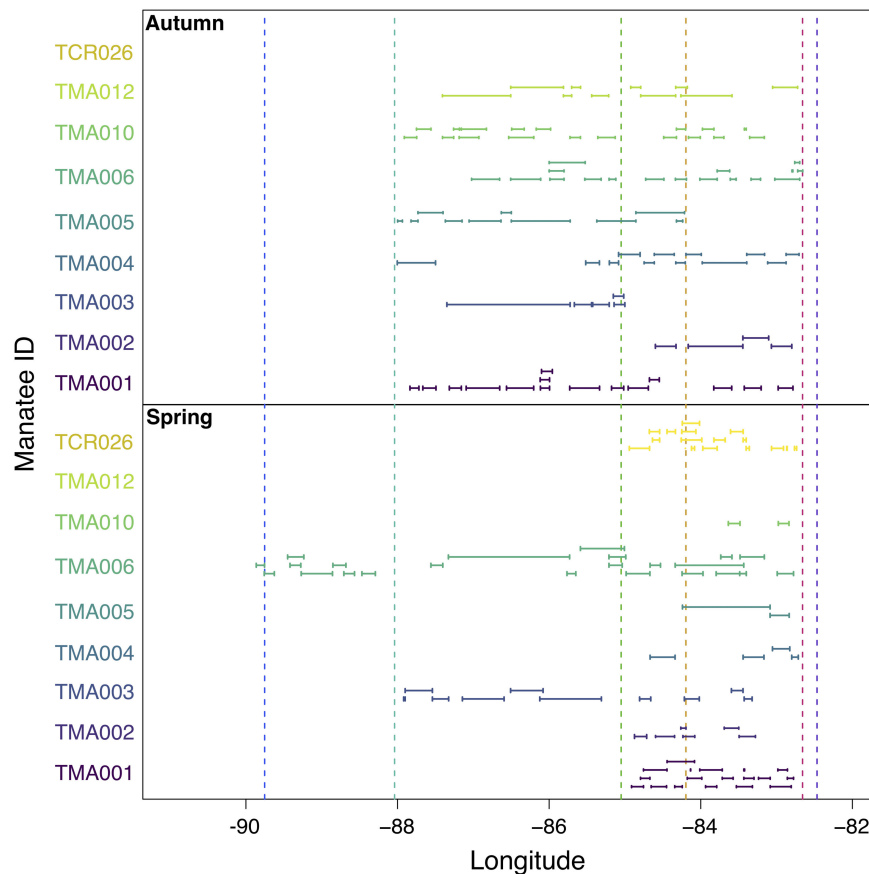


FIGURE 6 | Location of long step lengths (>20 km) during autumn and spring migrations. Line caps indicate start and end longitudes of the step length. Colored dashed lines refer to locations shown in **Figure 2**.

energy reserves (Gómez et al., 2017). For example, many birds use particular sites to resupply energy reserves and recondition their bodies before or after arduous sections of migratory routes (Buchanan et al., 2012; Hasselquist et al., 2017). Terrestrial herbivores often track resource quality as they move from winter to summer ranges (i.e., the green wave hypothesis; Bischof et al., 2012; Aikens et al., 2017). For manatees, migration distance had little effect on the duration of migrations, and individuals made long distance migrations sometimes slowly (using many stopover locations) and sometimes quickly, demonstrating that no single stopover site was essential to replenishing energy reserves during migration. Although Mobile Bay and Crystal River were the most used western and eastern terminal locations, respectively, some animals opted to travel farther west to Lake Pontchartrain (TMA003, TMA006) or east to Tampa (TMA006). In some cases, terminal locations were the conservative end points because tags were lost, particularly during spring migration, resulting in shorter tracking durations, and animals may have traveled farther west than known. The similarity in phenology of annual plant cycles across sites in the nGoM along with ready access to freshwater and a variety of vegetation types known to be used by manatees may enable manatees to flexibly use stopover sites and endpoints along the migration route from the Florida

panhandle to eastern Louisiana (Hillmann et al., 2019). These observations suggest that manatees have flexible migratory patterns for which the distance and duration are not strictly driven by environmental or physiological needs once the basic parameters for survival are met.

Multiple factors, including season, use of stopover sites, and directedness of travel, contributed to variation in the duration of nGoM migrations (Erni et al., 2002; Nilsson et al., 2013; Michelot et al., 2017). Manatee migrations tended to be shorter in duration during autumn when manatees used stopovers for shorter periods of time (~30 days), and manatees that commenced autumn migration earlier made more stopovers. Manatees that left the nGoM late in the season (i.e., November) returned directly (indicated by long average step lengths) to peninsular Florida, suggesting that skipping stopovers may have been necessary to arrive in Florida before water temperatures in the nGoM became too cold (Irvine, 1983; Bossart et al., 2003; Deutsch et al., 2003). The somewhat longer but more variable duration of springtime migrations were likely possible because of the lack of a looming or eminent driver of migration such as the threat of cold temperatures. Manatees that migrate long distances along the southeast Atlantic coast of the U.S.A. also have shorter autumn than spring migrations that are faster when they leave

later in the season (Deutsch et al., 2003). In contrast, several individual manatees in this study promptly left Crystal River in the early spring and swam with direct movements to Suwannee River or Apalachicola, suggesting that resource availability may become limited at high-density overwintering sites and affect the timing and duration of migration in some years (Littles et al., 2019). Of note, during 2020–2021 there has been an unusual mortality event for manatees on the U.S.A. Atlantic coast attributed largely to starvation from limited food resources in key peninsular habitats (Deutsch et al., 2021). Coincidentally, the first documented nGoM mortality of a manatee previously known only from the Atlantic coast occurred in Mississippi waters during February 2021 (Carmichael et al., 2021). Seasonal differences in the duration of migrations are found in a variety of species, typically due to variation in suitability of environmental conditions, including food availability and temperature (Nilsson et al., 2013; Martin et al., 2018; Deng et al., 2019). These findings suggest that seasonal and inter-annual variation in factors such as resource availability and water temperature affect immediate variation in the timing and duration of migration, with longer-term implications for range expansion.

Directed movements during migration likely reflect location-specific variation in habitat quality and structure. First, many segments in which movements were most directed (step lengths >20 km) were areas where freshwater and dietary resources were absent or uncommon. For many species, migration and movements between sites and resource patches are often very directed with long step lengths and small angles between steps (De Knecht et al., 2007; Michelot et al., 2017; Cloyed and Dell, 2019). Second, manatees often used the Intracoastal Waterway and inshore waters and rivers or followed the coastline during migrations, making their movements frequently constrained by land and conducive to long steps (Cloyed et al., 2019). Manatees also performed long step lengths across open sections of water such as crossing Apalachee Bay near Wakulla River and from Cedar Key, just south of Suwannee River, to Crystal River. This combination of traveling among resource-rich sites and in areas where movements were constrained to follow the coast or east-west waterways resulted in similar spatial patterns of directed movements among manatees.

The increased presence of manatees in the nGoM raises new conservation concerns. Our results revealed migration to a series of sites in the nGoM that are currently important for manatees, particularly Mobile and Apalachicola Bays. In populations of other species that are comprised of both migrants and residents, ecological conditions such as competition, predation, and resource abundance all contribute to switching among tactics (Brodersen et al., 2011; Chapman et al., 2011; Mysterud et al., 2011; Eggeman et al., 2016) and are likely to affect manatee migrations. TMA010 did not migrate to the nGoM during the summer of 2013, even though he migrated in years preceding and following 2013. Although more work is needed to determine the factors driving manatee geographic distributions and their specific habitat use in the nGoM into the future, this study makes an important contribution to the growing body of data needed to understand mechanisms of migration under heterogeneous and changing environmental conditions. Detailed information on

species occurrence and habitat use will enable identifying critical resources along expanding migratory routes and implementing location-specific strategies to reduce injury and mortality (Hieb et al., 2017). For example, manatees may be at greater risk from vessel interactions and strikes, other types of human interaction (Hieb et al., 2017, 2021; Cloyed et al., 2019), and cold stress associated with migrations to the nGoM. An increasing number of tropical species, from primary producers to large vertebrates like manatees, have recently become established in the nGoM, leading to the hypothesis that these waters will continue to tropicalize, significantly impacting ecosystem functions (Heck et al., 2015). These observations have raised local management and conservation concerns and make manatees an excellent sentinel species to monitor migratory behaviors and help define the broader effects of climate change on tropicalization of the nGoM and similarly affected waters elsewhere (Bonde et al., 2004; Heck et al., 2015; Scheffel et al., 2018).

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: http://cf.disl.org/datamanagement/metadata_folder/DISL-Carmichael-MSN-010-2016.xml.

ETHICS STATEMENT

The animal study was reviewed and approved by the University of South Alabama (581568 and 1038636) and Sea to Shore Alliance (S2S201003) IACUC protocols.

AUTHOR CONTRIBUTIONS

CC analyzed the data, wrote the main draft of the manuscript, and participated in editing the manuscript. EH, KD, MR, and RC contributed to collection and analysis of data from tagged and sighted manatees and participated in writing and editing the manuscript. RC and MR conceived the project. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2021.725837/full#supplementary-material>

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Ecological Trap or Favorable Habitat? First Evidence That Immature Sea Turtles May Survive at Their Range-Limits in the North-East Atlantic

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Unusual environmental events can push marine animals outside their physiological tolerances through changes in trophic and/or thermal conditions. Such events typically increase the risk of stranding. Rescue Centers offer a unique opportunity to report animals in distress and satellite track rehabilitated individuals to identify potential new habitats and support an effective conservation of these endangered species. By combining sightings (1988–2020) and tracking data (2008–2020) collected along the French Atlantic and English Channel coasts, our study assessed if the Bay of Biscay is an ecological trap or a favorable habitat for immature sea turtles. The largest tracked individuals migrated westward to pelagic waters, likely toward their natal beaches, while smaller individuals remained within the Bay of Biscay (BoB) and crossed colder (mean: $17.8 \pm 3.0^{\circ}\text{C}$) but more productive waters. The turtles' directions differed from the ones of ocean currents, excluding a passive advection to these unexpected habitats. Although the BoB might be thermally unsuitable in winter, the higher micronekton biomass predicted in this region could offer a productive foraging habitat for immature turtles. However, the majority of the sightings referred to individuals stranded alive (75%), suggesting this area could also act as an ecological trap for the smallest individuals that are mostly reported in winter suffering cold-stunning. Assumed to be outside the species range, our results reveal a potential foraging ground in the North-East Atlantic for these young turtles, confirming the crucial role of the rehabilitation centers and the need to continue prioritizing conservation of these endangered species, particularly vulnerable at this stage and at such temperate latitudes.

Keywords: Bay of Biscay, loggerhead turtle, green turtle, micronekton, sea surface temperature, Kemp's ridley turtle

INTRODUCTION

Unusual environmental conditions can push marine animals outside their physiological tolerances through changes in trophic and/or thermal conditions. In sea turtles, such events are commonly caused by a drop in sea surface temperature (SST) below 10°C , making individuals lethargic and floating at the sea surface. The risk of stranding is inevitably increased during such cold-stunning

events (George, 1997; Spotila et al., 1997). Rescue Centers offer a unique opportunity to satellite track the rehabilitated individuals to identify potential new habitats (assumed to be unfavorable due to extreme thermal conditions), and redefine Regional Management Units to ensure the conservation of these endangered species. Hypothermia of sea turtles induced by cold weather episodes have been reported in the North-West Atlantic (Burke et al., 1991; Still et al., 2005; Roberts et al., 2014; Griffin et al., 2019; Innis et al., 2019), Gulf of Mexico (Foley et al., 2007; McMichael et al., 2008; Avens et al., 2012; Shaver et al., 2017), Mexican coast (Koch et al., 2013; Salinas-Zavala et al., 2020) and Western Europe (Davenport, 1997; Witt et al., 2007; Bellido et al., 2008, 2010; Monzón-Argüello et al., 2012; Nicolau et al., 2016), affecting three main species, i.e., the green, the Kemp's ridley and the loggerhead turtles.

The loggerhead turtle (*Caretta caretta*) is the most studied of the seven sea turtle species (Hays and Hawkes, 2018) and has a complex life cycle, being distributed in oceanic waters during its juvenile stage before recruiting to coastal habitats (Bolten, 2003). The movements and habitat use of immature individuals directly caught at-sea at their developmental habitats have been largely documented in the Mediterranean Sea (Cardona et al., 2005; Revelles et al., 2007; Casale et al., 2012; Abalo-Morla et al., 2018; Chimienti et al., 2020), Pacific (Polovina et al., 2001, 2004, 2006; Kobayashi et al., 2008; Briscoe et al., 2016b, 2021), Indian (Dalleau et al., 2014; Bousquet et al., 2020), and Atlantic Oceans (Mansfield et al., 2009, 2014; Varo-Cruz et al., 2016; Chambault et al., 2019). However, the spatial patterns of individuals after rehabilitation in unusual habitat (outside their geographical range-limit) remain undocumented in most regions, in particular in Western Europe.

Stranding events of sea turtles occur annually along the Western European coasts, including the Spanish (Bellido et al., 2010; Orós et al., 2016), Portuguese (Nicolau et al., 2016), British (Botterell et al., 2020) and French coasts (Witt et al., 2007; Morinière and Dell'Amico, 2011). Genetic analysis have demonstrated that immature loggerhead turtles stranded along the French Atlantic and English Channel coasts mostly originate from the North-East American coast (51%), and to a lesser extent to Cape Verde (26%) (Monzón-Argüello et al., 2012). Hatchlings emerging from Florida rookeries are known to perform a transatlantic oceanic migration toward several developmental habitats located in the Azores, Madeira, Cape Verde, and Canary Islands (Bolten et al., 1998). But despite the large number of stranding events observed each year (Witt et al., 2007; Bellido et al., 2010; Morinière and Dell'Amico, 2011; Nicolau et al., 2016; Orós et al., 2016; Botterell et al., 2020), no favorable developmental habitat has been identified yet along the continental European coast due to potentially unfavorable thermal conditions and the high latitudinal location of this areas, assumed to be outside the species usual range (Wallace et al., 2010). In addition to loggerhead turtles, green (*Chelonia mydas*) and Kemp's ridley sea turtles (*Lepidochelys kempii*) originating from North-West Atlantic, Caribbean, and Gulf of Mexico (Manzella et al., 1988; Marquez, 2001; Wallace et al., 2010) are, two species rarely seen in European waters, annually gathering

in lower proportions along the French Atlantic coast and English Channel coasts.

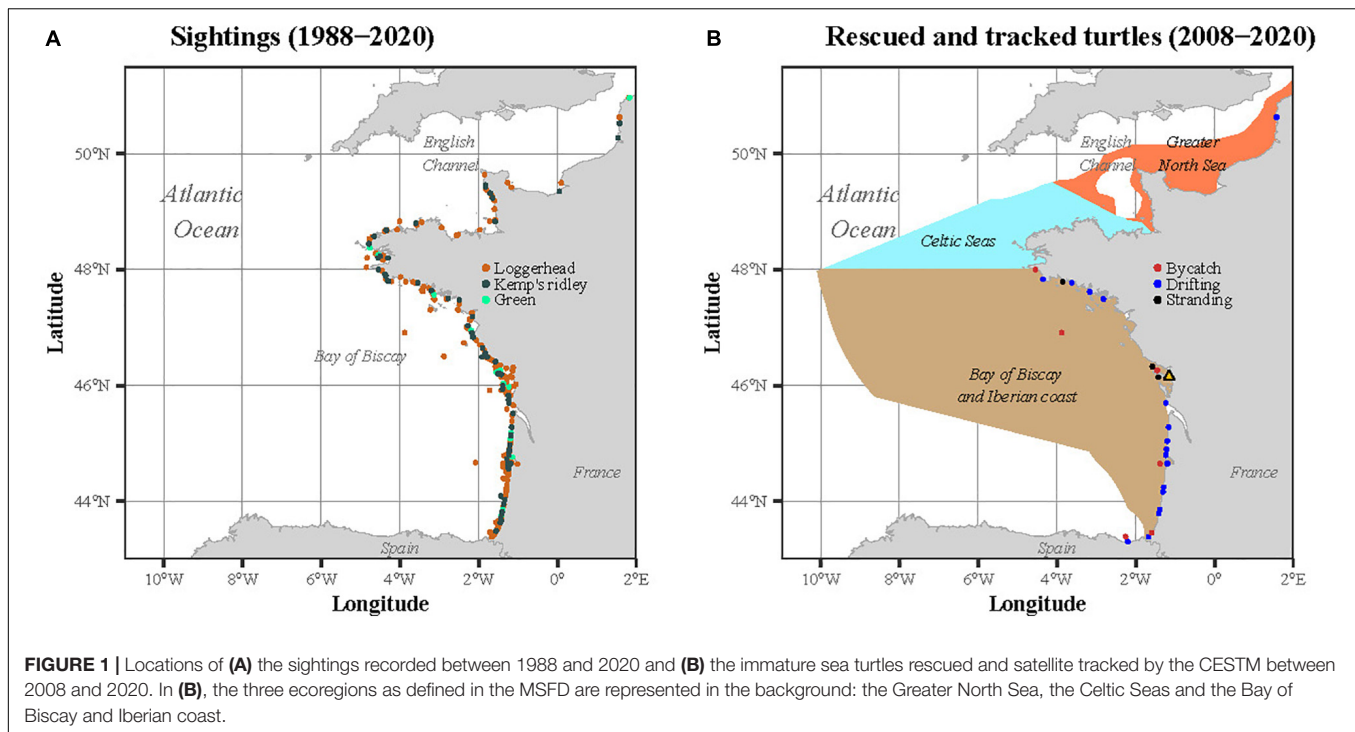
In 2010, Wallace et al. (2010) delineated 58 Regional Management Units (RMUs) based on published satellite tracks, tag returns and demographic and genetic data collected from nesting populations for the seven sea turtle species worldwide. However, these units have not incorporated some sites of immature turtle aggregation, in particular in the North-East Atlantic where immature loggerheads, greens and Kemp's ridleys are frequently observed (Bellido et al., 2010; Morinière and Dell'Amico, 2011; Monzón-Argüello et al., 2012; Nicolau et al., 2016; Orós et al., 2016; Botterell et al., 2020). Satellite tracks and stranding reports collected from European waters therefore provide a unique source of data to update these RMUs and design more appropriate units of protection taking into account juvenile sea turtle habitats.

By combining sightings (1988–2020) and tracking data (2008–2020) collected by the CESTM (Center d'Études et de Soins pour les Tortues Marines) of the Aquarium La Rochelle along the French Atlantic and English Channel coasts, our study aims to assess if the Bay of Biscay could be a favorable habitat or rather an ecological trap for immature sea turtles. Depending on their size, we expect that the rehabilitated immature individuals will either: (i) remain in the North-East Atlantic ecoregion (smaller individuals) or (ii) migrate toward their natal beaches located along the North-Eastern American coast or Cape Verde islands (larger individuals). Our study provides the first evidence of new habitats for rehabilitated immature sea turtles across the North-East Atlantic. Our findings will support the use of sea turtles as bioindicators in the context of the European Marine Strategy Framework Directive (MSFD) and will help redesigning the Regional Management Units (Wallace et al., 2010) to prioritize conservation of these endangered species, particularly vulnerable at this stage.

MATERIALS AND METHODS

Sightings

Sightings of sea turtles are reported throughout the year to the CESTM from the English Channel-North Sea to the Bay of Biscay-Iberian Coast (**Figure 1A**). This large dataset covering 33 years of sightings (1988–2020) complements the work of Witt et al. (2007) to investigate the temporal variability of the turtle size throughout the year, over a longer period. These sightings gather individuals stranded, bycaught in fishing nets or drifting at sea. Initiated in 1988 and compiling data from the four species found along Western Europe (leatherback, loggerhead, Kemp's ridley and green), this dataset has been partly published (Witt et al., 2007; Morinière and Dell'Amico, 2011). To be consistent with the tracking analysis, we restricted this dataset to the three species satellite tracked in our study, i.e., the loggerhead, the Kemp's ridley and the green turtle. The sightings located outside the three marine ecoregions defined by the MSFD were also discarded from the analysis.



Ethics Statements

This study meets the legal requirements of the country and the Rescue Center where this work was carried out, and follows all institutional guidelines. The Prefectoral Order N°2004-1104 approved the opening of the CESTM and delivered to Mrs. Florence Dell'Amico a certificate (n°2017 02173) to conduct care practices on non-domestic animals. The protocol was approved by the French “Regional environment, planning and housing” agency (DREAL, permit number: DREAL/56-2020), authorizing the transportation, tag deployment and release of endangered species. The Ministerial Order (30/12/2020) acts as an exception to the strict protection of species, authorizing the manipulation of protected species when found bycaught, drifting at sea or stranded.

Rescue and Rehabilitation

Between 2008 and 2020, 66 immature sea turtles were rescued and rehabilitated by the CESTM of the Aquarium La Rochelle. Among these 66 individuals, 28 were then equipped with satellite transmitters. The rescued individuals (one rescued twice) were found stranded ($n = 17$), bycaught ($n = 8$) or drifting at the sea surface ($n = 3$) within the three regions defined by the MSFD along the Atlantic French and English Channel coasts: the Greater North Sea, the Celtic Seas and the Bay of Biscay and Iberian coast. The majority of the rehabilitated individuals were loggerhead turtles ($n = 23$), but some were also Kemp's ridley ($n = 4$) and green ($n = 1$) sea turtles. When rescued, each individual was measured (minimum Straight Carapace Length, hereafter SCLmin) and weighed. The same morphometric measures were also taken before attaching the tag, a few days before release.

Tag Deployment

Different tags types were used between 2008 and 2020. They all recorded Argos locations. In 2008, a KiwiSat® Argos tag (SirTrack manufacturer) was deployed on the first individual after rehabilitation using the attachment procedure described in Balazs et al. (1996) for the biggest individuals. The 27 remaining tags (two SPLASH and 25 SPOT) deployed between 2009 and 2020 were provided by Wildlife Computers® and attached using the procedure developed by Seney et al. (2010) for the smallest individuals. This technique incorporating a neoprene layer takes into account the rapid growth of immature individuals to prevent the tags to detach too quickly, extending therefore the tracking duration. The complete list of deployed tags is given in **Supplementary Table 1**.

Data Prefiltering

Location data were obtained from the Argos Data Collection and Location System. The Least Square positioning algorithm was used for tags deployed before 2011 and the improved Kalman filtered positions were obtained for the other tags (Lopez et al., 2014). All statistical analyses were performed using R software version 4.0.2 (R Core Team, 2021). We restricted our dataset to positions associated with a travel speed lower than 10 km/h (Fossette et al., 2010). Locations on land and those associated with a location class Z were also discarded.

Movement Analysis

The individual tracks were then predicted daily using the *foieGras* package with a simple continuous-time random walk algorithm (Jonsen and Patterson, 2020; Jonsen et al., 2020). The algorithm accounted for the Argos quality to predict the

daily locations using Argos error ellipses for the tags deployed after 2011, while the location classes (0, 1, 2, 3, A or B) were used for the remaining tags. Following Hays et al. (2021) and Hart et al. (2021), assessment of tag failure was conducted on the data available using the three following metrics: battery voltage, wet/dry switches and the number of Argos transmissions.

To identify turtle aggregation and hotspot habitats, we generated hexagonal maps by summing the number of predicted locations (from the random walk) in each grid cell of 0.5 and 0.1 degrees, respectively. To reduce tagging location and track length biases, the first week of tracking was removed for each individual.

Spatial patterns were visually identified based on the geographic difference between the last position recorded for each individual and the release site. Intrinsic (morphometric measurements) and extrinsic factors (environmental conditions encountered) were then compared according to the spatial pattern. The effect of rehabilitation time on the spatial pattern was tested using a Kruskal-Wallis test.

In order to assess if the behavior of the turtles was typical, we then compared the movement characteristics (tracking duration, swimming speed and distance traveled) of the injured individuals that were amputated ($n = 4$, **Table 1**, IDs with the asterisk) to the “not injured” turtles. The interaction between distance traveled and tracking duration was also tested. This was conducted using a Generalized Linear Model with a binomial distribution, and the state (injured vs. not injured) as a response variable.

Environmental Drivers

To assess the habitat used and selected by the turtles, a series of environmental variables were then extracted at each predicted daily location. Three oceanographic variables were extracted daily from E.U. Copernicus Marine Service Information¹ at a resolution of 0.08 decimal degree: the zonal component of the surface currents (U, positive eastward), the meridional component of surface current (V, positive northward) and the Sea Surface Temperature (SST). Two products were used depending on the period: the *Global Ocean Physics Reanalysis Glorys S2V4* (PHYS_001_024, after 2016) and the *Global Ocean Physics Reanalysis Glorys12v1* (PHY_001_030, before 2016).

Predicted daily positions were used to compute the daily ground speeds of each turtle. The swimming speed of each individual was then calculated by subtracting the modeled ocean current velocity from the ground speed (Gaspar et al., 2006). Turtles and ocean currents headings were then estimated at each position. To assess if the habitats experienced by the turtles were productive, two low and mid-trophic level (LMTL) variables were also extracted daily from the Spatial Ecosystem and Populations Dynamics Model (SEAPODYM) at a 0.08 decimal degree (Lehodey et al., 2010): the mesozooplankton biomass (200 μm to 2 cm) and the epipelagic micronekton biomass (2–20 cm). Unlike primary productivity or chlorophyll *a* that are commonly used to predict the distribution of megafauna species, micronekton and zooplankton refer to mid-trophic levels encompassing the potential prey of sea turtles. Micronekton

group gathers organisms of different taxa (e.g., fish, cephalopods, crustaceans) and these model outputs are made available through the CMEMS web portal (BGC_001_033). Due to the dive behavior of immature turtles of this size, we restricted our analysis to the epipelagic layer.

Habitat Modeling

The geographic space available to each animal was assessed by simulating a series of tracks for each individual using the *availability* package (Raymond et al., 2021), i.e., $n = 50$ simulated tracks per individual as suggested by Hindell et al. (2020). Using the *mgcv* package (Wood, 2017), the habitat selected by the turtles was then characterized using a Generalized Additive Model to relate the presence of the turtles to a series of environmental factors, i.e., SST, zooplankton biomass, micronekton biomass, ocean current velocity, zonal and meridional components of ocean currents and sea surface salinity. The turtle's presence was used as a binary response variable (real track vs. simulated tracks). All numeric variables were first checked for collinearity using the VIF function from the *usdm* package (Naimi et al., 2014). To account for the inter-individual variability, turtle ID was added as a random factor. An autocorrelation term was also added to the model to account for the correlation structure in the data. A threefold cross-validation was used by partitioning the dataset into the training (2/3 of the data) and the validation dataset (1/3). Model evaluation was then done on the validation dataset using four performance metrics calculated for each model: the area under the curve (AUC), the sensitivity, the specificity and the true skill statistics (TSS).

To test the influence of the spatial pattern on the thermal and biological habitat used by the turtles, a generalized logistic model was performed using the *mlogit* package (Croissant, 2020) using the data collected along the entire route for each individual. The response variable was the spatial pattern with the four modalities, and the explanatory variables the environmental conditions encountered by the individuals: SST, zooplankton and micronekton biomasses.

RESULTS

Sightings (1988–2020)

The sightings were reported throughout the year between 1988 and 2020 along the French Atlantic and English Channel coasts (**Figure 1A**). A total of 449 sightings of immature sea turtles were reported, including a majority of loggerhead turtles ($n = 353$), followed by Kemp's ridleys ($n = 75$) and greens ($n = 21$). No green turtle was observed in spring and summer while a very few Kemp's ridley were seen in April and late summer. The majority of the sightings referred to individuals stranded alive (65.5%), followed by stranded dead (23%), captured alive (6.9%), drifting alive (2.7%), captured dead (1.3%), drifting dead (0.4%) and observed in the water alive (0.2%). A larger proportion of sightings occurred during late autumn and winter, with a peak in February and March, representing 39% of the sightings (**Figure 2A**). The smallest individuals (≤ 32 cm) were mostly observed between

¹<https://resources.marine.copernicus.eu>

TABLE 1 | Characteristics of the rescued turtles and after release with the satellite tags.

ID	Species	Obs.	Rehab.	Haplotype	Track start	Track end	Distance	Duration	Duration BoB	Speed	Swim speed
							(km)	(days)	(days)	(m/s)	(m/s)
ANTIOCHE	<i>Caretta caretta</i>	Stranding	257	CC-A10.1	29/07/2008	16/11/2008	960	110	110	0.1	0.13
ANTIOCHE 2	<i>Caretta caretta</i>	Stranding	101	CC-A10.1	24/09/2009	16/06/2010	3,600	265	67	0.15	0.20
BAMBI	<i>Caretta caretta</i>	Drifting	49	CC-A1.1	25/09/2009	01/04/2010	2,100	188	188	0.12	0.13
BELINE	<i>Caretta caretta</i>	Stranding	194	CC-A1.3	09/07/2009	30/09/2009	1,100	83	79	0.14	0.17
BOUTON D'OR	<i>Caretta caretta</i>	Stranding	99	CC-A2.1	09/07/2009	31/10/2009	1,700	114	63	0.16	0.17
BULLE	<i>Caretta caretta</i>	Bycatch	287	CC-A1.1	09/07/2009	31/07/2009	270	22	22	0.13	0.16
CHACAHE	<i>Caretta caretta</i>	Bycatch	209		05/07/2011	23/07/2011	470	18	18	0.30	0.28
DANAE	<i>Lepidochelys kempii</i>	Bycatch	210		10/07/2012	18/09/2012	250	70	70	0.05	0.08
DELTA	<i>Lepidochelys kempii</i>	Bycatch	46		10/07/2012	03/09/2012	300	55	55	0.06	0.12
DOMINO	<i>Caretta caretta</i>	Stranding	188		10/07/2012	12/11/2012	1,600	125	125	0.14	0.14
ECUME	<i>Caretta caretta</i>	Drifting	102		24/09/2013	29/09/2013	160	5	5	0.37	0.36
FLAMME	<i>Caretta caretta</i>	Stranding	122		02/07/2014	01/10/2014	2,200	91	23	0.28	0.25
FLOT	<i>Chelonia mydas</i>	Bycatch	253		02/07/2014	07/08/2014	190	36	36	0.06	0.13
FRANCESCA	<i>Caretta caretta</i>	Stranding	79		02/07/2014	04/08/2014	1,100	33	23	0.39	0.33
FUTE	<i>Lepidochelys kempii</i>	Stranding	551		17/08/2015	03/10/2015	920	47	21	0.22	0.21
GLOBE-HELENA	<i>Caretta caretta</i>	Bycatch	83		08/07/2016	04/11/2017	6,900	484	319	0.16	0.16
HORIA	<i>Caretta caretta</i>	Stranding	428		08/08/2017	27/11/2017	1,800	111	18	0.18	0.19
ICARE*	<i>Caretta caretta</i>	Stranding	177		29/06/2018	08/05/2020	11,000	679	31	0.19	0.16
IDOLE	<i>Caretta caretta</i>	Stranding	203		29/06/2018	09/01/2019	2,100	194	38	0.12	0.19
ILE DE RE	<i>Caretta caretta</i>	Drifting	319		29/06/2018	27/01/2019	1,800	212	212	0.09	0.13
INDIGO	<i>Caretta caretta</i>	Stranding	94		30/06/2018	25/11/2018	1,900	148	148	0.14	0.14
IODEE*	<i>Caretta caretta</i>	Stranding	87		29/06/2018	13/11/2018	2,700	137	48	0.22	0.19
JUPITER	<i>Lepidochelys kempii</i>	Stranding	207		04/07/2019	19/11/2019	3,900	138	53	0.33	0.30
KAROLINA	<i>Caretta caretta</i>	Stranding	30		22/07/2020	17/08/2020	610	26	26	0.26	0.27
KAWAI	<i>Caretta caretta</i>	Bycatch	371		23/06/2020	08/10/2020	760	107	107	0.08	0.11
KEMEN*	<i>Caretta caretta</i>	Stranding	180		23/06/2020	15/06/2021	5,700	357	32	0.18	0.14
KERCAMBRE*	<i>Caretta caretta</i>	Stranding	128		23/06/2020	30/08/2020	1,400	68	25	0.23	0.2
							2,129 ± 1,562	145 ± 101	73 ± 52	0.61 ± 0.43	0.17 ± 0.11

"Obs." stands for the type of observation, "Rehab." is the rehabilitation time (in days) spent at the CESTM (in parentheses is the total duration between rescue and release). Speed refers to the average travel speed (not corrected from ocean currents) in m/s (in parentheses is the maximum speed). IDs with an asterisk are injured turtles.

January and April, while largest turtles (>40 cm) were found year-round (**Figure 2B**).

Rehabilitation and Tracking Data (2008–2020)

Among the 28 satellite tracked turtles, one was removed from the analysis due to a very short tracking duration and only a few locations transmitted (Ino). This turtle was found stranded dead with the tag still attached only 10 days after release, so the end of transmission was not due to battery exhaustion (**Supplementary Figure 1A**). Among the 27 remaining turtles, four were amputated (Icare, Iodée, Kemen, and Kercambre). These injured individuals behaved similarly (in terms of swimming speed, tracking duration and distance traveled) compared to the "not injured" turtles (generalized linear model: all $p > 0.05$). Rehabilitation time had no effect on the spatial pattern (Kruskal-Wallis rank sum test, $p > 0.05$).

Sightings occurred throughout the year but there was a peak in fall and winter, representing 64% of the observations. The individuals were either found stranded ($n = 17$), bycaught ($n = 7$) or drifting at sea ($n = 3$) along the French Atlantic coast, from Bretagne to the Spanish border (**Figure 1B**). The duration between the observation and the release lasted between

32 (Karolina) to 4239 days (Francesca), and on average (\pm SD) 373 ± 771 days (**Table 1**). Most individuals were rehabilitated at the CESTM, but one turtle remained in another center for 12 years before being transferred to the CESTM for release with a satellite tag. The rehabilitation time spent at the CESTM varied between 30 and 551 days for an average of 190 ± 122 days. When released, the turtles measured between 21.5 and 87.5 cm in SCLmin (mean \pm SD: 41.6 ± 16.6 cm), for a body mass ranging from 1.8 to 93.2 kg and a mean of 17.7 ± 21.6 kg.

Among the 27 satellite tracked turtles, one was found stranded again a few months after release (Antioche), and then equipped a second time in 2009 (Antioche 2). The average tracking duration was 145 ± 152 days, for an average traveled distance of $2,129 \pm 2,409$ km (range: 160–11,000 km) (**Table 1**). The time spent within the BoB varied between 5 and 319 days (mean \pm SD: 73 ± 52 days). The total travel speed (including ocean currents) was 0.17 ± 0.12 m/s (max: 0.9 m/s). The haplotype was available for six individuals (**Table 1**) and have been previously published in Monzón-Argüello et al. (2012). The natal origin of five individuals could be determined and have already been published in Monzón-Argüello et al. (2012): one originates from Cape Verde, one from Dry Tortugas, Mexico or South Florida, and three could have multiple origins (e.g., Florida, Dry Tortugas, Mexico, Cape Verde).

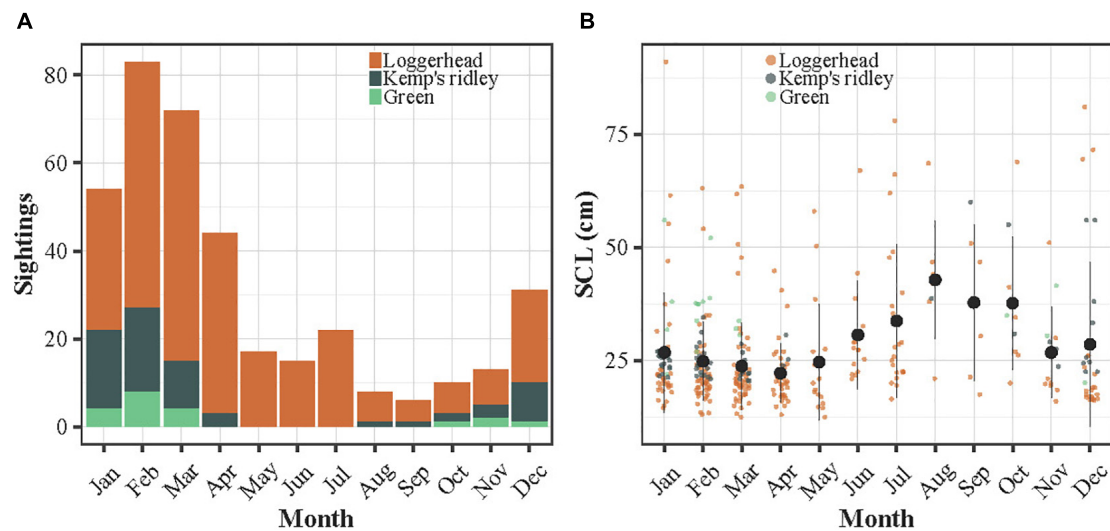


FIGURE 2 | (A) Histogram of the number of sightings according to month and species. **(B)** Distribution of the SCL (SCLmin or SCL in cm) of the sightings over month. In **(B)**, the dots refer to the monthly means and the bars to the standard errors.

Assessment of tag failure was conducted over the 27 individuals, and for only four turtles, the drop in battery voltage below 3.0 V was indicative of battery exhaustion at the end of the tracking (**Supplementary Figure 1A**). Data on the wet/dry switches was available for only 13 individuals. Except for Antioche 2, the clear difference between “dry” and “wet” states suggested biofouling was not the reason for the cessation of transmissions (**Supplementary Figure 1B**).

Spatial Patterns

The 26 turtles dispersed largely from the European west coast to Bermuda, passing near the Azores and Canary Islands (**Figure 3**). Among the four Kemp's ridleys, two migrated northward while the last two remained within the BoB. The only green turtle satellite tracked (Flot) remained within the BoB during the entire tracking duration (36 days). According to the last position recorded for each individual compared to the release site, four different spatial patterns were identified: Bay of Biscay, North, South and West (**Figure 3**). The Bay of Biscay pattern refers to 11 resident individuals that remained within this region along the French Atlantic coast. The North pattern includes three individuals that migrated north toward United Kingdom, the Netherlands and Norway, crossing the English Channel and the North Sea. Among the three North individuals, two were Kemp's ridley turtles. The South group ($n = 3$) headed toward Portugal, the Mediterranean Sea and Western Sahara, while the West group ($n = 10$) migrated westward within the North Atlantic in the open ocean, targeting the Azores, the Canary Islands or even Bermuda.

Figure 4A shows a heatmap over the entire study region, highlighting the habitats of interest located mainly in the Bay of Biscay. This map confirms that the individuals crossed both international waters and numerous Exclusive Economic Zones (16 ZEEs, e.g., Spain, France, Portugal, Western Sahara. At a

finer scale, the heatmap in **Figure 4B** confirms that the area of turtle aggregation is located close to the shoreline near the release site, and is included into the Gironde estuary and sea of Pertuis Marine Natural Park.

The SCLmin and body mass varied significantly according to the spatial pattern (**Figure 5**). The SCLmin was significantly larger for individuals migrating westwards (mean \pm SD: 53.1 ± 14.9 cm) and northwards (mean \pm SD: 61.9 ± 13.5 cm), and minimum for the resident turtles that remained in the Bay of Biscay (BoB, mean \pm SD: 32.7 ± 9.3 cm) and the South group (mean \pm SD: 44.9 ± 10.1 cm, Kruskal-Wallis rank sum test, $p < 0.001$). Similarly, body mass differed significantly with the spatial pattern (Kruskal-Wallis rank sum test, $p < 0.001$). Body mass was maximum for the North (mean \pm SD: 39.4 ± 19.9 kg) and West (mean \pm SD: 31.3 ± 19.8 kg) groups and minimum for the BoB (mean \pm SD: 7.7 ± 6.5 kg) and South (mean \pm SD: 17.7 ± 16.0 kg) groups, being below the average values (mean \pm SD: 41.6 ± 16.6 cm and 17.7 ± 21.6 kg).

Active Swimming or Passive Advection?

We found differences between directions of ocean currents and those of the turtles across the four patterns (**Figure 6**). For the Bay of Biscay group, ocean currents flowed mainly south-eastwards while the individuals headed north-west in the opposite direction (**Figures 6A,B**). For the South and the West group, ocean currents flowed south-west and south-east, while the turtles swam mainly west for both groups (**Figures 6C-F**). The North individuals headed northwest and northeast and the ocean currents mainly west and north-east (**Figures 6G,H**). The swim speeds of the turtles were significantly faster (mean \pm SD: 0.17 ± 0.11 m/s) than the speed of ocean currents (mean \pm SD: 0.10 ± 0.08 m/s, Mann-Whitney U -test, $p < 0.001$). The turtle swimming speed was positively correlated to the velocity of ocean

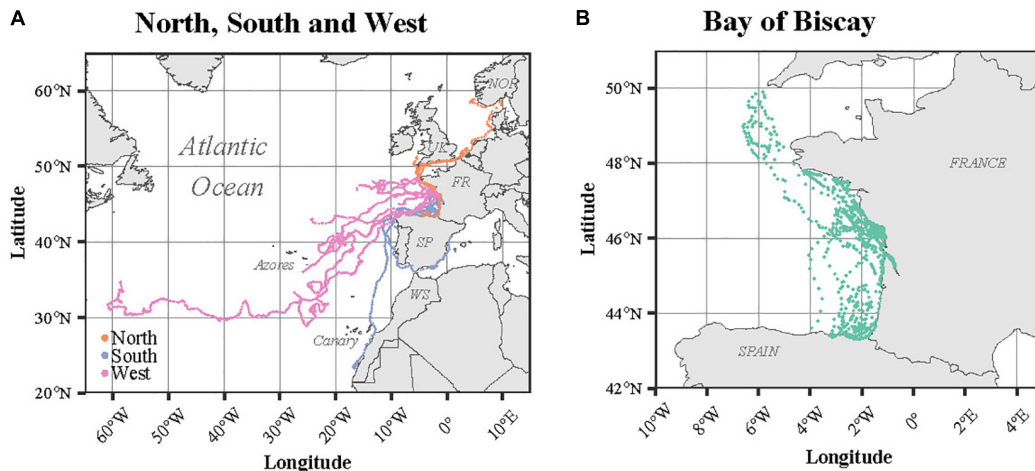


FIGURE 3 | Satellite tracks of the immature turtles according to their spatial pattern: **(A)** North ($n = 3$), South ($n = 3$) and West ($n = 10$) and **(B)** Bay of Biscay ($n = 11$). The names of the countries are indicated in capital letters: NOR (Norway), UK (United Kingdom), FR (France), SP (Spain), and WS (Western Sahara).

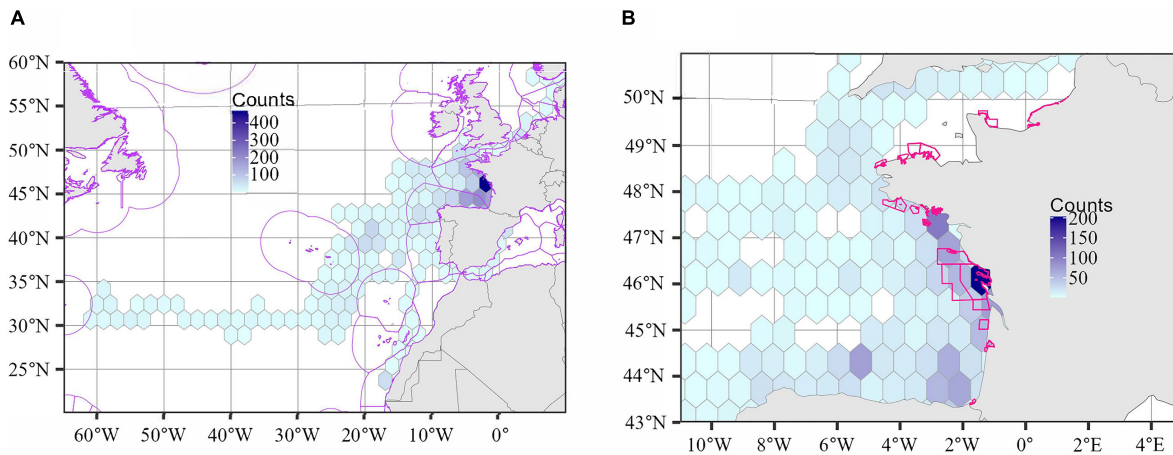


FIGURE 4 | Density plots of the 26 sea turtles **(A)** over the entire study region and **(B)** a focus over the French Atlantic coast and English Channel. The counts refer to the total number of locations recorded in each grid cell. The first week of tracking was removed to discard the potential effect of the release site and atypical behavior after release. Exclusive Economic Zones were overlaid (in purple, left) and Marine Protected Areas (in pink, right) in **(A,B)**, respectively.

currents and to the zonal component of the currents U (LMM, $p < 0.001$).

Habitat Selection

The explained deviances derived from the GAMs ranged between 23.1 and 23.4%, and the seven predictors were highly significant ($p < 0.001$). The performance of the models was high and negligible variability was noticed across the models: $0.270 < R^2 < 0.273$, $0.79 < AUC < 0.80$, $0.68 < \text{sensitivity} < 0.69$, $0.740 < \text{specificity} < 0.741$ and $0.42 < TSS < 0.43$. Current velocity and SSS had a negative relationship with the turtle's presence, while micronekton and zooplankton biomasses increased with the probability to find a turtle (Figure 7). Turtle's presence was at its highest for low and high values of U and V currents. The GAM indicated an optimum SST around 17–18°C, showing lower probabilities of turtle's presence at both

low and high sea temperatures. The SST extracted at turtle's locations varied between 8 and 27.6°C for an average temperature of $18.4 \pm 3.3^\circ\text{C}$ (Supplementary Table 2). The SST varied significantly according to the spatial pattern, being minimum for the North group ($16.1 \pm 3.8^\circ\text{C}$, logistic model estimate: -0.28 , $p < 0.001$) and maximum for the West group ($19.8 \pm 2.7^\circ\text{C}$) (see Figure 8A, logistic model estimate for BoB = -0.30 , $p < 0.001$ and south = -0.16 , $p < 0.001$).

When all individuals and the four patterns were pooled together, the seasonal trend was also observed and differed according to the size of the turtles with the smallest individuals ($SCL_{\min} \leq 29$ cm) exploiting waters generally colder ($17.2 \pm 2.6^\circ\text{C}$) than the largest individuals ($SCL_{\min} \geq 41$ cm, $18.9 \pm 3.7^\circ\text{C}$) (see Figure 8B). Nearly half of the locations recorded (49%) were associated with waters between 15 and 20°C, and only 18% below 15°C (Supplementary Figure 2).

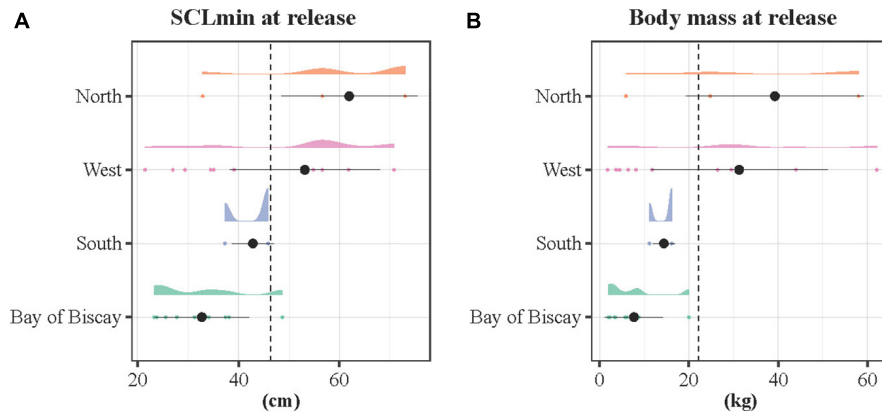


FIGURE 5 | Density distributions of the (A) SCLmin and (B) body mass at release according to the spatial pattern. The density distributions are color-coded by spatial pattern, with a cloud of points below. The dotted lines refer to the average SCLmin and body mass considering the 26 tracked individuals (Francesca was removed because unrepresentative of the sample size). The black dots stand for the mean and the bars the standard deviation for each group.

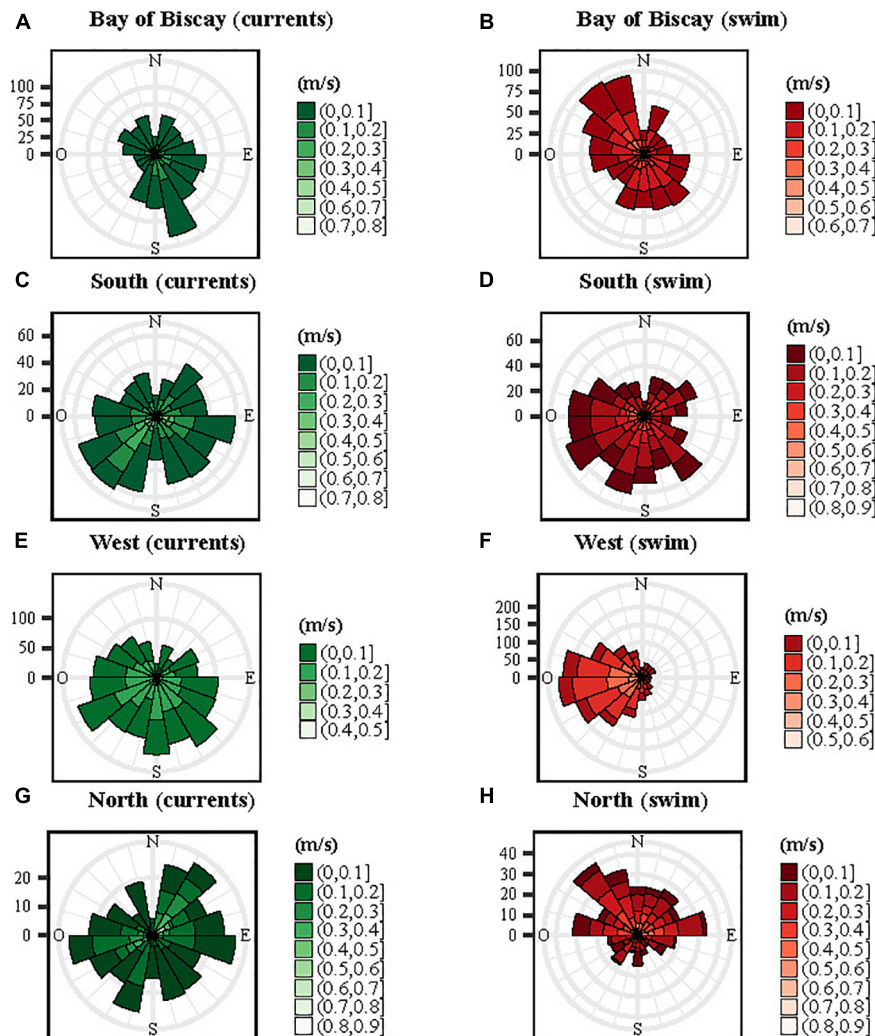


FIGURE 6 | Rose diagram frequency distributions of ocean currents (in green) and turtles (in red) orientation and velocity (in m/s) for the four spatial patterns: Bay of Biscay (A,B), South (C,D), West (E,F) and North (G,H). The currents were extracted at each turtle location.

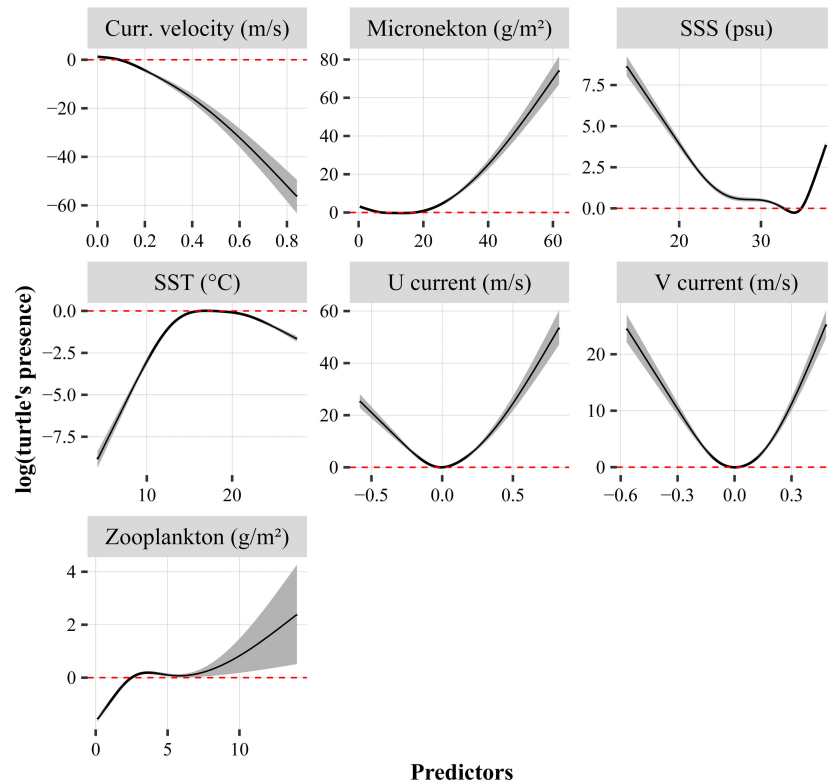


FIGURE 7 | Relationships between turtle's presence (y-axis) and their associated environmental variables obtained from the GAMs. The solid black line in each plot is the smooth function estimate and the shaded regions refer to the approximate 95% confidence intervals. The y-axis represents the response variable expressed in log scale. Positive values on the y-axis indicate a high probability of turtle's presence, and conversely. The horizontal dotted lines indicate the probability of turtle presence is not significantly positively or negatively influenced by the predictor. SSS refers to Sea Surface Salinity.

The zooplankton biomass varied between 0.10 and 9.0 g.m^{-2} for an average biomass of $2.3 \pm 1.4 \text{ g.m}^{-2}$ (Figure 8C and Supplementary Table 2). The zooplankton biomass varied significantly according to the spatial pattern (logistic model estimates: BoB = 0.32, north = 0.60, south = 0.23, $p < 0.001$), being minimum for the West group ($1.4 \pm 1.1 \text{ g.m}^{-2}$) and maximum for the North group ($3.7 \pm 1.5 \text{ g.m}^{-2}$). The micronekton biomass varied between 0.48 and 49.9 g.m^{-2} for an average biomass of $6.4 \pm 4.9 \text{ g.m}^{-2}$. The micronekton biomass varied significantly according to the spatial pattern (logistic model estimates: BoB = 0.60, north = 0.66, south = 0.12, $p < 0.001$), being minimum for the West group ($3.3 \pm 2.5 \text{ g.m}^{-2}$) and maximum for the North group ($12.9 \pm 7.4 \text{ g.m}^{-2}$) (see Figure 8D).

DISCUSSION

By compiling the sighting data from three species together with the first dataset on rehabilitated individuals satellite tracked from the French Atlantic coast, our study sheds light on contrasting spatial patterns driven by individual size, and provided evidence that the Bay of Biscay might act as an ecological trap for the smallest individuals in winter due to

low sea temperatures, but also as a potential foraging habitat in summer and autumn.

Spatial Pattern Driven by Turtle Size

The four spatial patterns identified seemed mainly driven by the size of the individuals, with the smallest turtles remaining in close proximity to the release site in the Bay of Biscay, while the largest turtles migrated either northwards or performed long westward migration in pelagic waters. The majority (51%) of the immature loggerhead turtles frequently observed along the French Atlantic coast originate from Florida (Monzón-Argüello et al., 2012), suggesting that the largest turtles heading westward in our study were targeting their natal beach as observed for other sea turtles species in the Indian Ocean (Dalleau et al., 2014) and the Caribbean (Chambault et al., 2018). The size of mature individuals in loggerhead turtles ($80\text{--}90 \text{ cm}$, Wyneken et al., 2013) is larger than any in the West group of oceanic turtles tracked in our study (SCLmin: $52.2 \pm 14.6 \text{ cm}$). However, these immature individuals might well initiate their return journey early, possibly stopping at an intermediate foraging site to develop and reach sexual maturity. Similar to some immature loggerhead turtles satellite tracked from the North-East American coast (Mansfield et al., 2014), one of our individuals reached Bermuda where the tag stopped

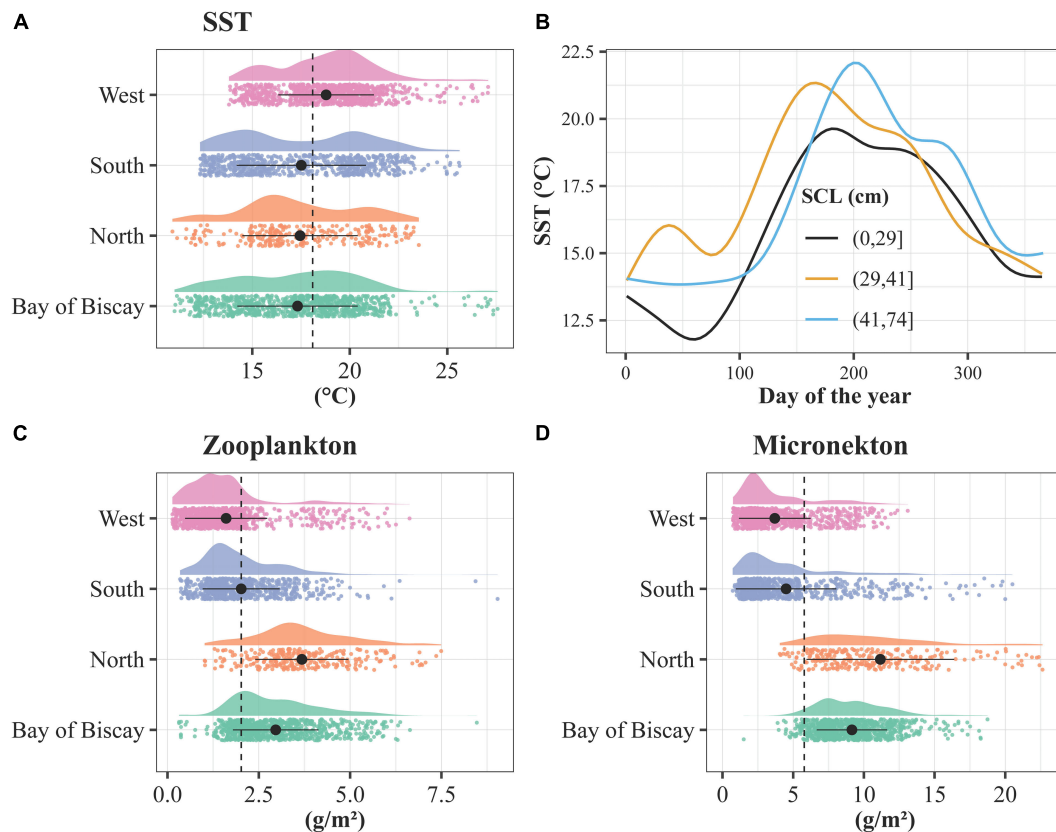


FIGURE 8 | (A) Smooth lines of the SST at turtle's locations according to days of the year and SCLmin classes (in cm). Density distributions of the **(B)** SST, **(C)** zooplankton biomass and **(D)** micronekton biomass extracted at the turtle's locations according to the spatial pattern. The density distributions are color-coded by spatial pattern, with a cloud of points below. The dotted lines refer to the average zooplankton and micronekton biomasses considering the 26 tracked individuals. The black dots stand for the mean and the bars the standard deviation for each group.

emitting. Located 1,600 km from Florida, these oceanic islands could be a stopover before reaching the nesting beach in Florida or a permanent foraging ground, as it has been evidenced in immature loggerhead turtles originating from Florida (Mansfield et al., 2009). The clear westward heading of the turtles in the West group, independently of the current direction also confirms that these turtles are willingly migrating westwards. Furthermore, the haplotypes of five of the 26 satellite tracked turtles were available, showing that these turtles mainly originated from Florida, Dry Tortugas or Mexico. Among the satellite tracked turtles, only Beline originated from Cape Verde. Genetic samples were collected from all the satellite tracked individuals, allowing in the near future the comparison between their natal origin and their trajectory to confirm this natal homing hypothesis (Meylan et al., 1990).

Among the largest individuals tracked in our study (SCLmin > 45 cm), three turtles headed northwards in critically unsuitable habitats due to a strong thermal constraint in winter (SST < 8°C). It is worth noting that among these three turtles, two were Kemp's ridley turtles, a species originating from the Gulf of Mexico and the Atlantic coast of the United States (Manzella et al., 1988; Marquez, 2001). The reasons for this surprising northward migration of this species remain unclear

but could be due to either a disorientation or unusually productive and/or warm waters masses, channeling turtles out of their common range (Griffin et al., 2019). The higher micronekton and zooplankton biomasses found along the tracks of these three individuals compared to the three other spatial patterns reinforce the assumption that they were actually targeting productive waters. The low bathymetry and the narrow strip characterizing the English Channel and North Sea could, however, be responsible for the underestimation of the coastal circulation in this region in the framework of the SEAPODYM model, possibly resulting in an overestimation of the primary productivity by remote sensing. Consequently, zooplankton and micronekton biomasses might be slightly overestimated in this area (Conchon, personal communication). More Kemp's ridley turtles need to be satellite tracked from the French Atlantic waters in order to elucidate these unexpected movements toward higher latitudes.

The coastal behavior of the smallest individuals was surprising and against the main hypothesis that the rehabilitated turtles would migrate back to the open ocean after release. The majority of immature loggerhead and green turtles are known to spend many years in the open ocean to grow and avoid predators, before swimming back to coastal habitats (Bolten, 2003). Coastal

migrations have also been observed in some juveniles loggerheads (Mansfield et al., 2009), but only in much larger individuals (SCL: 64.8 ± 10.9 cm) than the ones remaining in European coastal waters (SCL: 32.9 ± 9.6 cm). The location and the date of the release might partly influence the individuals' movements. Similar to a recent study conducted in Australia (Robson et al., 2017), future work should focus on simulating the active dispersal of turtles (size of the rehabilitated individuals) to confirm that the location and date of release are optimal for the rescued individuals, but also to determine if this coastal behavior is the result of environmental variability.

Resident Behavior in European Coastal Waters

Forty-one percent of the satellite tracked individuals exhibited a coastal behavior in the French Atlantic waters during the entire tracking duration, with a strong aggregation close to the release site off La Rochelle that could be partly attributed to the release location. Release sites are voluntarily located in close proximity to the CESTM (< 1 h) to prevent a stress induced by a long transportation of the rehabilitated turtles to be released (Hunt et al., 2019). The timing of the release is also strongly based on tidal cycles (during ebb tides, strong coefficients) to help the individuals swimming away from the shore. Despite a similar behavior has been observed in other taxa such as birds (Giunchi et al., 2003; Wallraff and Wallraff, 2005), this aggregation close to the release site is probably more intentional and indicative of a productive and favorable area, likely due to the presence of several river plumes acting as nursery grounds for a wide variety of fish (Yamashita et al., 2000; Le Pape et al., 2003). Alternatively, these small individuals might not be strong enough to swim away from the shore and migrate back to oceanic waters. But given their good condition after rehabilitation and the relatively small size of several turtles migrating westward to the open ocean, this hypothesis is unlikely. Among the 11 turtles that used the BoB the entire tracking duration, tag failure could be assessed for three of them, and evidence of battery exhaustion was only demonstrated for one turtle (Indigo). For two other individuals, biofouling was not indicative of tag failure, but the decrease in swimming speed might suggest that the turtles could have died due to cold-stunning in winter. The rapid growth of immature loggerhead turtles could also explain a premature tag detachment (Hays et al., 2021), leading to a shorter tag life (mean: 145 ± 152 days, range: 18–679 days) compared to other studies based on adult individuals, e.g., loggerheads retain 50% of their tags for 584 days (Hart et al., 2021). For future deployments, we recommend a careful battery management based on a severe duty cycling to extend tag life in immature individuals (Christiansen et al., 2016).

Although these results are in agreement with a previous study based on aerial surveys (Darmon et al., 2017), this finding is surprising because our individuals were relatively small (SCL: 32.9 ± 9.6 cm), a range of size at which they are thought to be fully pelagic (Bolten, 2003). Also, a recent study has demonstrated that European waters were not a suitable habitat for immature loggerhead turtles (Harrison et al., 2021). The authors restricted

the model simulations to a passive dispersal of neonate turtles during the first year at sea, rather than simulating the active movements of immature turtles, probably explaining why the BoB was not identified as a suitable habitat for this species. New simulations using recent active dispersal models (Gaspar and Lalire, 2017; Lalire and Gaspar, 2019), should be performed to verify if loggerheads born in Florida might reach the BoB and find there suitable habitats, at least during part of the year.

Tidal currents are indeed known to play an important role in the coastal circulation of the BoB (Karagiorgos et al., 2020). A higher resolution regional ocean reanalysis including tidal forcing (IBI: Atlantic-Iberian Biscay Irish Ocean Physics Reanalysis, Sotillo et al., 2015) is available from the Copernicus Marine Service, but was not used as this reanalysis does not cover our entire tracking period at the finest resolution ($1/36^\circ$ decimal degree). Further work with the fraction of our tracking data covered by the IBI reanalysis should be conducted in the near future to more precisely investigate the role of tidal currents on turtles' movements within the BoB.

The BoB is a highly dynamic ecosystem characterized by several currents flowing in opposite directions. There is also a seasonal inversion, with the main slope current flowing northwards in winter while toward the equator in summer and fall (Michel et al., 2009), making this region highly variable in terms of oceanic circulation. Together with the main oceanic circulation in fall, the Iberian shoreline might also act as a physical barrier, preventing the southward migration of these individuals at this period. That might explain why no seasonal north-south pattern was observed for the resident turtles, unlike their conspecifics in the Pacific (Polovina et al., 2001; Briscoe et al., 2016b) and Atlantic (Mansfield et al., 2009). The active swimming in young turtles has recently been detected by numerous studies (Gaspar et al., 2012; Briscoe et al., 2016a; Putman et al., 2016). Chambault et al. (2019) observed that large immature loggerheads (SCL: 36.3–61.1 cm) tracked around the Azores were clearly active. Our results confirmed that active swimming behavior is already present in the smaller individuals tracked in this study. Our findings therefore exclude the hypothesis that the turtles remained in their habitats due to ocean currents transport after release, but rather suggest a real habitat use (at least during summer and autumn), indicating that the Bay of Biscay might provide a suitable habitat in terms of both thermal and trophic conditions. This hypothesis was supported by two turtles from the BoB group which transmitted data until the next winter and even the next spring.

Trophic and Thermal Constraints

Mid-trophic level models (zooplankton and micronekton) confirmed the high productivity of the BoB, suggesting that coastal turtles could be feeding during the tracking period. Indeed, the BoB hosts all-year-round a wide variety of marine megafauna species, from seabirds to cetaceans (Lambert et al., 2017). The highest zooplankton and micronekton biomasses found in this area compared to the three other spatial patterns confirmed that this presumably unsuitable habitat could be used as an important feeding ground for immature sea turtles. The lack of seasonality for micronekton biomass also suggests this

area is a favorable foraging ground for these species throughout the year. The analysis of stomach contents from necropsied individuals found along the French Atlantic coast also confirms that some turtles were feeding in proximity to their stranding site (Dell'Amico, personal communication). The numerous river plumes along the French Atlantic coast (Gironde, Charente, Loire) could also contribute to the high productivity of this area, and constitute a critical habitat for many species (Lambert et al., 2018). Unlike other marine species that use the shelf edge and the abyssal margin of the BoB, the tracked turtles remained in close proximity to the shore (75% of the locations < 100 m isobaths) and occasionally exploited river plumes, with two individuals using the Gironde Estuary. The importance of the BoB as a critical habitat or an ecological trap should be further investigated using longer tracking durations, additional individuals and model simulations. But so far, the 449 sightings collected over 33 years by the CESTM tend to show that immature individuals from the three species use these waters year-round, including the smallest ones mostly in winter, probably due to cold-stunning.

While a suitable habitat should be productive, it also needs to be thermally optimal or at least acceptable for the species to survive. Similarly to other ectotherm species, ambient temperature plays a crucial role in reptile development and survival (Angilletta et al., 2002), driving the at-sea distribution of sea turtles. For this reason, immature loggerhead and green turtles during their pelagic phase generally target the 17–18°C isotherms (Polovina et al., 2000; Mansfield et al., 2014, 2021; Patel et al., 2021), and are rarely seen in habitats colder than 14°C (Robinson et al., 2020). Ten percent of our dataset was, however, associated with such cold waters, including 26% of the individuals remaining in these unsuitable areas for weeks or even months (range: 5–128 days, mean: 53 days). Similar to other loggerheads populations, smaller individuals experienced colder waters compared to larger ones (Abecassis et al., 2013), which could be related to increasing diving capacities with increased size. The larger turtles could target deeper, richer but colder layers, and therefore need to rewarm at the sea surface. Similar thermoregulation behaviors have been evidenced in other marine ectotherms (Di Santo and Bennett, 2011). The colder temperature range experienced by the smaller individuals could also partly explain why five of these small turtles (range: 3.3–8.7 kg) were found dead ($n = 4$) or stranded again alive ($n = 1$) during the following winter after release in European waters, possibly due to cold-stunning. This phenomenon is not uncommon as in Australia, 8.6% of the rehabilitated turtles were recaptured (Flint et al., 2017). This raises a serious concern regarding the thermal favorability of the BoB, where satellite-derived SSTs range between 10 and 20°C (Huret et al., 2018). Water temperatures can even drop below 10°C in very coastal areas used by the resident turtles. All the rescued turtles were in distress when found, suggesting that the BoB might act as an ecological trap for these young individuals in winter.

It is worth mentioning that the European waters are also commonly used by sub-adult and adult leatherback turtles (Witt et al., 2007; Nicolau et al., 2016), especially in summer, likely due to large aggregations of jellyfish (Houghton et al., 2006).

Unlike the hard-shelled species (loggerhead, Kemp's ridley and green turtle), leatherback strandings occur mainly during fall when weather conditions favor carcasses to drift to the shore before being stranded. Although the cause of mortality is in most cases difficult to determine, due to the level of decomposition, the endothermic ability of this gigantotherm species should make them less vulnerable to cold temperatures in such temperate habitats. But in response to global warming, these temperate habitats might become more and more thermally suitable as SST is expected to increase in the future, e.g., 0.23°C/decade in the Western English Channel coastal waters (L'Hévéder et al., 2017). As it has already been predicted for many species (Walther et al., 2002; Parmesan and Yohe, 2003), immature sea turtles might therefore experience a northern shift toward new habitats in response to global warming (Patel et al., 2021). However, the rise of temperature could be associated with a decrease in ocean productivity, leading to a trade-off between a more thermally favorable habitat but less abundant resources.

Conservation Implications

The identification of a species geographical range is crucial to implement effective management of endangered species, reinforcing the interest of our findings. All sea turtle species inhabiting the North Atlantic are listed on the IUCN Red list, with status vulnerable (loggerhead turtle), endangered (green turtle) and critically endangered (Kemp's ridley turtle, Wibbels and Bevan, 2019). The French East Atlantic sea turtle network (RTMAE), coordinated by the CESTM of Aquarium La Rochelle, therefore provides an unprecedented dataset to confirm the turtle presence in the BoB. It is worth mentioning that all the satellite tracked turtles were found in distress (stranded, bycaught or drifting at the sea surface), supporting the idea that without the rescue center and rehabilitation, these turtles may have likely died. Given the number of rescued individuals per year is relatively low, it is hard to estimate the real proportion of immature sea turtles inhabiting the European waters, especially in winter. Future work should therefore be dedicated to genetic analysis and model simulations to assess if the BoB is either an ecological trap or an important habitat used by these immature sea turtles year-round. Such results will undoubtedly support conservation measures, especially the update of the RMUs by potentially including the BoB as an important habitat for loggerhead turtles. As RMUs are population specific, the dataset of the two other species (Kemp's ridley and green turtles) need to be first augmented to draw reliable conclusions regarding their distributions. Alternative approaches such as aerial surveys are available to assess marine megafauna species distribution in the BoB and English Channel (Darmon et al., 2017; Lambert et al., 2018), but such observations generally miss small individuals like immature sea turtles, preventing the identification at the species level, and inevitably leading to an underestimation of the population. Our findings also confirm the importance of the Marine Protected Areas, including the small MPA located off the CESTM (Gironde estuary and the Sea of Pertuis Marine Natural Park), where a large proportion of the tracked individuals aggregated.

Although some individuals were found in bad condition (four were amputated), they showed no sign of atypical behavior after release, which is in agreement with other immature turtles satellite tracked from North-East America (Robinson et al., 2020). Among these four injured individuals, the longest tracking duration was even recorded for one of them (679 days), a sub-adult loggerhead turtle describing a typical trajectory despite being amputated from the left pectoral flipper, probably due to vessel collision or entrapment in fishing gear. Even though sea turtles are not the main marine megafauna species bycaught in the North East Atlantic (Bonanomi et al., 2019; Peltier et al., 2021), 29% of our rehabilitated and tracked individuals were found bycaught dead or alive ($n = 3$), stranded alive ($n = 1$) or stranded dead ($n = 4$) only few weeks after release. Indeed, the BoB hosts large populations of heavily small pelagic fishes (anchovy, sardine), in particular along the Spanish Atlantic coast (Ruiz et al., 2021), where several turtles aggregated. This clearly increases the entrapment risk in fishing nets.

In addition to bycatch, sea turtles face many other threats at sea such as marine debris (entrapment or ingestion) and organic pollutants, which are two of the 11 Descriptors listed in the Annex I of the European Marine Strategy Framework Directive (MSFD, 2008/56/EC), aiming to determine the Good Environmental Status (GES) of the EU's waters by 2020. Among other marine megafauna species (e.g., cetaceans, seabirds), sea turtles are used as bioindicators of the ocean health to reach the good environmental status. The work carried out by Rescue Centers such as the CESTM of Aquarium La Rochelle is therefore critical and should be supported since they offer the unique possibility to collect a wide variety of data from both rescued and dead animals, e.g., satellite tracking for movement analysis (Descriptor 1), tissue sample for genetics (Descriptor 1), pollutants analyses (Descriptor 8) and interactions with marine litter from necropsies (Descriptor 10).

DATA AVAILABILITY STATEMENT

The datasets presented in this article are not readily available because the dataset concerns endangered species and cannot be communicated. Requests to access the datasets should be directed to FD'A, tortues@aquarium-larochelle.com.

ETHICS STATEMENT

The animal study was reviewed and approved by the Prefectoral Order N°2004-1104 DREAL permit number: DREAL/56-2020 Ministerial Order (30/12/2020).

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AUTHOR CONTRIBUTIONS

FD'A: designing experiment and data collection. PC: data analysis and writing. FD'A, PC, and PG: interpretation of the results. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2021.736604/full#supplementary-material>

Supplementary Figure 1 | Metrics used to assess tag failure: (A) battery voltage, (B) Wet-dry switches (dry state in red and wet state in blue) and (C) the total number of Argos transmissions over time. For (A), the red lines (3.0 V) refer to the threshold below which there was a drop in battery voltage indicative of battery exhaustion. In (B), no data regarding wet-dry states was available for 15 individuals. In (C), the red lines refer to the threshold before battery exhaustion (26,688 transmissions) calculated from Horia based on the battery voltage graphic.

Supplementary Figure 2 | Individual tracks colored by the SST for the (A) North, (B) South and (C) Bay of Biscay groups. The black triangles refer to the last location recorded.

Supplementary Table 1 | Summary of the types of tag deployed on the 28 immature turtles.

Supplementary Table 2 | Characteristics of the habitat used (thermal and trophic) for each individual. The column SST refers to the mean \pm SD and the numbers in parentheses to min and max in °C. Zooplankton and micronekton biomasses are expressed in $g.m^{-2}$.

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Using Predicted Patterns of 3D Prey Distribution to Map King Penguin Foraging Habitat

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King penguins (*Aptenodytes patagonicus*) are an iconic Southern Ocean species, but the prey distributions that underpin their at-sea foraging tracks and diving behaviour remain unclear. We conducted simultaneous acoustic surveys off South Georgia and tracking of king penguins breeding ashore there in Austral summer 2017 to gain insight into habitat use and foraging behaviour. Acoustic surveys revealed ubiquitous deep scattering layers (DSLs; acoustically detected layers of fish and other micronekton that inhabit the mesopelagic zone) at c. 500 m and shallower ephemeral fish schools. Based on DNA extracted from penguin faecal samples, these schools were likely comprised of lanternfish (an important component of king penguin diets), icefish (*Channichthyidae* spp.) and painted noties (*Lepidonotothen larseni*). Penguins did not dive as deep as DSLs, but their prey-encounter depth-distributions, as revealed by biologging, overlapped at fine scale (10s of m) with depths of acoustically detected fish schools. We used neural networks to predict local scale (10 km) fish echo intensity and depth distribution at penguin dive locations based on environmental correlates, and developed models of habitat use. Habitat modelling revealed that king penguins preferentially foraged at locations predicted to have shallow and dense (high acoustic energy) fish schools associated with shallow and dense DSLs. These associations could be used to predict the distribution of king penguins from other colonies at South Georgia for which no tracking data are available, and to identify areas of potential ecological significance within the South Georgia and the South Sandwich Islands marine protected area.

Keywords: acoustic surveys, *Aptenodytes patagonicus*, diving behaviour, foraging habitat, king penguin, prey distribution, Southern Ocean, South Georgia

INTRODUCTION

The Southern Ocean is one of the most pristine ecosystems on the planet. At present, 7.2% of the ocean surface is protected, and this may expand to 11.2% if proposed marine protected areas (MPAs) are sanctioned (Hindell et al., 2020). As part of the Global Ocean Alliance push for '30 by 30', there is an aspiration to afford protection to more. Understanding the distribution of predators at sea is part of the process of developing spatial management plans. Hindell et al. (2020) proposed areas of ecological significance (AESs) based on predator tracks, but these AESs do not consider prey distributions directly. Determining how marine predators find their prey and hence better understanding their foraging ecology and role in ocean food webs is important for marine conservation.

Foraging habitat choices by central-place foragers during the breeding season are determined by their colony locations and dive capabilities, relative to the three-dimensional spatial distributions of prey (that may themselves show diel or seasonal variability due to migration) and competition with conspecifics and other predator species (Fauchald, 2009; Boyd et al., 2015). In turn, the self-organising behaviour of prey into, e.g., schools, swarms, patches and layers for protection from predation (Brierley and Cox, 2015; Rieucou et al., 2015) leads to prey aggregating at multiple spatial scales (10s of m for schools to 100s of km for layers). The ability of predators to track prey aggregations across these different scales depends on their search strategies (Sims et al., 2008), that typically involve a mixture of memory, social facilitation and area-restricted search (ARS) (e.g., Davoren et al., 2003; Wakefield et al., 2013). The strength of predator-prey relationships are therefore often scale-dependent, since large, persistent and predictable prey aggregations are more likely to be found than small, ephemeral patches (Fauchald, 2009). Small patches may be nested within larger aggregations, adding further complexity (Benoit-Bird et al., 2013). Spatial distribution of air-breathing predators at sea will also vary as a function of prey depth and predator diving capability, so predator distribution may also be more closely linked to accessibility of prey rather than abundance (Boyd et al., 2015). This can lead in some instances to apparent avoidance of dense prey patches that are too far from the colony (Bertram et al., 2017), or too deep in the water column (Boyd et al., 2015). Predators may also not show strong associations with prey when food is superabundant (Bertram et al., 2017), distributed uniformly (Logerwell et al., 1998), or very scarce (Smout et al., 2013; Campbell et al., 2019). Studies of predator distribution relative to that of prey therefore need to be conducted in the context of the predators' foraging behaviour and the spatial and temporal scales at which prey aggregate (Benoit-Bird et al., 2013).

In the open ocean, fish and zooplankton form super-aggregates that are typically 10s of m in height and that can extend for 100s of km. These structures, known as deep scattering layers (DSLs; often observed between 200 and 1000 m, but have been observed outside this range) since they are readily detectable using echosounders, may offer an almost ubiquitous prey field, potentially providing deeper diving predators (e.g., elephant seals; Robinson et al., 2012) with a

reliable and predictable food source. Mesopelagic fish are an important component of DSLs whose global biomass is estimated to be between 1,800 and 16,000 million tonnes (Irigoin et al., 2014; Proud et al., 2019), making them a major component of ocean ecosystems (Saunders et al., 2015). Myctophids are a small (2–20 cm) but abundant forage fish present in most oceans (Gjøsaeter and Kawaguchi, 1980; Catul et al., 2011) and form an important component of mesopelagic biomass in the Southern Ocean (Hulley, 1981; Lubimova et al., 1987). They comprise the main prey of numerous diving predators such as southern elephant seals (*Mirounga leonina*) and king penguins (*Aptenodytes patagonicus*) (e.g., Adams and Klages, 1987; Cherel et al., 2002; Bradshaw et al., 2003). However, since we lack observational data on the underwater distribution of potential prey across seascapes (conventional acoustic surveys are limited to observations along transects, but see Makris (2006) for areal acoustic observations), the times and depths at which prey become accessible to predators remains unclear.

Tracking seabirds in the horizontal dimension enables exploration of drivers of distribution in the context of widely available physical variability (from remote sensing). Typically, tagged seabirds are tracked from their colonies or counted from vessels, and their density is either related to the distribution of prey (from vessel-based acoustic/net/environmental sampling, e.g., Logerwell et al., 1998; Hentati-Sundberg et al., 2018; Campbell et al., 2019), or associated with remotely sensed oceanographic variables that influence prey densities like sea surface temperature (SST), bathymetry, chlorophyll concentration and the locations of oceanographic fronts (e.g., Bost et al., 2011; Scheffer et al., 2012; Scales et al., 2014; but see Grémillet et al., 2008; Sherley et al., 2017). As the climate changes, foraging habitats are expected to shift geographically in line with these associations, and this could have consequences on marine predator populations (Sherley et al., 2017; Cristofari et al., 2018).

King penguins are distributed widely across the Southern Ocean and breed on subantarctic islands such as Kerguelen, Crozet, Macquarie and South Georgia (Woehler, 1993; Ratcliffe and Trathan, 2011). These islands, and much of the penguin foraging grounds, are protected by MPAs, e.g., the South Georgia and the South Sandwich Islands (SGSSI) MPA (2012). The diet of king penguins is predominantly comprised of myctophids, particularly *Krefftichthys anderssoni* at South Georgia, whose predominance in the diet is associated with higher king penguin breeding success (Perissinotto and McQuaid, 1992; Olsson and North, 1997). King penguin foraging distributions have been associated with warm-core eddies and strong temperature gradients in the Antarctic Polar Frontal Zone (Scheffer et al., 2010). For example, the effects of a one degree latitude shift in SST anomalies on the location of the Polar Front could extend the travel distance of king penguins breeding at Crozet Islands by 130 km, which is a substantial proportion of their expected foraging range (typically between 300 and 600 km) (Bost et al., 2015). But since king penguins are central place foragers, that have fixed breeding localities (islands) and a scarcity of alternative breeding sites, their ability to change foraging distribution in response to spatial shifts in prey distributions may be limited (Bost et al., 2009; Sherley et al., 2014). Constraints on foraging

include distance that an individual can travel from its colony that may vary with stage of the breeding season (Scheffer et al., 2016), diving capability (<400 m; Charrassin et al., 2002) and the fact that king penguins are visual foragers, which means foraging is predominantly carried out in daylight (Bost et al., 2002); this limits their ability to feed on myctophids within DSLs that migrate to the surface at night (Hazen and Johnston, 2010). These constraints lead us to expect that king penguins would preferentially target fine-scale (10s of m) dense fish schools rather than larger scale prey structures (10s–100s of km) such as DSLs that may be inaccessible most of the time, conditional on the schools being at relatively shallow depth during the day and within the stage-specific foraging range of the colony.

In this study, we attempt to relate the distribution of king penguins during guard stage tracked with GPS, time-depth recorders (TDRs) and accelerometers from South Georgia to that of their prey, inferred from diet studies and acoustic surveys conducted during the Antarctic Circumnavigation Expedition (ACE, December 2016 to March 2017). Despite our best intentions, we were not able to obtain coincident observations of predators and prey, simply because the penguins did not forage close to the vessel: hence we built models to predict prey distribution at penguin dive locations. The specific objectives of this study were to (i) compare fine-scale (10s of m) vertical distributions of fish schools and layers (determined from low frequency echosounder observations) and king penguin prey encounters (analysis of accelerometry data) observed in the same interfrontal zone (located between the Antarctic Polar Front and the Southern Antarctic Circumpolar Current Front) and during the same period (February and March 2017) off South Georgia; (ii) combine *in situ* echosounder observations recorded during ACE with environmental data to build predictive models of local-scale (10s of km) fish echo intensity and vertical distribution for the Southern Ocean, and (iii) model the horizontal habitat suitability of king penguins based on predicted prey distributions to answer the question: what characteristics of prey do penguins prefer to travel to? Note that this is different to modelling prey encounter dives versus non prey encounter dives which asks a different question (i.e., what characteristics of the prey are associated with penguins finding prey).

MATERIALS AND METHODS

Data were collected as part of the ACE (20th December 2016 to 18th March 2017, **Figure 1**) aboard the research vessel '*Akademik Tryoshnikov*'. Echosounder data were collected continuously throughout the voyage and king penguin foraging behaviour data were collected simultaneously off South Georgia using data loggers. Unfortunately, the ACE vessel was not equipped to carry out net tows and therefore no biological sampling was conducted. However, DNA was extracted from penguin faecal samples collected during the study period to determine penguin diet and provide information on prey consumed.

King Penguins

King penguins breeding at Hound Bay (54°23'S, 36°15'W), South Georgia, were studied between 20th February and the 22nd

March 2017. This period coincided with the passage of the ACE voyage past South Georgia (2nd to the 8th March 2017). Only adult chick-rearing king penguins in guard stage were included in this study.

Animal Handling and Instrumentation

A total of 18 individual king penguins were captured as they were leaving on foraging trips. They were instrumented with miniature data-loggers attached to their lower backs with waterproof Tesa® tape and quick-drying two-part epoxy, and marked on their front with permanent black hair dye to aid in reidentification and device recovery (Scheffer et al., 2010). At-sea movements were followed using GPS (Pathtrack nanofix GEO, weight: 32 g; size: 54 × 23 × 17 mm), and dive profiles were recorded using TDRs (G5, CTL, Lowestoft, United Kingdom; weight: 6.5 g; size: 12 × 35.5 mm) recording at 1 Hz. Prey strikes were measured using a tri-axial accelerometer (X8M-3, Gulf Coast Data Concepts, Waveland, MS, United States, weight: 34 g; size: 51 × 25 × 16 mm) recording surge, heave and sway at 25 Hz. Birds were recaptured after one foraging trip and the loggers were retrieved. Battery capacity limited the observation period for both TDR and accelerometer tags. Typically, the accelerometer tags ran out of battery 4–5 days before the penguins returned from foraging at sea.

Foraging Behaviour

Trip characteristics were extracted from GPS data using the 'trip' package in R (Sumner et al., 2009) following the application of a speed filter of 14 km h⁻¹ (e.g., Cotté et al., 2007) (which is the fastest observed swim speed of a penguin, see Kooyman and Davis, 1987) to remove any erroneous position estimates (<0.1% of all positions). For each bird, trip duration (days), path length (km), maximum distance from colony (km), and mean and maximum speed (ms⁻¹) were calculated. TDR data were processed using IGOR Pro (WaveMetrics, Version 7, OR, United States) to calculate maximum dive depth; dive duration; number of undulations (also called 'wiggles', defined as a depth change rate < 0.25 ms⁻¹); bottom phase duration; and post dive duration (see Ropert-Coudert et al., 2007, for parameter definitions). Depth undulations (wiggles) are indicative of either prey search, prey encounter, predator interaction or other movement, and hence are not a reliable source for detecting prey capture attempts. Shallow travelling dives ≤4 m were excluded (Charrassin and Bost, 2001; Charrassin et al., 2002). For five individuals, the GPS battery expired before completion of the foraging trip so the location of subsequent dives could not be determined.

Prey Encounters

Prey capture attempts were identified using the accelerometry data (e.g., Ropert-Coudert et al., 2006; Zimmer et al., 2011). Vectorial Dynamic Body Acceleration (VDBA), a commonly used proxy of whole body activity (Gleiss et al., 2011), was calculated as:

$$VDBA = \sqrt{(A_x^2 + A_y^2 + A_z^2)} \quad (1)$$

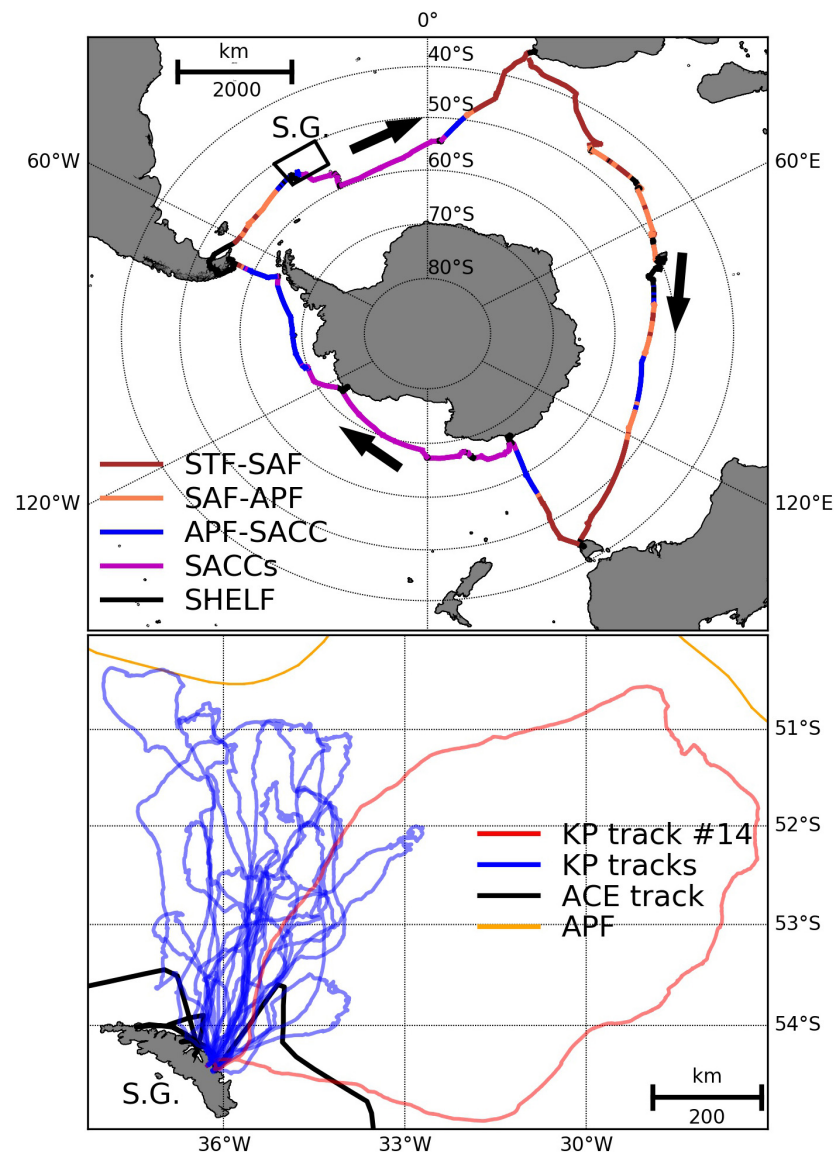


FIGURE 1 | The track of the Antarctic Circumnavigation Expedition (ACE) research vessel (**Top**) plus GPS positions of the 18 tagged king penguins (**Bottom**) foraging from Hound Bay. In the top plot, the ACE track is colour coded by interfrontal zone as experienced during the voyage (i.e., fronts are calculated *in-situ* at a daily time resolution): STF-SAF (sub-Tropical Front to sub-Antarctic Front), SAF-APF (sub-Antarctic Front to Antarctic Polar Front), APF-SACC (Antarctic Polar Front to Southern Antarctic Circumpolar Current Front) and SACCs (Southern Antarctic Circumpolar Current Front to the southern boundary of the Antarctic Circumpolar Current). In the bottom plot, 17 king penguin tracks are shown by blue lines (birds 1–13 and 15–18) and a single red line indicates the anomalous trip of bird 14 that performed a far eastern loop uncharacteristic of birds during the guard breeding stage. The ACE track in the vicinity of South Georgia is indicated by a black line, and the mean position of the Antarctic Polar Front (Orsi et al., 1995) is shown by an orange line. South Georgia (S.G.) is also indicated on both maps.

where A_x , A_y and A_z are the dynamic accelerations of the surge, heave and sway axes respectively, calculated by subtracting the static acceleration of each axis (a smooth over 1 s) from the total acceleration (Shepard et al., 2008). There was an upper inflection point at 2.5 m s^{-2} in the frequency of VDBA across all birds, and this was used as a threshold for diagnosis of prey capture attempts (**Supplementary Figure 1**), i.e., when VDBA (at 1 Hz) became higher than 2.5 m s^{-2} during a dive, we inferred that there was a prey encounter and pursuit (Sánchez et al., 2018). This meant that multiple prey encounters (e.g., multiple

captures of prey) might be detected as a single prey capture attempt. This was deemed acceptable since our analysis is reliant on the identification of prey encounter dives and prey encounter depths, not the absolute number of prey items (which would require additional sensors, e.g., cameras). For each foraging dive (dives > 4 m) with a prey capture attempt, the depth at which the first VDBA point exceeded 2.5 m s^{-2} was considered as the prey encounter depth (m). The first 4 m of the descent phase were excluded from the acceleration analysis to be consistent with the dive data and because birds perform strong wing beats at

the beginning of a dive to overcome the effects of buoyancy and inertia (Zimmer et al., 2011).

Diet Study

During the same period as the biologging study, 47 faecal samples were collected from other (i.e., not the instrumented birds) king penguins (Le Guen et al., 2020). Ideally, we would have collected samples from the instrumented birds, but due to limited resources and sampling logistics, we were only able to collect samples from birds at the colony whilst the instrumented birds were at sea. Since all the instrumented birds were rearing chicks, only samples taken from chick-rearing birds were considered in this study (16 out of 47 samples collected between 22nd February and 11th March 2017). It is likely that samples were taken from different individuals as they were collected from different nests across the colony (c. 100–150 penguins in total), but it is possible that faeces from the same bird were sampled more than once since adults swap nests regularly. Contamination was minimised during collection by maintaining strict sampling protocols, e.g., sterilising apparatus with ethanol between sampling and only taking samples from the surface of the faecal matter, i.e., not making contact with the underlying soil (for more information, see Le Guen et al., 2020). These data provide vital information on colony-specific diets, which could potentially change seasonally and/or annually in response to changes in prey distributions (e.g., Saunders et al., 2013). Prey taxa for each bird were identified using DNA sequencing (for DNA extraction and sequencing protocols see **Supplementary Material**).

Echosounder Observations

Echosounder observations were collected continuously along the ACE track (**Figure 1**) using a Simrad (Bergen, Norway) EK80 echosounder operating a single-beam (10–20 kHz) Wärtsilä ELAC Nautik GmbH (Keil, Germany) LSE179 transducer. Prior to the survey, at-sea trials were conducted to find the optimum settings (i.e., high signal-to-noise ratio) for detection of mesopelagic fish communities: frequency = 12.5 kHz, ping interval = 8 s, power = 150 W, and pulse duration = 16 ms. At this frequency (wavelength c. 12 cm), the majority of the returned signal is expected to originate from large organisms (fish, squid, etc., not zooplankton; Simmonds and MacLennan, 2005), and organisms that possess gas bladders (Proud et al., 2019), e.g., *K. anderssoni*. An echosounder calibration was conducted at South Georgia using the standard target method (Demer et al., 2015).

Echosounder Data Processing

Raw echosounder data were imported into Echoview version 8 (Myriax, Hobart, Tasmania) and the calibration parameters were applied. Transient noise, impulse spikes and attenuated pings were removed. Data were gridded at a resolution of 5 m depth by 10 km along track, and integrated values (Mean Volume Backscattering Strength, MVBS, dB re 1m^{-1}) were exported to provide data for modelling. Data were also integrated and exported at fine-scale (i.e., 1 ping \times 1 m sample) to facilitate comparisons with fine-scale king penguin prey encounters. MVBS values were used to calculate the nautical area scattering

coefficient (NASC, average echo intensity per nautical mile squared; $\text{m}^2 \text{nmi}^{-2}$) and weighted mean depth (WMD, mean depth weighted by linear values of MVBS) values for two depth zones: (1) the penguin foraging zone, between the surface and the depth at which 95% of prey encounters occurred, and (2) the mesopelagic zone, this – by common definition – extended between 200 and 1000 m, and was expected to contain king penguin prey (e.g., myctophids), some of which would have been deeper than the dive range of penguins. At the 12.5 kHz echosounder frequency used, the local WMD value for the mesopelagic zone is essentially equivalent to the mean depth of the principal (strongest) DSL, since during ACE a single broad DSL was observed through most of the expedition. Following the same logic, NASC values calculated between 200 and 1000 m were effectively a proxy for DSL NASC. NASC and WMD values calculated between 200 and 1000 m will be referred to as DSL NASC and DSL depth hereafter.

Predicting Nautical Area Scattering Coefficient and Weighted Mean Depth Using Neural Networks

To model prey availability within the foraging domain of the king penguins at South Georgia (**Figure 2**), neural networks were built to predict NASC and WMD along the entirety of the ACE voyage track (see **Figure 1**). Using the entire expedition (as opposed to using a subset of the data close to South Georgia) increased the size of the training set by a factor of 25 and enabled daily and weekly variability (recorded away from the South Georgia foraging site) in prey characteristics to be captured. Environmental variables used as inputs for the neural networks (**Table 1**) were selected based on previous studies and known relationships between NASC, WMD and the environment (e.g., Klevjer et al., 2016; Aksnes et al., 2017; Proud et al., 2017). To explain diel variation in the depth distribution of biomass resulting from diel vertical migration, sun angle was included as an input variable (see **Table 1**). All input variables were at the same or higher spatial resolution as the summarised track echosounder observations (10 km), except for sea-level anomaly, which was gridded at a resolution of $0.25^\circ \times 0.25^\circ$. Values of the input variables were assigned positions along the vessel track using linear interpolation.

Each 10 km position along the ACE cruise track was classified as belonging to one of four interfrontal zones (**Figure 1**) evident in vertical potential temperature profiles. Daily mean potential temperature data at 25 m depth intervals from 100 m to 300 m depths were extracted from the Global coupled FOAM quarter degree model run by the United Kingdom Met office¹ along the ACE track for each day of the cruise. Each ship location was then associated with a interfrontal zone based on the potential temperatures at 200, 300, and 500 m (**Figure 1**) evident in previous work (e.g., Orsi et al., 1995; Belkin and Gordon, 1996; Boehme et al., 2008). All locations associated with a water depth of less than 1000 m were classified as being on the shelf.

¹<http://marine.copernicus.eu>

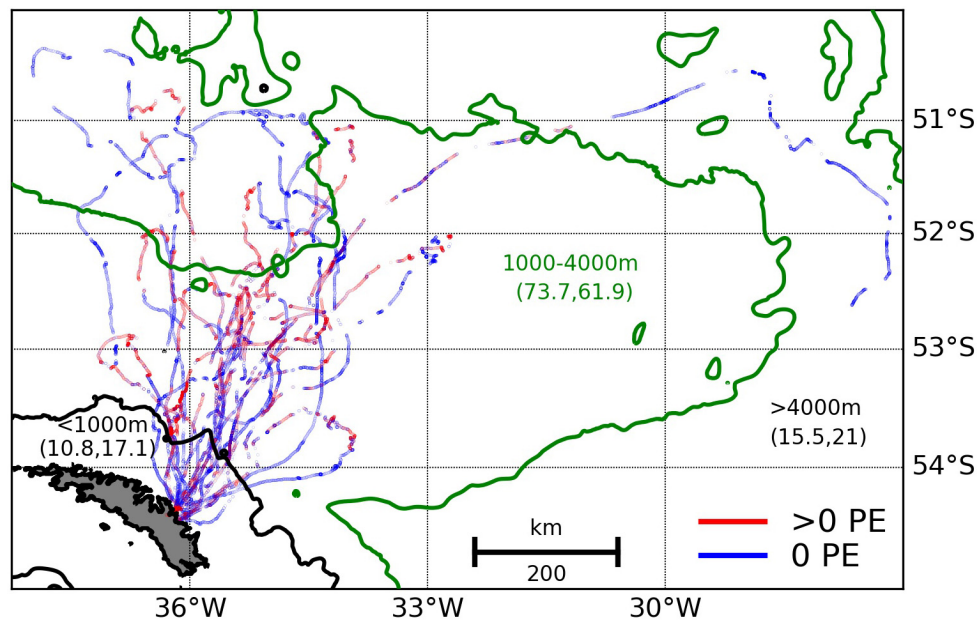


FIGURE 2 | King penguin dive locations (maximum depth > 4 m) where at least one prey encounter (PE) was detected (red points) and where zero prey encounters were detected (blue points). Colour-coded contours split the dives into three depth zones (inshore: <1000 m, and two offshore zones: 1000–4000 m and >4000 m) and the percentage of dives and PEs in each zone is given in parentheses (%dives, %PEs). All dives occur in the Antarctic Polar Front to Southern Antarctic Circumpolar Current Front interfrontal zone. Time-depth recorder loggers and accelerometers ran out of battery for some birds before they returned to South Georgia so not all tracks close.

Neural network inputs (Table 1) and outputs (NASC and WMD calculated over the penguin foraging zone and mesopelagic zone) were scaled to between 0.0001 and 0.9999 (weighting the contribution of each input equally). Temporal inputs were predominantly at daily resolution apart from PP (see Table 1), which was monthly and hence values for February and March were assigned to penguin dive locations over the study period. R-packages ‘caret’ (Kuhn, 2008, 2020) and ‘nnet’ (Venables and Ripley, 2002) were used to train and test the neural networks (10-fold cross validation; 80%/20% split for train/test data, respectively). A standard 3-layer setup (input, hidden layer, output) was used. The number of nodes in the hidden layer (6–30 nodes) and decay parameter (regularization parameter to avoid over-fitting; 0.001–0.1) varied, and optimum models were selected based on validation set mean root-mean-square error (RMSE) values (mean over the 10 folds).

Penguin Habitat Selection Modelling

We did not have direct echosounder observations at penguin dive locations, so took a modelling approach to infer the likely prey-field characteristics at dive sites on specific days during the study period. This was made possible by including ACE day (see Table 1) in the NASC and WMD models to capture daily and weekly variability; note that we used ACE day rather than day of year to avoid forcing the model to weight day 1 (January 1st) and day 365 (December 31st) very differently, when in fact these 2 days should be weighted similarly since they are only 1 day apart. Daytime king penguin dive data that could be associated with valid GPS locations were used to study king

penguin habitat use. Bird 14 was excluded from this analysis due to anomalous behaviour (see trip with far eastern loop in Figure 1), which was not consistent with other studies for birds in this stage (Scheffer et al., 2012), and also because its TDR logger ran out of battery (note absence of eastern loop in Figure 2). Habitat selection models (e.g., Aarts et al., 2008) were used to define the pelagic foraging habitat suitability of the king penguins. The outer limit of available habitat was set conservatively (to limit spatial extent of sampling domain, see Hazen et al., 2021) as a circle with a radius of $1.1 \times$ the maximum foraging range from the Hound Bay king penguin colony (Wakefield et al., 2017). Dives where the seabed was <600 m (the expected maximum depth of DSLs in this region) were excluded from this analysis and hence habitat suitability in this context refers to pelagic dives as opposed to shallow inshore/benthic dives (where we did not have acoustic observations). Dive locations were assigned values of the environmental variables (see Table 1) at the same scale as the modelled NASC and WMD observations. Environmental variables were averaged over an area demarked by a circle (diameter = 10 km) centred on each dive location. Predicted NASC and WMD, distance to colony and seabed depth were extracted for each dive (presence) location and day (Figure 2) as well as for three randomly chosen pseudo-absence locations (three points drawn from the entire accessible geographic area) for every dive location to represent habitat availability (Aarts et al., 2008). Binomial generalised additive models (GAM; logit link function) with presence/pseudo-absence location as the response, and the prey indices (predicted NASC and WMD), seabed depth and distance to colony as explanatory

TABLE 1 | Neural network model inputs.

Input	Main justification	Data source
Latitude	Spatial trends in PP (i.e., biomass), light regime, fish size (Saunders and Tarling, 2018) and swimbladder morphology (Dornan et al., 2019).	Vessel GPS.
Longitude	Spatial trends in fish distributions.	Vessel GPS.
Sun angle (second)	To account for diel variation in the depth distribution of fish biomass that is predominantly caused by diel vertical migration.	Derived from position and time of day using 'suncalc' R-package (Thieumel and Elmarhraoui, 2019).
ACE day (daily)	Seasonal influences on fish distributions.	First day of expedition = 1, last day = 85.
Distance to land (0.0042° × 0.0042°)	Island effect on production.	GEBCO (version 2020, www.gebco.net).
Seabed depth (0.0042° × 0.0042°)	Pelagic-benthic coupling.	GEBCO (version 2020, www.gebco.net).
SST (daily; 0.083° × 0.083°)	Species distributions and metabolic rates.	CMEMS global reanalysis product daily mean fields (www.resources.marine.copernicus.eu).
PP (monthly; 0.083° × 0.083°)	Food availability.	Ocean Productivity website (www.science.oregonstate.edu).
Mean (2007–2017) PP (monthly; 0.083° × 0.083°)	Food availability over longer time periods.	Ocean Productivity website (www.science.oregonstate.edu).
SD (2007–2017) PP (monthly; 0.083° × 0.083°)	Variability in food availability.	Ocean Productivity website (www.science.oregonstate.edu).
Sea level anomaly (daily with respect to a 20-year mean; 0.25° × 0.25°)	Changes in production related to mesoscale oceanic features, e.g., eddies.	Global Ocean Gridded L4 Sea Surface Heights and derived variables reprocessed (1993–ongoing) (https://marine.copernicus.eu/access-data).

Justification is provided for inclusion of each input in the neural network, along with data source. Where relevant, the spatial and temporal resolution of source data is indicated.

variables were fitted using the R package 'mgcv' (Wood, 2006). Models were fitted using interactions between related covariates (using tensor smooths; Wood, 2006), e.g., an interaction between seabed depth and distance to colony is expected to influence habitat suitability since birds only utilise shallow water when close to the colony; note that some degree of correlation is expected between seabed and distance to colony. GAMs were parameterised using full tensor product smooth terms: (te1) distance to colony * seabed depth; (te2) $NASC_{50-260\text{ m}}$ * $WMD_{50-260\text{ m}}$, representing the penguin 'prey' component, and (te3) $NASC_{200-1000\text{ m}}$ * $WMD_{200-1000\text{ m}}$ representing the 'DSL'

component (i.e., addressing the question does the depth and intensity of DSLs influence diving behaviour?).

For each model, the random pseudo-absence selection was repeated 30 times, resulting in 30 model iterations. Model selection was conducted using Akaike Information Criterion (AIC), cross validation and Area Under the Receiver Operating Curves (AUC), which are conservative and permit violation of model assumptions relating to non-independence of errors that are inherent in tracking data (spatial and temporal autocorrelation). Three candidate models were compared using AUC: (1) the null model (te1), (2) the 'prey' model (te1+te2), and (3) the 'prey+DSL' model (te1+te2+te3). Selected GAMs were then averaged over the 30 iterations using the 'MuMIn' R package (Barton, 2020) and used to predict habitat use probabilities around the Hound Bay colony. Since predictions of NASC and WMD will have an associated error (RMSE from neural networks), uncertainty associated with the habitat model will be biased low.

RESULTS

In total, 18 birds were tracked, and faecal samples were collected from 16 non-instrumented birds. Bird 14 was excluded from dive analysis due to anomalous foraging behaviour that was not consistent with previous studies, and no accelerometer data were collected from bird 16 due to a tag malfunction.

King Penguin Foraging Trip Characteristics

All king penguin foraging trips headed north from South Georgia in the direction of, but never reaching, the Antarctic Polar Front. The birds remained in the APF-SACC interfrontal zone during guard stage (consistent with other studies; see Scheffer et al., 2012). Foraging trips took place between 20th February and 22nd March and had an average duration of 10.2 days (range = 4.8 to 17.8 days; 183.8 days total), path length of 820.7 km (range = 293.9 to 1837.2 km) and mean maximum distance from colony of 317.2 km (101.7 to 672.8 km). Specific details of individual trips are given in **Supplementary Table 1**.

A total of 37,275 dives deeper than 4 m were identified during 165.3 days of total tracking time across all birds between February 20th and March 20th (using TDR tags; see **Figure 2** and **Supplementary Table 2**). On average, birds dove 228 times per day and each dive included 8.2 undulations/wiggles (i.e., potential prey encounters). The maximum dive depth recorded was 352 m and the maximum dive duration was 9 min 10 s. Birds dived mostly during the day (c. 73% by dive duration), with depths increasing progressively after sunrise and reduced around sunset (**Supplementary Figure 2**) in keeping with both diel vertical migration (DVM) of prey and increased visibility with depth as sun angle increases (Bost et al., 2002; Pütz and Chérel, 2005).

King Penguin Prey Encounters and Pelagic Vertical Habitat Use

A total of 45,958 (43,063 with valid GPS locations) prey encounters deeper than 4 m were detected during 99.3 days

of total tracking time across all birds between February 20th and March 16th (using accelerometer tags; see **Figure 2** and **Supplementary Table 3**). On average there were 462.8 prey encounters per day and hence around 2 prey encounters per dive (i.e., 462.8 prey encounters per day/228 dives per day). The average prey-encounter depth was 107.1 m (lower quartile = 67.1 m; upper quartile = 174.8 m), and 95% of encounters occurred at a depth ≤ 260 m, which was used to define the lower boundary of the king penguin foraging zone (see sections “Predicting Fish Distributions Using Neural Networks”, “King Penguin Habitat”, and “King Penguin Habitat Suitability”); very few prey encounters occurred deeper, so including acoustic backscatter from beyond this depth as ‘prey’ would have resulted in inclusion of features (such as DSLs occurring deeper than 260 m) that were not typically accessed by king penguins. The vast majority of the birds’ foraging effort was off shelf (seabed > 1000 m; 38,394 out of 43,063 prey encounters were offshore). We thus compared the vertical distribution of prey encounters offshore to offshore echosounder observations (seabed > 1000 m; c. 465 km of vessel track) made in the same interfrontal zone (APF-SACC; see **Figure 1**) between 4th March and the 18th March 2017. Echosounder observations recorded in the top 50 m were excluded due to surface noise. We compared day (29,877 prey encounters; see **Figure 3A**) and night (8,517 prey encounters; see **Figure 3B**) separately to avoid complications associated with prey DVM. MVBS was plotted for each depth interval (0–600 m by 10 m intervals) and MVBS level (–80 to –40 dB re 1m^{-1} by 3 dB re 1m^{-1} intervals) e.g., the cell in the bottom left-hand corner of **Figures 3A,D** is the MVBS value calculated by first thresholding the data by the MVBS level (–80 to –77 dB re 1m^{-1}) and then integrating the remaining observed echo intensity over the depth interval (590 to 600 m).

Acoustically Detected Prey Field

DSLs, which were ubiquitous throughout the APF-SACC interfrontal zone, were the source of most of the recorded echo energy (78.3% during the day and 92.4% during the night; note that the top 50 m was excluded) but even at night these DSLs appear to be deeper than the dive capability of the king penguins (**Figure 3**). Fish schools (isolated echogram features, 10s of m in width and height) occurred ephemerally in the epipelagic zone, observed at both low echo intensity (prey type 1: MVBS level = –70 to –65 dB re 1m^{-1} ; see **Figure 3A**) and high echo intensity (prey type 2: MVBS level = –50 to –40 dB re 1m^{-1} ; see **Figure 3A**). The differences in MVBS level imply that prey types 1 and 2 differ in numerical fish density, target strength or both. A third prey type, which we termed ‘prey patches’ (Béahle et al., 2017) (prey type 3: MVBS level = –70 to –60 dB re 1m^{-1} ; see **Figure 3A**), comprised clusters of linked schools (see **Supplementary Figure 3**) that, due to echosounder beam geometry, would appear as layers if they were observed deeper in the water-column (the echosounder beam broadens with depth and hence sampled volume increases with depth, reducing horizontal resolution and blurring the boundaries between discrete prey structures giving them a continuous appearance). The vertical distributions of prey types 2 and 3 shifted markedly between day and night (see **Figures 3A,D**) and hence were likely

composed of species that performed DVM. The modal depth in daytime penguin prey encounters matched with the modal depth of prey type 2 (high energy fish schools) NASC (**Figure 3**). Prey type 1 was persistent throughout the daily cycle and matched with peaks in penguin prey encounters both during the day and night (**Figure 3**).

Diet Analysis

Only 9 of the 16 chick-rearing penguin faecal samples returned useful DNA data (likely due to degradation of the DNA in the gut during digestion). Of these, eight contained DNA of eight species of fish (**Table 2**) but only two contained euphausiid crustacean DNA (*Euphausia superba* and *Thysanoessa macrura*). Fish also eat krill and so it is possible that presence of krill DNA in penguin faecal samples is a consequence of secondary ingestion. Higher occurrences of krill were found in the other breeding stages (3 out of 16 samples for incubating birds, and 5 out of 16 samples for non-breeding birds). No prey species were encountered in the procedural blanks, thus it is likely that no contamination occurred during the DNA extraction phase.

Consideration of the known DVM behaviour, biology, and depth distribution of these fish species (**Table 2**) links them to the three prey types observed (see section “Acoustically Detected Prey Field” and **Figure 3**). Both adult icefish (*Channichthyidae* spp.) and painted notothen (*Lepidonotothen larseni*) are associated with the seabed so probably do not make up a large percentage of the penguins’ diets (90% of prey encounters are pelagic; these fish may be taken opportunistically at the start or end of trips). However, larvae and juveniles of these species occur within the epipelagic zone and since they are without gas-filled swimbladders are relatively weak scatterers, which matches with prey type 1 (icefish also do not perform DVM, which is consistent with the observed DVM pattern). The other two prey types (2 and 3) likely correspond to rhombic lanternfish (*K. anderssoni*), since they are known to perform DVM, have gas-filled swimbladders (i.e., high intensity acoustic targets) and occur in both the epipelagic and mesopelagic zone.

Predicting Fish Distributions Using Neural Networks

NASC and WMD were calculated for the penguin foraging zone (50–260 m; defined in **Figure 3**) and the mesopelagic zone (200–1000 m), resulting in four model outputs (NASC and WMD for both depth zones) and hence four neural networks. Models were trained using 80% of the ACE echosounder data ($n = 1,636$ samples), and model selection and evaluation was based on validation set ($n = 164 \times 10$ folds) and test set ($n = 409$ samples) RMSE, respectively. Optimum networks for each of the outputs were as follows (see **Figure 4**): (A) NASC_{50–260 m}, nodes = 22, decay = 0.001 (test RMSE = $295.6 \text{ m}^2 \text{ nmi}^{-2}$; $R^2 = 0.66$); (B) NASC_{200–1000 m}, nodes = 30, decay = 0.001 (test RMSE = $289.9 \text{ m}^2 \text{ nmi}^{-2}$; $R^2 = 0.81$); (C) WMD_{50–260 m}, nodes = 28, decay = 0.001 (test RMSE = 18.4 m; $R^2 = 0.73$),

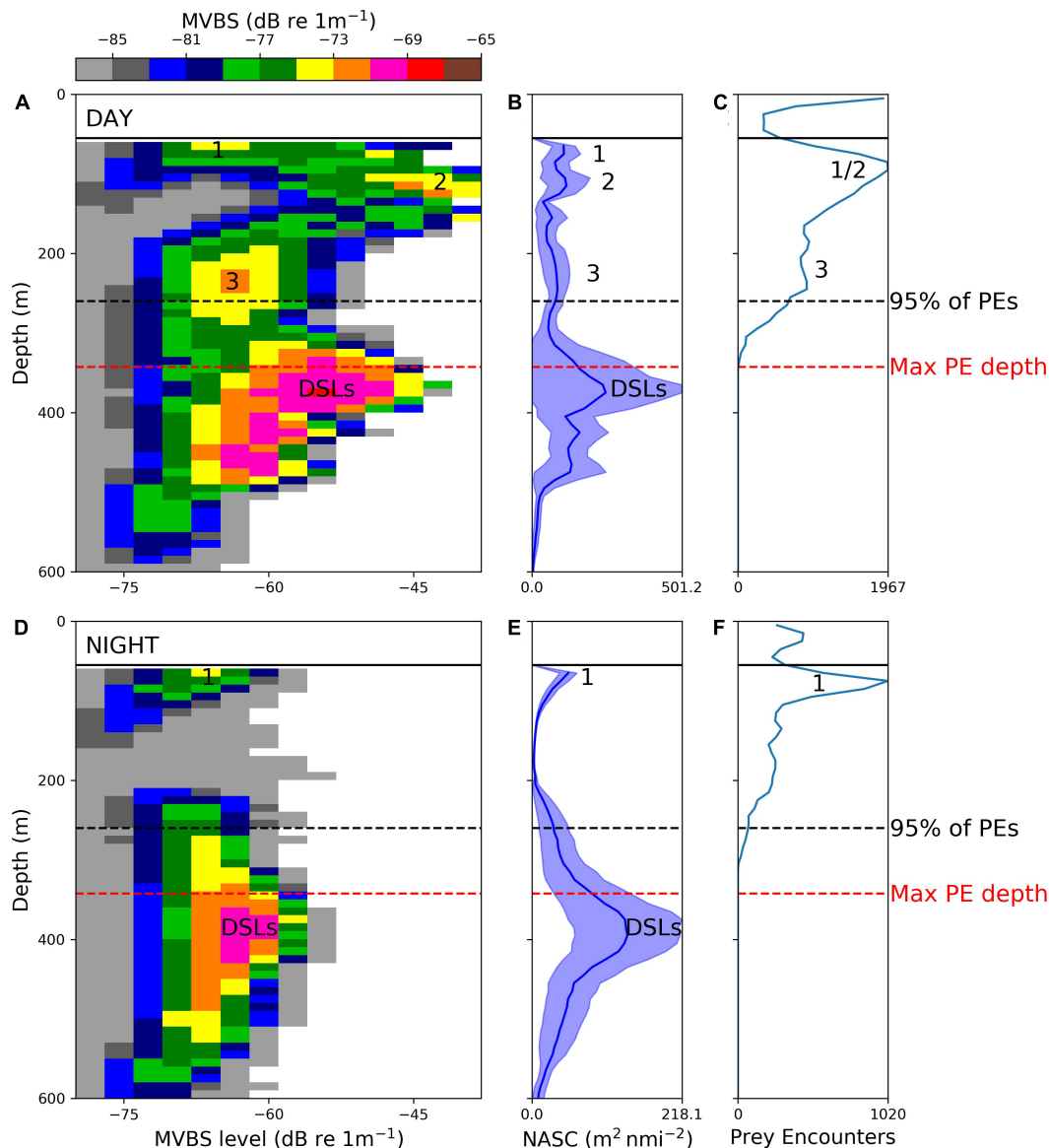


FIGURE 3 | Offshore (seabed depth > 1000 m) king penguin prey encounters (PEs) detected between 20th February and 16th March 2017 and acoustic observations of water-column backscattering intensity distribution in the Atlantic sector of the Southern Ocean (Antarctic Polar Front to Southern Antarctic Circumpolar Current Front interfrontal zone; 4th March to 18th March 2017). Panels (A,D) show observed mean volume backscattering strength (MVBS, -80 to -65 dB re 1 m^{-1}) by depth interval (0 to 600 m in 10 m intervals) and MVBS level (-80 to -40 dB re 1 m^{-1} in 3 dB re 1 m^{-1} intervals) during day and night, respectively. Panels (B,E) show MVBS collapsed into 1D mean nautical-area scattering coefficient (NASC) values, integrated over 10 m intervals between 50 and 600 m (echosounder observations recorded in the top 50 m were excluded from analysis due to surface noise), blue shading represents variability (95% confidence intervals) in calculated NASC values (standardised into 1 km along-track segments). Panels (C,F) show numbers of prey encounters by 10 m depth intervals from 0 to 600 m. Numbers indicate different prey types (1 = low intensity schools, 2 = high intensity schools, and 3 = clusters of schools termed 'prey patches'; see section "Acoustically Detected Prey Field" for more information). Deep scattering layers (DSLs) were labelled where values of MVBS peaked in the mesopelagic zone. 95% of all prey encounters occurred shallower than 260 m (black dashed line). Red dashed line is the maximum depth of all recorded prey encounters.

and (D) $\text{WMD}_{200-1000\text{ m}}$, nodes = 28, decay = 0.001 (test RMSE = 47.8 m; $R^2 = 0.75$).

King Penguin Habitat

Predicted gridded NASC and WMD daily values (sun angle was set to the local daily maximum value) were averaged over the king penguin foraging period and plotted (Figure 5; standard

deviation plotted in Supplementary Figure 4). Mean areal values of $\text{NASC}_{50-260\text{ m}}$ and $\text{NASC}_{200-1000\text{ m}}$ over the penguin foraging domain were c. 322 and 335 $\text{m}^2\text{ nmi}^{-2}$, respectively. Mean areal values of $\text{WMD}_{50-260\text{ m}}$ and $\text{WMD}_{200-1000\text{ m}}$ over the penguin foraging domain were c. 78 and 336 m, respectively. King penguin dive locations were associated with shallow prey (Figure 5C) that had high NASC values (Figure 5A)

TABLE 2 | Fish species detected in king penguin (chick rearing stage = 8 penguins) DNA faecal samples.

Species	Common name	%DNA	Stage	Depth zone	DVM	Gas	Prey type	Source
<i>Kreftichthys anderssoni</i>	Rhombic lanternfish	88%	Adult	Epipelagic Mesopelagic	Yes	Yes	2/3	Duhamel et al. (2000); Collins et al. (2008); Lourenço et al. (2017)
<i>Lepidonotothen larseni</i>	Painted notothen	50%	Adult	Epi-benthic	Yes	No	NA	De Witt et al. (1990); Loeb et al. (1993); Frolkina et al. (1998); Bushula et al. (2005); Curcio et al. (2014); Deli Antoni et al. (2019)
			Larvae or Juvenile	Epipelagic	Yes	No	1	Gon and Heemstra (1990); Loeb et al. (1993); Frolkina et al. (1998); Bushula et al. (2005); Curcio et al. (2014); Deli Antoni et al. (2019)
<i>Channichthyidae</i> spp.	Icefish	50%	Adult	Demersal	No	No	NA	Permittin (1973); Loeb et al. (1993); Kock (2005)
			Larvae or Juvenile	Epipelagic	No	No	1	Loeb et al. (1993); Kock (2005)
<i>Lepidonotothen nudifrons</i>	Gaudy notothen	38%		Demersal	No	No	NA	De Witt et al. (1990); Loeb et al. (1993); Deli Antoni et al. (2019)
<i>Parachaenichthys georgianus</i>	Antarctic dragonfishes	25%		Demersal	No	No	NA	North and Ward (1989); Gon and Heemstra (1990); Loeb et al. (1993); Kock (2005)
<i>Magnisudis atlantica</i>	Duckbill barracudina	13%		Mesopelagic and bathypelagic	No	No	NA	Fishbase (http://www.fishbase.org/)
<i>Acanthopterygii</i> spp. BD-2006	Bony/ray-finned fishes	13%			No	No	NA	NA
<i>Nototheria rossii</i>	Marbled rockcod	13%		Demersal	No	No	NA	De Witt et al. (1990); Barrera-Oro et al. (2014); Cali et al. (2017)

All fish were found within the king penguin foraging zone (top 260 m), but larvae and juvenile fish are generally shallower (top 200 m). Vertical extents of prey types are shown in **Figure 3**. Demersal and epi-benthic species do not have a corresponding prey type. %DNA is the percentage of samples that included fish species DNA. Gas denotes if the species possesses a swimbladder or not.

in their foraging zone (top 260 m), and with relatively shallow (**Figure 5D**) and high intensity DSLs (**Figure 5B**) in the 200–1000 m depth range. NASC and WMD were also predicted for the region surrounding the Kerguelen Islands (see **Supplementary Figure 5**), which is also home to colonies of breeding king penguins. Spatial patterns of prey were very different between the two regions: in the Kerguelen region, mean $NASC_{200-1000\text{ m}}$ was much higher (c. $1599\text{ m}^2\text{ nmi}^{-2}$), mean $NASC_{50-260\text{ m}}$ was much lower (c. $132\text{ m}^2\text{ nmi}^{-2}$), and DSLs were substantially deeper (c. 487 m; a depth far beyond the diving capabilities of king penguins).

King Penguin Habitat Suitability

Excluding Bird 14 (see section “Materials and Methods”) left a total of 19,504 dives (out of 23,646 daytime dives and 37,254 in total) available for the habitat selection models. The ‘prey+DSL’ model had significantly better support than the null and prey models (**Figure 6C**) and a substantially lower AIC value (mean over the 30 model runs was 18,472 compared with mean values of 21,226 and 30,717 for the prey and null models, respectively, indicating that the more complex prey-based models were not being overfit). The ‘prey+DSL’ model was used to predict mean habitat suitability over the period (**Figure 6D**); note that NASC values are integrated over the penguin foraging zone and the mesopelagic zone in these models and hence are much larger than

the values in **Figure 3**, which are integrated over 10 m depth intervals.

King penguin habitat suitability declined with distance from the colony, and since we used the distance to colony * seabed depth interaction (te1), shallow seabed depths tended to be used close to the colony but were avoided as distance from it increased. Habitat suitability increased in the presence of high intensity and relatively shallow DSLs (**Figure 6B**). Three distinct features were evident in the partial plot for the prey component of the GAM (te2; **Figure 6A**) that were related to the three prey types defined in **Figure 3** (based on WMD and NASC) and **Table 2** (based on diet studies).

DISCUSSION

Our results indicate that king penguins in guard stage at South Georgia do not feed directly on the ubiquitous DSLs around their colony, as these were found to be outside their diving range during the study period. Instead, they likely target smaller, ephemeral schools occurring above the DSLs. This offers strong support for the idea that availability and prey type (or quality), rather than abundance *per se* influences predator–prey interactions at fine (10s of m) vertical scales (e.g., Benoit-Bird et al., 2013; Boyd et al., 2015). The link between targeted fish schools and the inaccessible DSLs, which is evident at a 10 km horizontal scale, may be related to ontogeny (e.g., juveniles

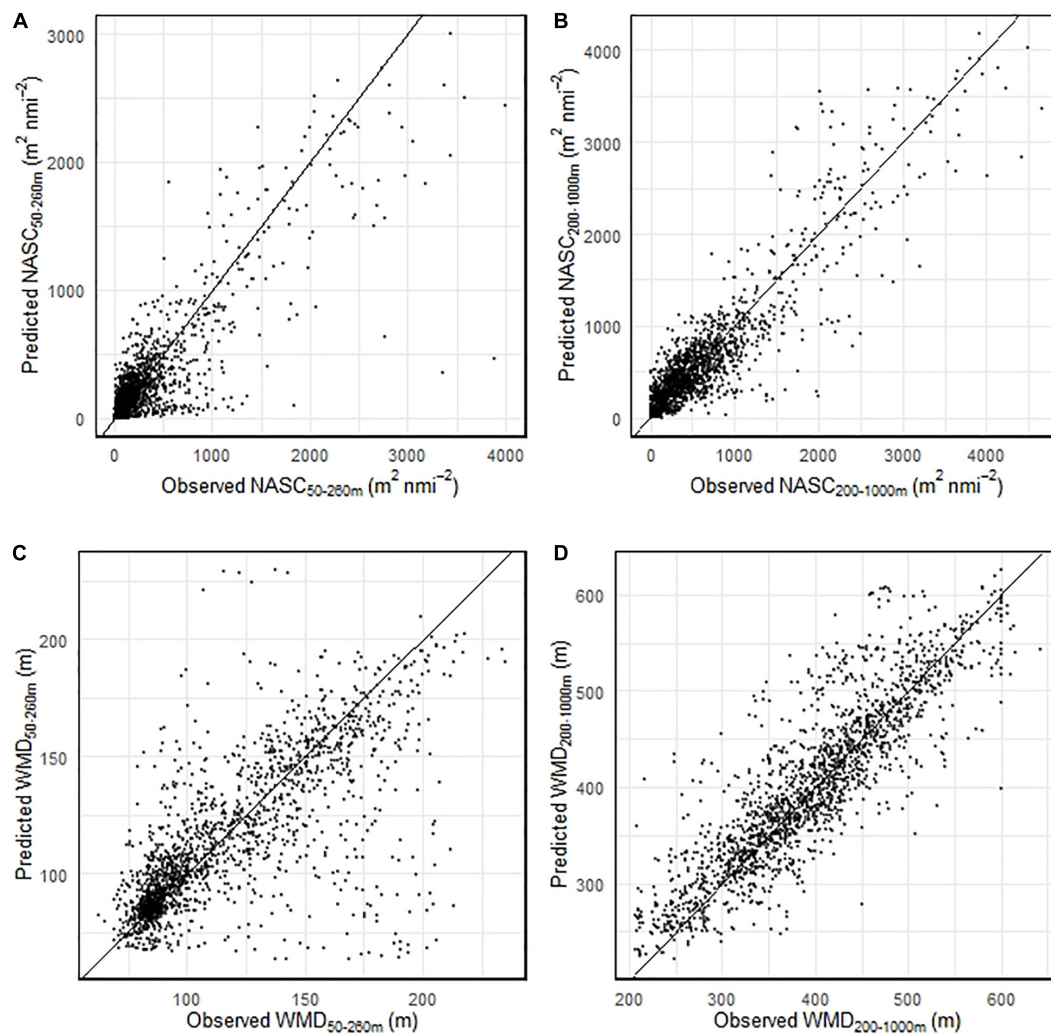


FIGURE 4 | Neural network predictions of nautical-area scattering coefficient (NASC; **A,B**) and weighted-mean depth (WMD; **C,D**) versus observations averaged over 10 km along track intervals collected during the Antarctic Circumnavigation Expedition.

forming clusters of shallower aggregates) or other food web links (e.g., changes in depth distribution related to species, size, DVM, or environmental conditions, e.g., light). However, these findings are based on a single site, breeding stage and year and warrant further investigation.

Study Caveats, Considerations, and Recommendations for Future Work

The approach taken here provides the foundations of a framework to tackle an important problem in marine ecology – linking at-sea diving predator distributions with their prey across multiple spatial and temporal scales – using a combination of acoustics, diet studies, animal tracking and modelling. Such a comprehensive and multi-faceted approach naturally incurs limitations, which will ultimately need to be addressed in future studies. For example, there was poor spatial overlap between penguin dive locations and the vessel track. Use

of a single echosounder frequency did not enable target identification. However, since the frequency used was relatively low (12.5 kHz), most of the received backscattering intensity could be attributed to fish. Due to surface noise, we were not able to make observations in the top 50 m and hence some schools at the surface may have been missed. This may explain why the shallow zone neural networks systematically underestimated NASC and WMD (see **Figure 4**). In future studies, structured and statistically robust (see Jolly and Hampton, 1990) multifrequency/broadband acoustic surveys with coincident trawling in known (or predicted) penguin foraging grounds should be conducted to enable prey species identification and provide information on prey size distribution.

We compared penguin prey encounters with predicted NASC values to study predator–prey interactions. However, not all predicted encounters will be a result of prey interactions since prey and predator encounter discrimination is not possible using accelerometry data alone, but the number of predation events

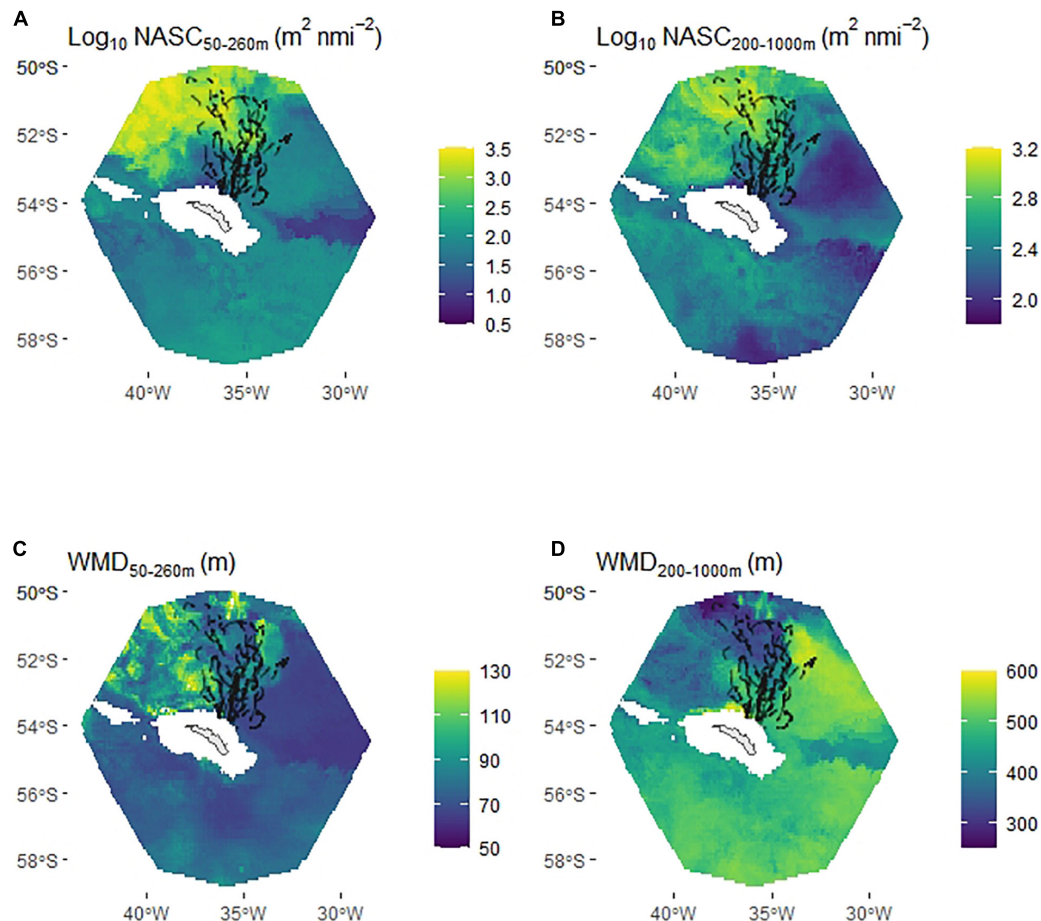


FIGURE 5 | Predicted mean (daily values averaged between 20th February and 18th March 2017) daytime nautical-area scattering coefficient (NASC; **A,B**) and weighted-mean depth (WMD; **C,D**) values for 17 (bird 14 excluded) chick-rearing king penguins foraging from South Georgia. Foraging domain defined as $1.1 \times \text{max foraging range} = 508.1 \text{ km}$. Grid cells that had a seabed $<600 \text{ m}$ were excluded. All penguin dive locations (with and without prey encounters) shown by black points.

is expected to be relatively low. We also used a neural network to predict prey characteristics because relationships between acoustic target strength and the environment are known to be non-linear and complex (e.g., see Jech et al., 2015). Neural networks provided very good predictive power but are hard to interpret, precluding any discussion related to the importance of the correlated model inputs.

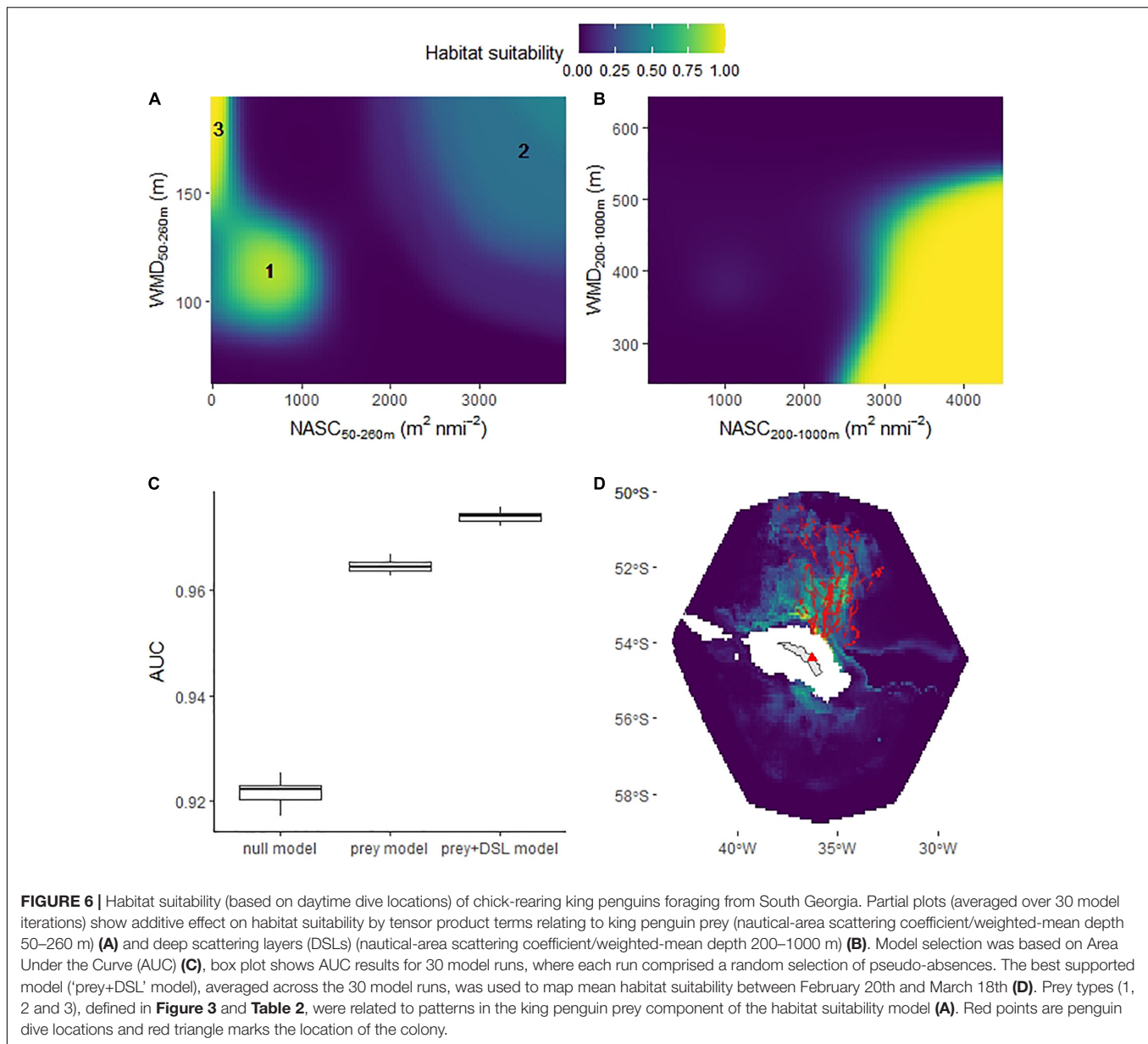
Spatially resolved ecosystem based management requires information on predator and prey distributions and on the interactions between them. We used model-predicted physical and biological variables to model prey NASC and WMD, which were then used to model predator habitat suitability. Instead of this multi-model approach, a single model based on the environmental covariates could have been used to predict habitat suitability. Whilst this less complex approach would ultimately be more statistically robust, it would not provide the means to determine the importance of the vertical distribution of different prey structures (e.g., scattering layers and schools) in predicting habitat suitability (i.e., providing information on predator-prey interactions). In the absence of coincident prey observations,

future modelling work should test the utility of our multi-model approach by comparing predictions with output from simpler models that only consider environmental observations.

We also modelled (binomial GLM) prey encounter dives ($=1$) versus non-prey encounter dives ($=0$) using the habitat suitability model predictors (analysis not presented) but did not find good agreement between the data and the models. This suggests that the data we used (predicted NASC and WMD values) do not explain the variance in prey capture well, which is likely to be better explained by environmental covariates that contribute to successful prey capture, e.g., surface illumination and light attenuation in the water-column (not available in this study).

King Penguin Prey

King penguins from South Georgia likely fed on barracudina close to the seabed and juvenile icefish and painted noties, that typically occupy reefs and kelp beds in the coastal region, on their return trips to the colony (Frolkina et al., 1998). Although relatively infrequent, occurring in just 13% of faecal samples that contained fish DNA from individual chick-rearing



penguins, barracudina may make up a relatively large proportion of king penguin diet by mass due to their large size (Olsson and North, 1997). In offshore regions, where the majority of foraging takes place, penguins targeted specific prey types (isolated and larger-scale patches of fish schools, comprised of various species across different life-history stages and depth ranges) within their diving range. Given that king penguins typically require c. 2.3 kg/day of fish (Bost et al., 1997; Putz et al., 1998), our results indicate that penguins must have on average obtained around 10.1 g of prey per dive or 5 g per prey encounter. Since adult *K. anderssoni* (main prey item of chick rearing penguins) weigh around 4 g at maximum standard length (c. 7 cm) (see Saunders et al., 2020), this would suggest that on average each prey encounter included capture of >1 fish. Penguins likely focused on juvenile (since they do not

eat larvae, see Ratcliffe and Trathan, 2011) fish species during the daytime that occurred in the mid-to-upper epipelagic zone (e.g., painted noties/icefish), but also probably fed on adult *K. anderssoni* both during the day and at dawn/dusk during fish vertical migration. Increases in shallow epipelagic prey density were related to relatively shallow and dense (high echo energy) DSLs, which is in agreement with the findings of Fielding et al. (2012) that acoustic backscattering intensity was positively related to the number of fish schools. This association can be explained by the strong coupling, via DVM and ontogenesis, between highly dynamic shallow water biomass (in the form of ephemeral schools and larvae/juveniles) and mesopelagic biomass (Pinti et al., 2021).

Electrona carlsbergi and *K. anderssoni* are known to be the dominant schooling myctophid species close to South Georgia,

and occur at depth of between 60 and 300 m (Saunders et al., 2013). King penguin chick rearing success has been found to increase when *K. anderssoni* form a large component of their diet (Olsson and North, 1997). We found that 88% of the chick-rearing birds had *K. anderssoni* in their diet, whereas no *E. carlsbergi* were found. Saunders et al. (2013) reported that *E. carlsbergi*, which are typically located in water associated with the Antarctic Polar Front (Hulley, 1981; Zaslavskiy et al., 1985; Saunders et al., 2014), were absent or in low abundance in some years, whereas *K. anderssoni* occurred more regularly every year. Since king penguins in guard stage do not feed at the Antarctic Polar Front, the absence of *E. carlsbergi* in the diets of birds in this study is likely to be a consequence of the constraints on foraging ranges during the guard stage of the breeding season (Olsson and North, 1997), but it is also possible that *E. carlsbergi* were consumed but not detected due to the relatively low sample size in our diet study.

Layers and associated patches of swimbladder fish have been observed during the daytime in the Scotia Sea (Saunders et al., 2015; Lourenço et al., 2017) and at Kerguelen (Béthague et al., 2017). Prey patches at Kerguelen, which were observed shallower than 180 m, were likely comprised of *K. anderssoni* and *Protomyctophum* spp. and disappeared at night owing to DVM (as observed here). The depth range of *K. anderssoni* around Kerguelen is between 100 and 150 m (Bost et al., 2002; Charrassin et al., 2004) and overlaps with the depth range of prey type 2 identified in this study, classified as *K. anderssoni* through diet analysis. This prey type may also include *Protomyctophum* spp., since *Protomyctophum choriodon* have been commonly found in king penguin diets, particularly during February and March (Olsson and North, 1997). Therefore, foraging behaviour of king penguins at South Georgia appears similar to that found at Kerguelen as is the apparent association between targeted prey patches and DSLs.

Predator–Prey Interactions

We found good agreement between the vertical distribution of acoustically detected fish schools and that of king penguin prey encounters at fine vertical scales (10s of m), and were able to map king penguin foraging habitat based on predicted 3D prey distributions at local horizontal scales (10 km) after controlling for regional-scale (10s–100s km) effects related to distance to colony and bathymetry. Within the habitat available to king penguins, defined to be $1.1 \times$ maximum foraging range from their colony, prey resources (full water-column NASC) were found to be relatively low when compared to other similar sites (e.g., Kerguelen, see **Supplementary Figure 5**). King penguins concentrated their diving effort in an area with relatively high levels of predicted NASC toward (but not reaching) the Antarctic Polar Front, likely containing relatively high densities of prey. Vlietstra (2005) found that in a similar resource-limited environment, fine-scale overlap of seabird and prey distributions increased when compared to resource-rich environments. Since prey distributions can shift significantly both seasonally and annually, e.g., presence/absence of *E. carlsbergi* around South Georgia (Saunders et al., 2013), potential king penguin foraging

habitat may change from being a resource-limited to a resource-rich environment. However, previous work has shown that king penguins have foraged in a similar area (Scheffer et al., 2010), suggesting that it may be characterised by predictability of resources and low variation in prey availability. It follows that the more constrained predators are by their environment (i.e., the harder it is to find prey compared with random search) the more tightly coupled the relationship between prey and predators will be. Perhaps the most important foraging constraint for king penguins is vertical accessibility, and studies of seabirds in the Humboldt Current have found that this is more important in predicting seabird foraging habitat selection than prey density throughout the water column (Boyd et al., 2015). It is perhaps no coincidence that DSL depth coincides with the maximum dive depth of king penguins: myctophids may go to these depths to reduce predation risk, as opposed to tracking isolumines (Røstad et al., 2016) or being physiologically constrained by swimbladder function (Bone et al., 1995). A relatively small shallowing of DSLs (10s of m), which is predicted by 2100 (Proud et al., 2017), could open up a very large resource to king penguins that is perhaps more reliable than the presently targeted ephemeral fish schools close to the surface. This would of course reduce prey variance at fine and local scales and make it very difficult to predict predator distributions (Logerwell et al., 1998), i.e., the spatio-temporal relationship between predator and prey would weaken as there would be a large number of areas with an abundance of food but no penguins. Under this scenario, availability of prey to king penguins would become analogous to present prey availability to elephant seals now: the very deep diving capability of elephant seals gives them access to the entire mesopelagic zone and the DSLs there, and so it is very difficult to predict elephant seal dive locations from modelled prey distribution patterns because prey is, to an extent, ubiquitous (McMahon et al., 2019). The degree to which DSLs become shallower around South Georgia in the future will depend on whether their depth is driven by environmental conditions (e.g., light) or predation risk – if the latter, they might not change.

Implications for Marine Spatial Planning and Conservation Management

Protection of key Southern Ocean predators and prey is becoming increasingly important as fishing of lower trophic levels (e.g., squid and toothfish; Agnew et al., 2005; Kock et al., 2007) continues and other fisheries expand (e.g., Antarctic krill; Nicol et al., 2012). In this study, we have linked high intensity (and likely high biomass) DSLs with penguin habitat suitability. Penguins are likely drawn to these locations to feed on DSL-associated schools that occur within their dive range. This result supports the approach taken by Hindell et al. (2020) for defining AESs, which assumes that predator aggregations are indicative of elevated productivity and biomass at lower trophic levels. Since DSL intensity is readily predictable at local scales, conservation management could use modelled DSL intensity as a proxy for important predator foraging grounds to designate AESs. However, strong correlation between predators and lower-trophic

level biomass is not ubiquitous (Boyd et al., 2015), and is likely to vary by species, season, access to habitat and prey distribution. Similarly, drivers of prey abundance are not always good predictors of predator distribution patterns, particularly in anthropogenically altered environments (Grémillet et al., 2008; Sherley et al., 2017). Therefore, it may not be prudent to define AESs over large areas based on ocean basin scale correlations. Instead, a regional approach, which considers seasonal variations in local populations (e.g., changes in predator distribution due to breeding stages, etc.), might provide a more informed basis for designating MPAs: the habitat suitability model developed in this study could be used to identify AESs within and beyond the SGSSI MPA (see Warwick-Evans et al., 2018; Handley et al., 2020).

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found at: <https://zenodo.org/record/3587678#.YPArB-hKiF4> and <https://doi.org/10.17630/d92c1af3-6149-4bb5-aa14-6fb00ef3a85a> for the acoustic and penguin tracking data respectively.

ETHICS STATEMENT

The animal study was reviewed and approved by the Government of South Georgia and the South Sandwich Islands (regulated activity permit number 2016/048), the British Antarctic Survey and the University of St Andrews.

AUTHOR CONTRIBUTIONS

RP collected the echosounder data, wrote the manuscript, and performed data analysis. CLG collected the echosounder data and king penguin data, performed preliminary analysis of king penguin and echosounder data, and produced a thesis chapter relating to the study. RBS collected the penguin data and contributed to writing the manuscript. AK helped with the accelerometry data analysis and contributed to writing the manuscript. YR-C provided guidance on data analysis methods and contributed to writing the manuscript. NR conceived the habitat preference analysis and contributed to writing the manuscript. SJ performed the DNA sequencing. AW performed

the DNA extraction and contributed to writing the manuscript. JPYA provided the accelerometry tags and contributed to writing the manuscript. RAS provided literature information on diet study species and contributed to writing the manuscript. PGF collected echosounder data, performed the calibration at South Georgia, and contributed to writing the manuscript. LB assigned frontal zones to track positions and contributed to writing the manuscript. ASB conceived the study, planned the field activities and contributed to writing the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2021.745200/full#supplementary-material>

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Foraging Behaviours of Breeding Arctic Terns *Sterna paradisaea* and the Impact of Local Weather and Fisheries

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During the breeding season, seabirds are central place foragers and in order to successfully rear chicks they must adjust their foraging behaviours to compensate for extrinsic factors. When foraging, arctic terns *Sterna paradisaea* are restricted to the first 50 cm of the water column and can only carry a few prey items back to their nests at once. In Iceland, where 20–30% of the global population breed, poor fledging success has been linked to low food availability. Using GPS loggers, we investigated individual foraging behaviours of breeding adults during incubation from a large colony over four seasons. First, we tested whether foraging trip distance or duration was linked to morphology or sex. Second, we examined how trips vary with weather and overlap with commercial fisheries. Our findings reveal that arctic terns travel far greater distances during foraging trips than previously recorded (approximately 7.3 times further), and they forage around the clock. There was inter-annual variability in the foraging locations that birds used, but no relationship between size or sex differences and the distances travelled. We detected no relationship between arctic tern foraging flights and local prevailing winds, and tern heading and speed were unrelated to local wind patterns. We identified key arctic tern foraging areas and found little spatial or temporal overlap with fishing pelagic vessels, but larger home ranges corresponded with years with lower net primary productivity levels. This suggests that whilst changing polar weather conditions may not pose a threat to arctic terns at present, nor might local competition with commercial fisheries for prey, they may be failing to forage in productive areas, or may be affected by synergistic climatic effects on prey abundance and quality. Shifts in pelagic prey distributions as a result of increasing water temperatures and salinities will impact marine top predators in this region, so continued monitoring of sentinel species such as arctic terns is vital.

Keywords: arctic tern, biologging, foraging behaviour, wind, fisheries

INTRODUCTION

Globally, populations of seabirds are declining, and pelagic species with expansive ranges are particularly vulnerable (Paleczny et al., 2015). There are numerous threats to seabirds including predation, disturbance and habitat loss, which particularly affect them during breeding, and bycatch, pollution and overfishing while they are at sea for much of the rest of the year (Croxall et al., 2012; Dias et al., 2019). As bioindicators, seabirds can offer insight into marine ecosystem changes (Piatt et al., 2007). They travel between profitable prey patches, and reduce movement when they reach profitable areas (Weimerskirch, 2007), so tracking seabirds can indicate areas of prey occurrence (Piatt et al., 2007). Seabird foraging ranges can be used to identify candidate locations for protection (Thaxter et al., 2012), and protecting these areas could benefit whole ecosystems (Hooker and Gerber, 2004).

While it is particularly challenging to understand and mitigate threats across seabirds' annual migratory ranges, which can be hundreds of thousands of square kilometres (Lascelles et al., 2014), there are opportunities to focus on threats and management at their breeding areas, which tend to be much more spatially restricted. In this study, we investigate the overlap of tern foraging areas with local fisheries and the impact of weather on the intra-breeding season foraging behaviour of arctic terns *Sterna paradisaea*, which are known to have poor breeding success in years with low prey abundance (Monaghan et al., 1992; Vigfúsdóttir et al., 2013).

Arctic terns annually undertake the longest recorded migration of any organism (Egevang et al., 2010), travelling over 100,000 km (Volkov et al., 2017) from circumpolar breeding locations in the Temperate (southernmost at 41°N) and Polar zones to overwintering sites in the Southern Ocean (Hatch, 2002). Populations appear to be declining at many locations across the breeding range [e.g., in Canadian High Arctic (Mallory et al., 2018), Western Iceland (Petersen et al., 2020), Greenland (Burnham et al., 2017), and Norway (Barrett et al., 2006)]. Generally there is high adult survival (Devlin et al., 2008; Mallory et al., 2018), with very high regional (Egevang and Frederiksen, 2011) and colonial breeding site fidelity (Devlin et al., 2008). Declines are therefore thought to be likely due to low recruitment or survival of juveniles, although some dispersal of adults to new breeding sites is possible (Vigfúsdóttir et al., 2013; Mallory et al., 2018). Food availability during the early stages of breeding will influence recruitment by altering laying date, clutch size or leading to egg abandonment (Suddaby and Ratcliffe, 1997). In Iceland, the collapse of sandeels (*Ammodytes* sp.), a key prey species, has coincided with lower adult survival since 2000 (Petersen et al., 2020), and low fledgling rates caused by starvation (Vigfúsdóttir et al., 2013). It is therefore key to understand how and where arctic terns forage during the breeding season, and whether their behaviour alters in relation to weather and fish stocks.

Wind is a key abiotic factor that impacts seabird demography; it can affect adult survival (Frederiksen et al., 2008), or breeding success (e.g., Robinson et al., 2002; Mallory et al., 2009; Johnson and Colombelli-Négrel, 2021). Changes to wind patterns can

alter foraging seabird behaviour, with strong winds impacting trip duration, flight speeds, trip success (e.g., foraging mass gain, capturing smaller prey, difficulty locating prey) and target prey species (Finney et al., 1999; Weimerskirch et al., 2012; Dehnhard et al., 2013; Elliott et al., 2014; Saraux et al., 2016). Breeding seabirds have been shown to mitigate the impact of strong winds during foraging trips by altering foraging search strategies (e.g., Scopoli's shearwaters, *Calonectris diomedea*; De Pascalis et al., 2020), flight altitudes (e.g., Antarctic petrels, *Thalassoica antarctica*; Tarroux et al., 2016), and altering flight air speeds (Spear and Ainley, 1997). In years with higher wind speeds, flight may be more costly for arctic terns, particularly if it is greater than their minimum power speed (i.e., the most energetically efficient speed to fly, 6.8 m.s⁻¹; Hedenström and Åkesson, 2016). During migratory flights, arctic terns adjusted air speed in relation to side-winds, but did not fully compensate for wind drift (Hedenström and Åkesson, 2016). It is therefore possible that during foraging trips arctic terns could also be impacted by wind speeds and may compensate by adjusting heading or air speed in order to maintain a course. In years with stronger winds, foraging trips may therefore be more energetically demanding. However, moderate increases in wind speed could have a positive effect on prey capture rate. For example, Sandwich terns *Sterna sandvicensis* exerted less effort hovering prior to a dive and the prey were less likely to see them in moderate winds due to the choppy waters (Dunn, 1973). Additionally, as a driver of oceanographic processes such as upwelling and vertical mixing, wind conditions can also impact prey availability and distribution (e.g., Cox et al., 2018). Therefore wind is likely to have indirect effects on arctic tern foraging behaviour as well.

Arctic terns have the capability to fly at high altitudes. During migration, radar observations recorded arctic terns flying at altitudes greater than 1,000 m (Gudmundsson et al., 1992) and they have been recorded traversing the Andes (Duffy et al., 2013). Arctic terns generally fly low whilst searching for food (Hedenström and Åkesson, 2016), but likely higher if transiting to a prey patch. We aim to describe arctic tern foraging flight altitudes using GPS devices for the first time.

Arctic terns feed on small schooling fish such as herring Clupeidae, sandeels, capelin *Mallotus villosus*, or crustaceans such as krill *Euphausiacea* (Hatch, 2002). They apparently have short foraging ranges, generally remaining within 10 km of the colony, only occasionally travelling further (Rock et al., 2007; Cabot and Nisbet, 2013). Foraging trip duration and distance are further constrained during chick rearing by arctic terns being limited to carrying only one to a few prey items at a time, and by shallow plunge dives to a maximum depth of 50 cm (Hatch, 2002). Arctic terns are therefore particularly vulnerable to local food shortages (Robertson et al., 2014b), such that smaller clutches are laid in response to lower quality food during courtship feeding (Suddaby and Ratcliffe, 1997), brood reduction is more likely in nests where adults have lower body condition (Monaghan et al., 1989), and breeding attempts are usually abandoned in years with low food availability (Monaghan et al., 1992). In addition, prey availability during the early stages of breeding can also impact the body condition of *Sterna* species, with significant declines in incubating female common tern *S. hirundo*

body mass reported in poor foraging conditions (Wendeln and Becker, 1996). Understanding arctic tern intra-seasonal foraging ecology is vital to investigate a key cause of low breeding success (Vigfúsdóttir et al., 2013), and could also identify early signs of changing conditions that will affect other seabird species foraging further from the coast (Pratte et al., 2018).

Iceland supports c. 20–30% of the world's population of breeding arctic terns (Asbirk et al., 1997), a population now listed on the Icelandic Red List as vulnerable due to recent population decline (Icelandic Institute of Natural History, 2018). In the warmer waters in the south and west of Iceland, seabirds rely mainly on sandeels, and in the cooler waters in the north and east on capelin and krill (Lilliendahl, 2009). Following the collapse of the sandeel population in 2000, annual arctic tern adult survival reduced by 10% in west Iceland (Petersen et al., 2020). The present study focuses on the foraging behaviours of arctic terns in the west and southwest regions (west of the Reykjanes peninsula and Faxaflói bay), and highlights potentially important foraging areas that are used by commercial fisheries.

Today, 38% of the Icelandic coastal fleet operate in the west and southwest regions (Þórðarson and Viðarsson, 2014), and in 2014 the majority of landings occurred at the harbour in Reykjavík (Edvardsson et al., 2018). The coastal fleet primarily lands cod *Gadus morhua*, which feeds on similar pelagic species to arctic terns, but the fleet also lands pelagic species such as lumpfish *Cyclopterus lumpus*, another arctic tern prey species (Þórðarson and Viðarsson, 2014). Demersal fisheries are the most valuable sector but the landed tonnage of pelagic fisheries, although very variable, is generally greater than that of the demersal (Edvardsson et al., 2018) and consists of c. 60–70% of the average annual catch by weight (Saevaldsson and Gunnlaugsson, 2015). Historically the pelagic fisheries in Iceland landed mostly capelin (a known prey species of arctic terns and other seabirds off the north coast of Iceland, but have not been documented in their diet in the south) for the fishmeal industry (generally greater than 80% of pelagic landings), but due to declines in capelin stocks and new, more valuable species (e.g., herring *Clupea harengus* and mackerel *Scomber scombrus*) entering Iceland's waters, capelin landings have declined recently (Saevaldsson and Gunnlaugsson, 2015). Given the importance of this area for breeding arctic terns and other seabird species (Garðarsson, 1999), the link between poor fledging success and food availability (Vigfúsdóttir et al., 2013; Petersen et al., 2020), and the increase in pelagic landings in the region (Edvardsson et al., 2018), it is important to investigate the potential impact of the fisheries industry. Addressing factors that influence arctic tern foraging success will shed light on the potential causes of the declines, which is key to preserve this population, and will also benefit the wide range of other species that breed in the rich waters around Iceland.

We aim to: (1) describe for the first time where and how far away from the colony Icelandic arctic terns forage, (2) to understand whether these movements can be explained by local wind conditions, and (3) to understand to what extent the movements and key foraging areas may overlap with local fisheries.

MATERIALS AND METHODS

Field Site

On the Southern Reykjanes Peninsula in Iceland is a breeding site with >10,000 pairs of arctic terns (near Sandgerði, Iceland, 64.015°N, 22.707°W). The colony is located in a privately owned site, Norðurkot farm, used as a nesting area for eider ducks (*Somateria mollissima*), and operated as a wild down farm. The study site was accessed annually, with landowner permission, for 3–4 weeks during June 2018, 2019, 2020, and 2021 for tracking device deployment and retrieval. Predation of arctic tern eggs and chicks was minimal due to local landowners monitoring and removing predators with 24/7 predator watches.

Animal Capture

Since June 2018, 331 breeding arctic terns have been caught and ringed at the study site using a tent spring trap (Moudry traps: TW45). The primed trap is placed on a nest with a trigger line over the eggs, which is triggered by the incubating bird landing back on the nest. This method does not cause damage to the adult or the eggs. The eggs in each nest were measured and the stage of development was determined with egg flotation (Liebezeit et al., 2007) adapted for arctic terns (**Supplementary Figure 1**). Any arctic tern captured with eggs less than a third of the way through development was not considered for tracking device deployment as birds captured on early stage eggs were more likely to abandon their nests (Vigfúsdóttir, Pers. Comm.). All birds were ringed on their right tarsus with a unique metal ring from the Icelandic Institute of Natural History, and 260 were fitted with leg flags (blue with a white two character alpha code, sealed with waterproof plastic glue) on the left tarsus. All captured terns were measured (head and bill length: from the centre of the back of skull to the tip of the bill, bill length: from the start of feathering to the tip, and bill depth: on a closed bill at the nostrils) with Vernier callipers (to 0.1 mm). Wing length was measured (1.0 mm accuracy) from the carpal joint to the tip of the longest primary and mass was measured using a cotton bag with a Pesola spring balance (to 1.0 g accuracy). Six breast feathers were plucked with the calamus attached and stored dry at room temperature in an envelope to determine sex using molecular techniques adapted from Fridolfsson and Ellegren (1999; **Supplementary Material**).

Tag Deployment

Tracking devices (Pathtrack GPS nanoFix Geo + RF) were deployed for one breeding season on 29 arctic terns, in June 2019 ($n = 11$), June 2020 ($n = 11$) and June 2021 ($n = 7$). They were scheduled to record GPS locations every 15 min and would transmit these data to a base station that was placed in the centre of the colony at a height of c. 2–5 m. Additionally, two archival devices were deployed in 2018 (Pathtrack GPS nanoFix Geo) and were recaptured within the same season; these were scheduled to record locations every 30 min. Tags were attached using a leg loop harness (using 2.54 mm Spectra tape, Bally Ribbons, PA, United States), and weighed 2.9 g (± 0.3 g), which is approximately 2.65% of the mean mass of all arctic terns caught

and ringed to date. The device was positioned on the lower back of the tern, with the antennae pointing toward the tail. Total handling time was always less than 12 min. Only arctic terns with a mass >100 g, and those that returned to incubate their eggs within 5 min after the trap was set, had tracking devices attached. Any individuals that were captured after more than 5 min were measured, ringed, and released without tracking devices, so that they could be considered as a control treatment to understand the effect of tracking tags on post release survival and nest return rate. If no incubating adult returned to the nest after 10 min the trap was removed. The nests of the tracked birds were monitored regularly during the deployment period between 05:00 and 00:00. Recapture of arctic terns carrying tracking devices was attempted prior to egg hatching within the same season.

Data Retrieval and Recapture

Of the 11 deployed tracking devices in 2019, nine were recaptured and the data successfully downloaded. No data were received remotely from the other two devices, and these birds abandoned their nests so device recapture was not possible. In 2020 data were received remotely from all 11 devices, and seven individuals were recaptured and the devices removed. The other four abandoned their breeding attempt, but continued to visit the colony, and data were therefore successfully downloaded remotely. In 2021 data were received from all seven devices, and four individuals were recaptured and devices removed. The other three did not return to their nests. Recapture and device removal was not possible without the birds returning to a consistent location. Additionally, two archival GPS devices were deployed and recaptured during the 2018 field season.

Wind Modelling

In order to investigate the effect of environmental variables, wind data were obtained from operational forecasts of the UK Met Office global deterministic numerical weather prediction model (Walters et al., 2019), with hourly wind forecasts for the duration of each field season on a horizontal grid of approximately 10-km spacing. Arctic terns consistently flew at a median height of 62.75 m above sea level (MASL; **Supplementary Figure 2**), so the modelled wind speeds used in all analyses were at 50 MASL, the closest height available. The model outputs included the *u* (zonal i.e., west: east) and *v* (meridional i.e., north: south) components of wind in netcdf format and these were accessed using the *ncdf4* R package (Pierce, 2019). Wind direction and speed were calculated using the *rWind* R package (Fernández-López and Schliep, 2018). The foraging season temporal mean wind speed and direction at each grid location was determined by calculating the mean of the *u* and *v* wind components separately at each location across the duration of the available tracking data, and the mean speed and direction at each location could be derived from these values [square root ($\text{mean } u^2 + \text{mean } v^2$)].

Net Primary Productivity

Vertically generalised production model (VGPM) “chlorophyll-based” net primary productivity (NPP) monthly averaged data ($\text{mg C m}^{-2} \text{ day}^{-1}$) were downloaded from the standard products section of the Ocean Productivity website in hdf format on a

global grid of $1,080 \times 2,160$ (Behrenfield and Falkowski, 1997).¹ Data were only available during the first 3 years of the study (2018–2020), and only productivity levels during the tracking period in June were used in analyses. Hdf files were opened in R using the *raster* package, and the raster layers were cropped to the area around the southwest peninsula of Iceland.

Overlap Between Arctic Terns and Fishing Vessels

Vessels in Icelandic waters are recorded using vessel monitoring systems implemented by the ICG Operations Centre, with the Icelandic Directorate of Fisheries (Fiskistofa) responsible for fishing related activities. The integrated system includes monitoring activities through radio-based systems such as the global Automatic Identification System (AIS), which records the locations of any vessels over 15 m in length and extends 30–60 nautical miles from shore, and satellite based systems that record the movements of all vessels through transmitters fitted to ships that send data to a land-based station via a satellite system (Geirsson, 2011).

Fishing vessel data were available from 1st June to 30th June (the period at this site where breeding arctic terns are incubating and chick rearing) for each of the four field seasons with tracking data (2018–2021), and in the range that the arctic terns travelled (63°N – 65°N and 25°W – 22.5°W). The data provided by Fiskistofa were downsampled to a position every 10 min and only included vessel locations whilst fishing, which was determined through a combination of logbook records and a speed filter. Demersal gear types were not used in analysis, and pelagic fishing gear types (longline, gillnet and handline) were retained (a total of 26,800 pelagic fishing gear type locations of 184,309 total locations during the 4 years). The frequency that they occurred in 0.01 degree grids were calculated with the *raster* package (Hijmans, 2020). The frequency in which arctic terns and vessels overlapped temporally as well as spatially was determined by matching tern locations within 1 km of vessels and 1 h and within 2 km of vessels and 6 h. The temporal scales were selected as they would include the average duration of a foraging trip recorded in this study, and the spatial scales were arbitrarily selected to be cautious and should be generous enough to include overlap.

Data and Analysis

Unless otherwise stated all analyses were conducted in R (R Core Team, 2018) and spatial calculations used the *geosphere* R package (Hijmans et al., 2017) using projected data (EPSG: 3057). The R scripts for the following analyses can be found at https://github.com/JoMort/ArcticTern_Foraging. Foraging trips by arctic terns were considered to begin as soon as any locations were received from more than 500 m from the colony area (to remove any locations where terns were visiting a freshwater bathing location c. 0.25 km from the colony). Flight bearing was calculated from the geodesic distance (the shortest path over an ellipsoid) between two subsequent locations using the *bearing* function. Arctic tern ground speed was calculated from the time and distance between two subsequent locations and the air speed was derived from

¹<http://sites.science.oregonstate.edu/ocean.productivity/standard.product.php>

the modelled wind velocities and the tracking location vectors using the triangle of velocities (see Hedenström and Åkesson, 2016). The outbound and return sections of foraging trips were compared separately using the maximum displacement from the colony (including the maximum displacement location) to mark the outbound section of a foraging trip, and locations recorded afterward were considered the return section of the foraging trip.

To test whether arctic tern size (mean, wing length, head and bill length, and culmen) was related to the mean distance travelled by each individual during foraging trips (for example whether larger birds flew further), we tested for normality and then calculated Pearson's correlations for each of the biometric measures (head-bill length was square transformed which yielded a normal distribution, all other variables were normally distributed). To describe the general body condition of the birds in the colony, the masses of all arctic terns captured in each of the study years were tested for normality and compared with a one-way ANOVA. If individuals were captured and weighed more than once either within or between years, only the first recorded mass was included to avoid pseudoreplication. Likewise, we also performed Welch's *t*-tests to determine whether there was a significant difference in the mean and maximum displacement (variables were tested for normality using Shapiro-Wilk test and then square and log transformed, respectively, for normal distributions) from the colony between males and females. The sex of one bird could not be determined so this individual was excluded from these analyses.

Due to the low sample size in 2018, the following analyses were only conducted on the 2019–2021 datasets. The mean wind direction in each year encountered by arctic terns during foraging trips was calculated with the R package *circular* (Agostinelli and Lund, 2017). To test for a significant relationship between the wind speed encountered at sea during foraging trips and arctic tern flight speeds, a repeated measures correlation was performed using the R package *rnmcorr* (Bakdash and Marusich, 2021). The mean ground speed per foraging trip was used, with arctic tern identity as the repeated measure. To test whether wind speed affected the outbound and return sections of foraging trips repeated measures correlations were also performed on the mean ground speed of outbound and return sections of foraging trip separately.

The autocorrelated kernel density estimates (AKDE) of each individual with five or more foraging trips were calculated using continuous-time movement modelling (ctmm) and implemented using the *ctmm* package (Fleming and Calabrese, 2021) following the workflow described in Calabrese et al. (2016). The *ctmm* package calculates the kernel density home range estimates from autocorrelated GPS data and is not biased by small sample sizes. The best performing model [Ornstein-Uhlenbeck-F (OUF)] was selected based on the lowest Akaike Information Criterion (AIC) for each individual. The smoothing bandwidth is calculated by the *akde* function. The estimated isopleths at 25, 50, 75, 90, and 95% for arctic terns tracked in 2019, 2020, and 2021 were then merged within years and their areas calculated using the *sf* package (Pebesma, 2018).

Spatial overlap of arctic tern locations with pelagic fishing vessels were determined using the R package *fuzzyjoin* (Robinson, 2020). All arctic tern locations with a great circle distance within a 1 km radius and ± 1 h of a fishing vessel location, and the number of arctic tern locations recorded within a 2 km radius and ± 6 h of a fishing vessel location, were extracted and then calculated as a percentage of the total locations.

RESULTS

Foraging Behaviour

During egg incubation, a total of 374 foraging trips were recorded for 29 individuals (2 in 2018, 9 in 2019, 11 in 2020, 7 in 2021). Devices were deployed in 2018 for 1 and 6 days respectively, in 2019 for 8–10 days, in 2020 for 3–8 days, and in 2021 for 5–9 days, but devices did not all function for the whole period (**Supplementary Table 1**). One trip in 2021 along the south coast by an individual that abandoned incubation lasted 3.3 days and was not considered a foraging trip during analyses. Trip duration varied from 14.9–2355 min (mean = 346.1 ± 384.7 min, median = 225 min) and was more variable within individuals in the 2020 [tracked individual foraging trip duration interquartile ranges (IQRs) ranged from 89.9–615.0] and 2021 (IQRs 285.0–663.8) breeding seasons compared to 2019 (IQRs 21.2–219.0; **Supplementary Figure 3**). The mean distance travelled per trip varied between individuals, and the mean displacement from the colony was 36.1 ± 37.1 km, with a recorded maximum trip distance of 218.9 km.

Arctic tern foraging locations varied between years. In 2018 they generally foraged to the west and south west of the colony, in 2019 to the west and north west, in 2020 they generally foraged to the south west with the exception of one individual that foraged within Faxaflói bay to the north of the colony, and in 2021 foraging locations were generally to the west and north west with occasional very long trips to the south and south east of the colony (**Figure 1**). In 2019 most tracked arctic terns departed toward the north west, whereas in 2020 the departure direction ranged from 180 to 360° and in 2021 trip departures were toward the west or south west (**Figures 2A–C**). Arctic terns departed for foraging trips throughout the day, including during the short “night” (the period between sunset and sunrise was less than 2 h throughout the study period). Of all the foraging trips recorded from 2019 to 2021, 25% fewer trips began in the 2 h preceding sunset compared with other times of day (**Figures 2D–F**). The sample size in 2018 (7 foraging trips) was too small to be included in these analyses.

There was no relationship evident from a visual inspection of arctic tern size and the mean distance travelled per foraging trip, suggesting that if any relationship were present (regardless of its shape) that the effect size would be very small. Nevertheless we tested for a linear relationship, in the absence of a rationale for using a quadratic model, and there was no statistical relationship either [mass $r_{(27)} = -0.16$, $p = 0.41$; wing length $r_{(27)} = 0.02$, $p = 0.93$; head and bill length (squared) $r_{(27)} = 0.06$, $p = 0.77$; culmen $r_{(27)} = -0.09$, $p = 0.66$; **Supplementary Figure 4**]. There was a significant difference in the mass of all arctic terns

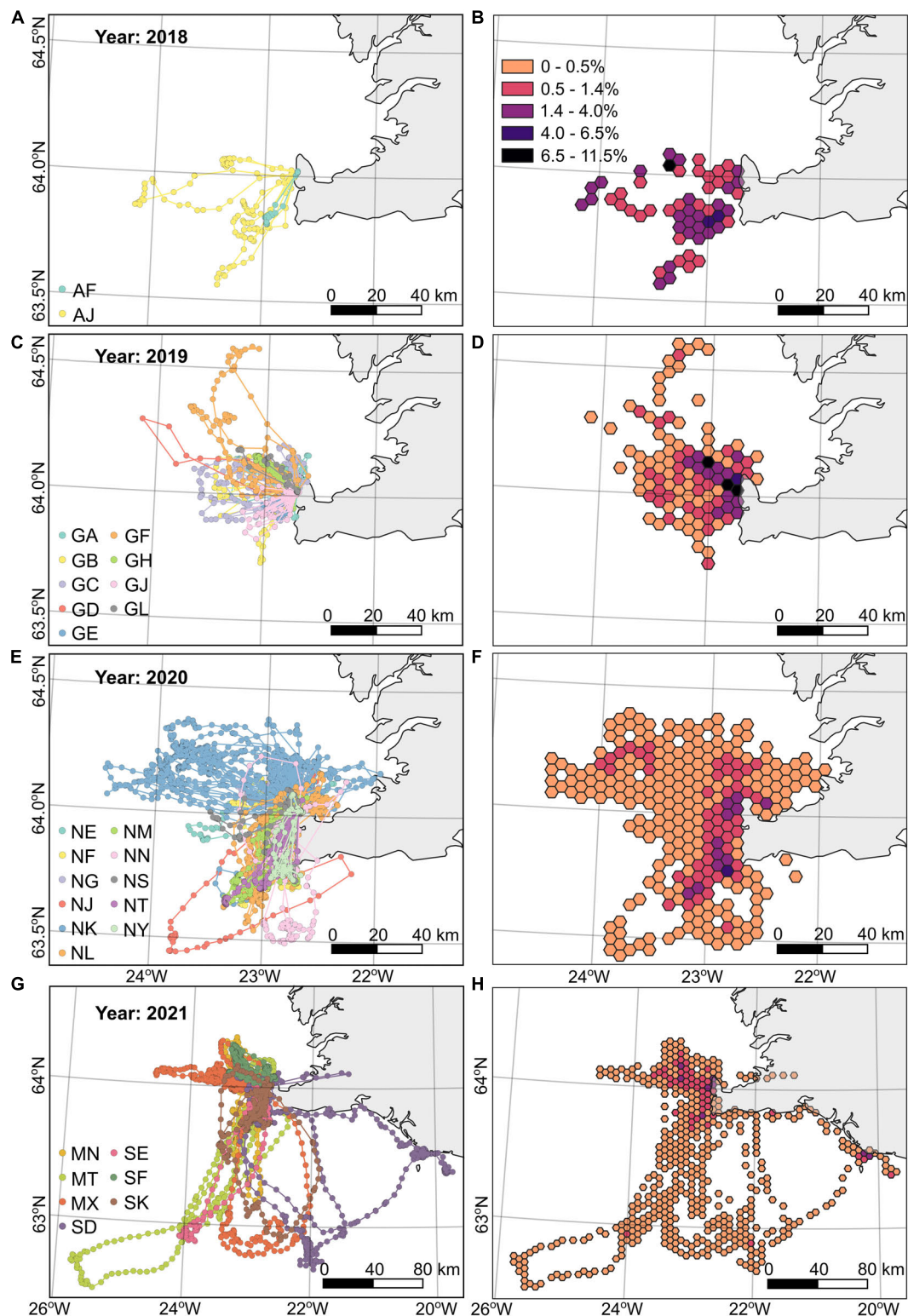
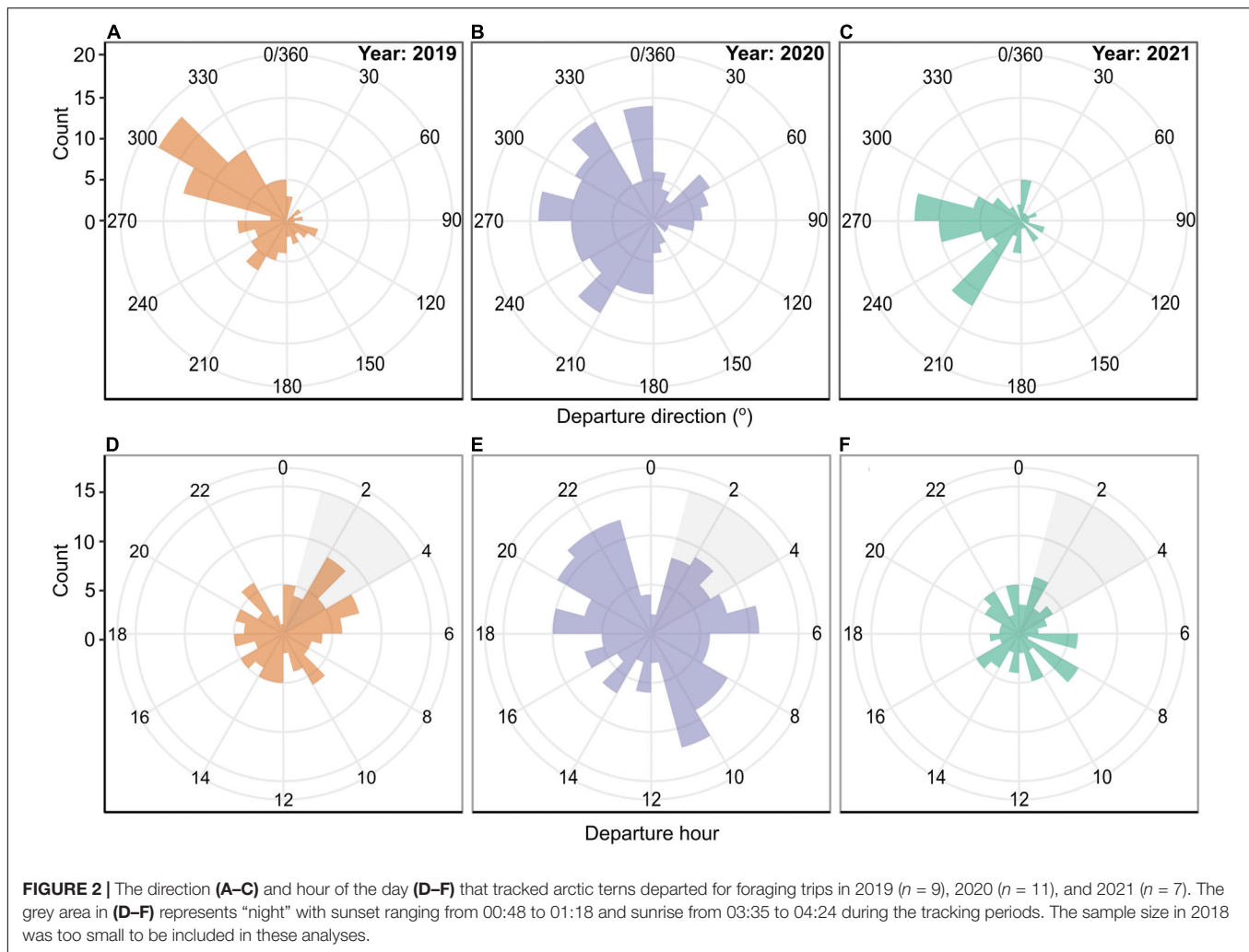


FIGURE 1 | Arctic tern foraging trips and location densities shown as hexbins in 5 km grids (cell area = 21.65 km^2 , short diagonal = 5 km; **B,D,F,H**) during four breeding seasons: (**A,B**) 2018, (**C,D**) 2019, (**E,F**) 2020, and (**G,H**) 2021 by 29 individuals ($n = 2$, $n = 9$, $n = 11$, and $n = 7$, respectively). The map extent in 2021 is larger due to the greater distances travelled in that breeding season. The projected coordinate reference system EPSG: 3057 is used.



(both controls and tagged with biologging devices) caught during each of the study years [$F_{(3)} = 20.86$, $p < 0.001$]. The mean mass of arctic terns captured in 2018 ($n = 73$, 105.4 ± 6.0 g) was significantly lower than terns captured in 2019 ($n = 144$, 110.5 ± 6.2 g) and 2020 ($n = 61$, 114.6 ± 8.7 g; Tukey's HSD $p < 0.001$, 95% CI = 2.5, 7.7 and $p < 0.001$, 95% CI = 6.0, 12.3, respectively). While there was no significant difference in mass, arctic terns captured in 2021 ($n = 36$, 107.4 ± 8.5 g) were significantly smaller than those captured in 2020 (Tukey's HSD $p < 0.001$, 95% CI = -11.0 , -3.4). There was also no significant difference between the square root transformed mean or log transformed maximum displacement distance that males and females travelled from the colony during foraging trips (t -test: $t = -1.44$, $p = 0.16$, and $t = -0.93$, $p = 0.365$, respectively).

The sizes of home ranges varied between individuals within years, with some foraging within much smaller areas (e.g., GA, GJ, NG, NY, SF) and others covering much larger areas (e.g., GB, GF, NE, NK, MT, SD; **Supplementary Table 2** and **Supplementary Figures 5–7**). The combined home range of tracked arctic terns with more than 5 foraging trips recorded in 2019 ($n = 6$; 50% AKDE 1136 km², 75% 2157 km², 95% 4309 km²) were 1.65 times

smaller than those tracked in 2020 ($n = 9$; 50% 1879 km², 75% 3562 km², 95% 7098 km²) and 15.9–18.2 times smaller than those tracked in 2021 ($n = 7$; 50% $20,677$ km², 75% $37,361$ km² and 95% $68,477$ km²; **Supplementary Table 2** and **Figures 3A,D,G,J**).

Impact of Wind Conditions on Foraging Behaviour

The wind speeds surrounding the Reykjanes peninsula (19.5 – 26° W and 62.5 – 64.6° N) during tracking device deployments were highest in 2018 and 2021 (median 8.1 and 8.3 m.s⁻¹, respectively), and lowest in 2020 [median 6.2 m.s⁻¹, compared with 6.8 m.s⁻¹ minimum power speed for arctic terns (Hedenström and Åkesson, 2016; **Figure 4**]. In 2018, 2019, and 2021, the average wind conditions experienced at the colony were westerly and faster compared to the average southerly and lower speed winds in 2020 (**Figures 4E–H**). Whilst foraging, the arctic terns encountered south westerly winds most often in 2019 (mean wind direction = 87.1°), with more occasional north easterlies (**Figure 5A**), compared to predominantly south easterly winds (mean wind direction = 330.5°) during foraging trips in 2020 (**Figure 5B**) and predominantly north westerlies with

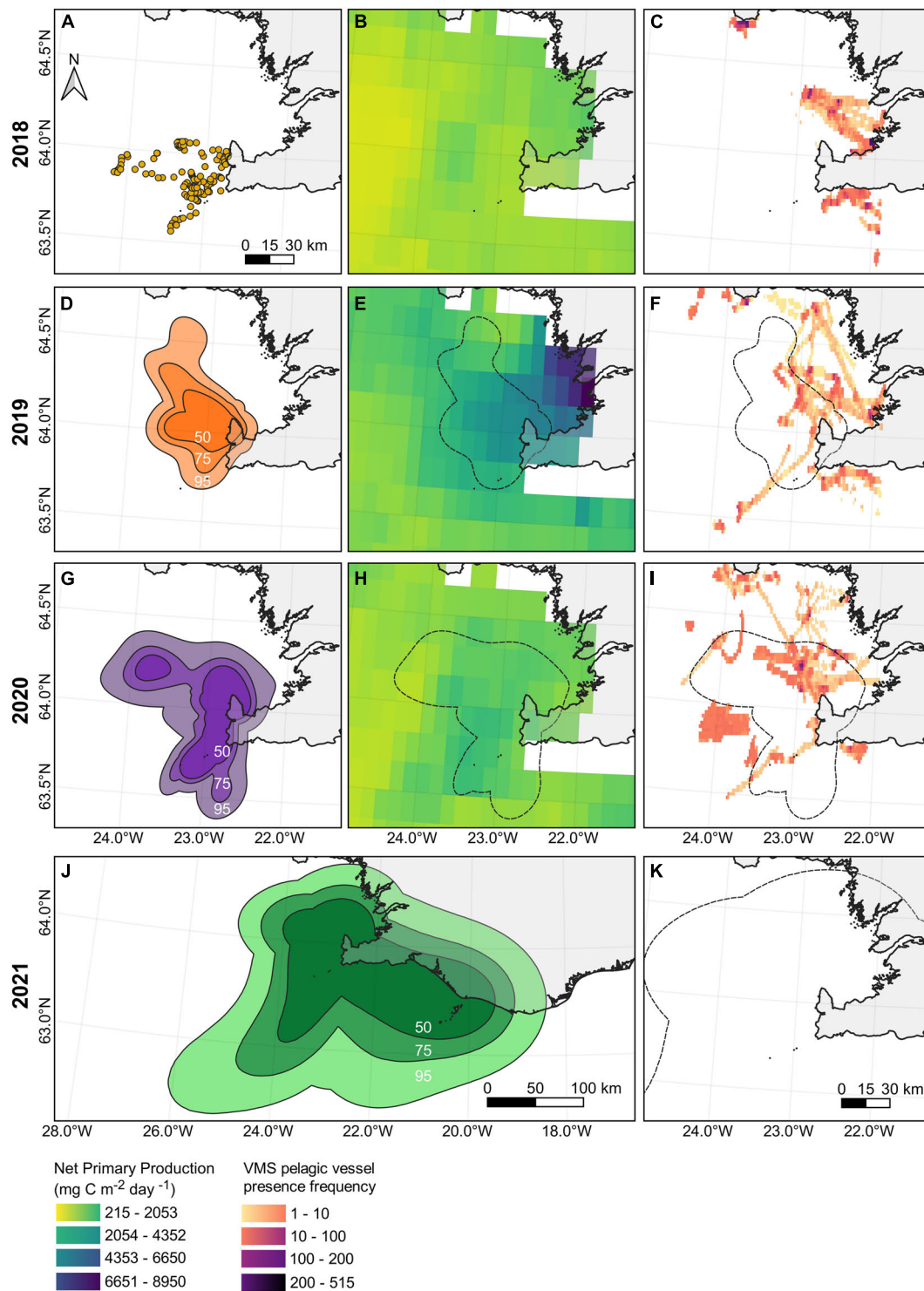


FIGURE 3 | Arctic tern locations, average monthly net primary productivity and fishing vessel locations in 2018 (A–C), 2019 (D–F), 2020 (G–I), and 2021 (J,H). The locations of arctic terns are shown in 2018 (A). In 2019 (D), 2020 (G), and 2021 (J), when there were larger sample sizes, automated kernel density estimations were calculated with the estimated isopleth sizes shown. The monthly average net primary productivity levels in June 2018 (B), 2019 (E), and 2020 (H) (estimated by Ocean Productivity Oregon State, 2021) are plotted on a grid with 100 degree resolution. Net primary productivity data were unavailable for 2021. Pelagic fishing intensity during June 2018 (C), 2019 (F), 2020 (I), 2021 (K). Arctic tern 95% isopleths are overlaid on the fishing data as dashed lines. The projected coordinate reference system EPSG: 3057 is used.

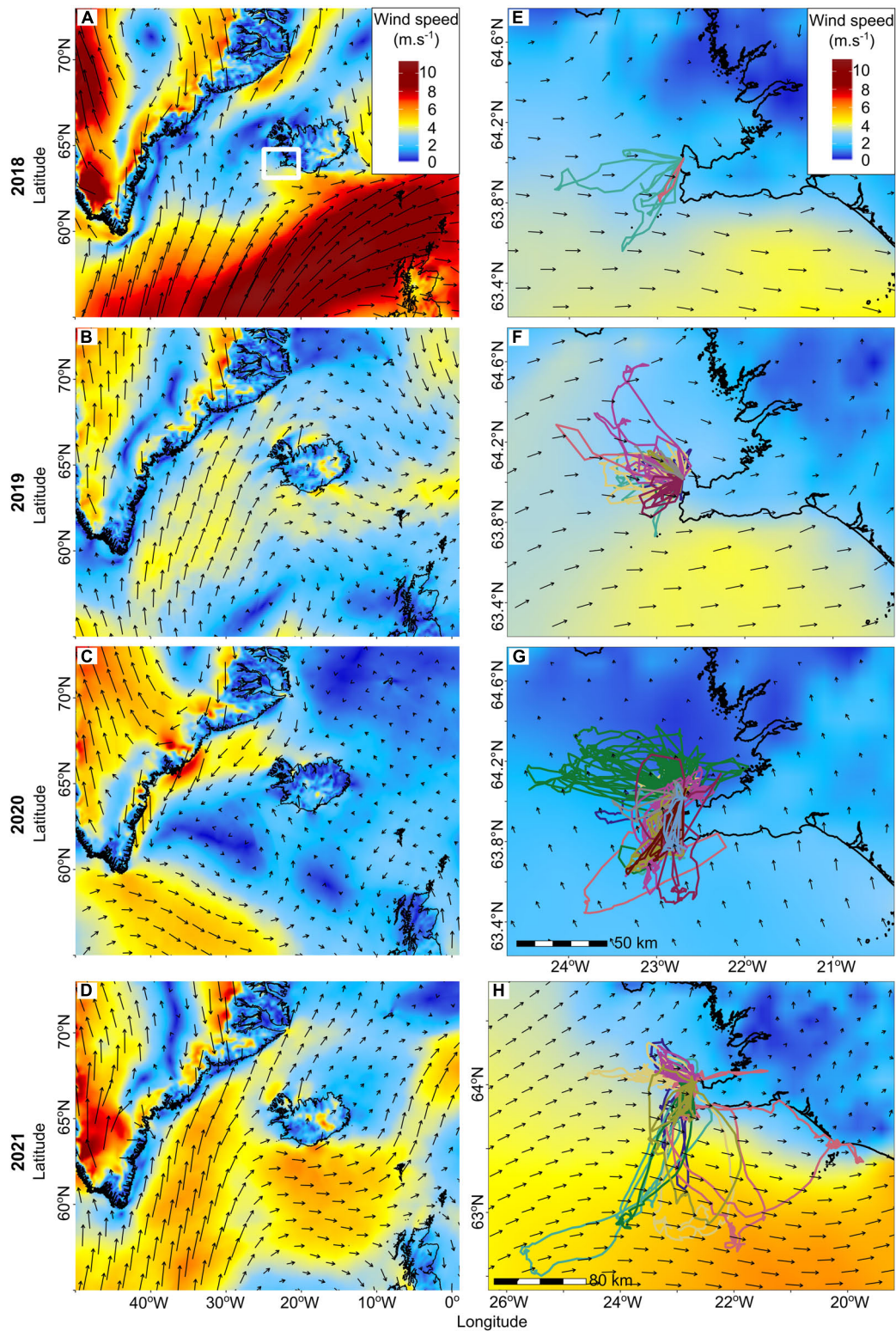
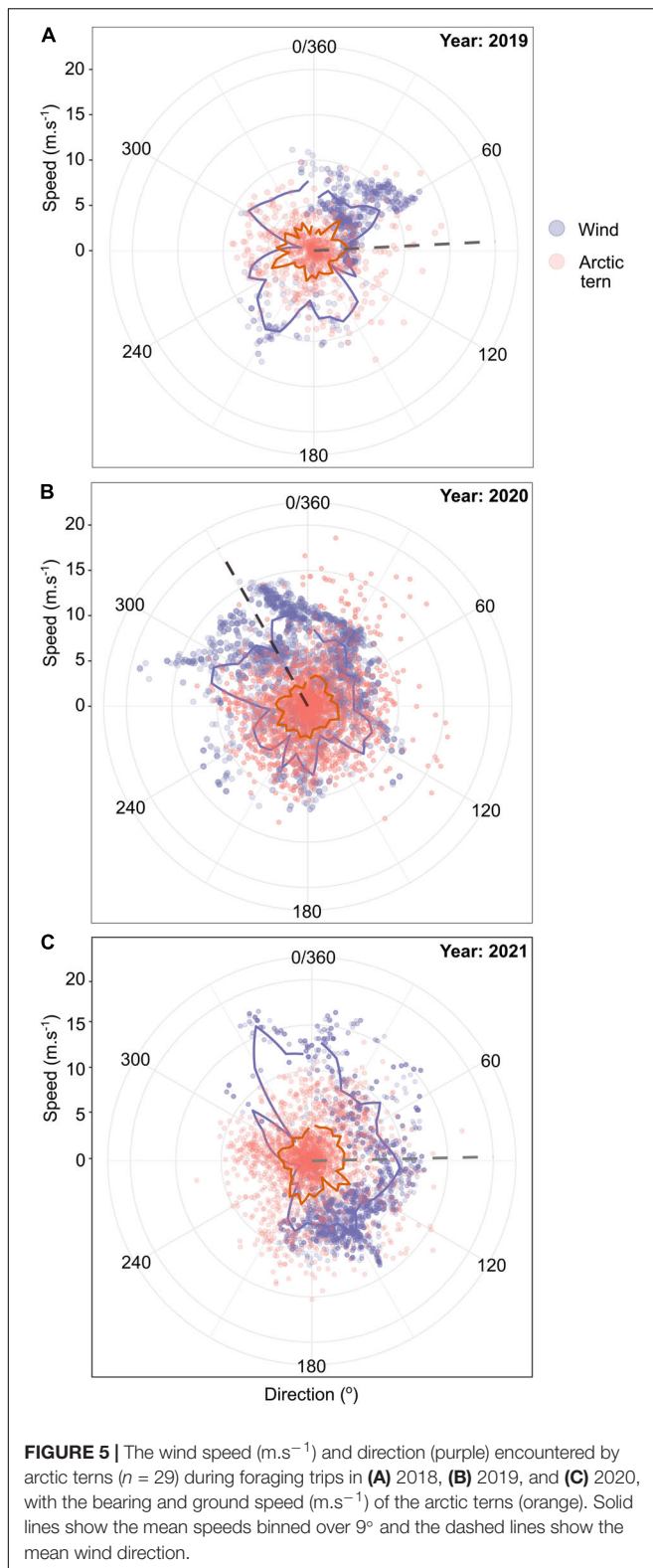


FIGURE 4 | Modelled mean wind speed and direction at 50 m altitude in the wider area around Iceland (A–D) and surrounding an arctic tern breeding colony (E–H). Arctic terns were tracked in 2018 (A,E), 2019 (B,F), 2020 (C,G), and 2021 (D,H) and the wind data were averaged for the duration of the tracking periods [17/06–23/06/2018 (6 days), 20/06–30/06/2019 (10 days), 10/06–09/07/2020 (29 days), 17/06–28/06/2021 (11 days)]. All recorded arctic tern foraging trips are shown (D–F), with colours corresponding to different individuals. The map extent in (H) is larger due to the greater distances travelled in that breeding season.



occasional south easterlies in 2021 (mean wind direction = 88.7° ; **Figure 5C**). Despite the wind being close to the minimum power speeds (most efficient forward flight speed) for arctic terns, there

was no evidence that they adjusted their direction of travel in relation to wind (**Figure 5**) and the ground speed travelled during foraging trips was not strongly correlated with the wind speed [repeated measures correlation 2019: $r(104) = -0.13$, $p = 0.19$, 2020: $r(171) = -0.08$, $p = 0.27$, 2021: $r(79) = -0.29$, $p = 0.01$; **Supplementary Figure 8**]. When the outbound and return sections of foraging trips were considered separately the relationship between arctic tern ground speed and wind speeds were either not significant, or had very weak negative correlations [repeated measures correlation 2019: $r(97) = -0.04$, $p = 0.67$ (outbound), $r(70) = -0.21$, $p = 0.08$ (return), 2020: $r(163) = -0.22$, $p = 0.01$ (outbound), $r(132) = -0.05$, $p = 0.6$ (return), 2021: $r(78) = -0.29$, $p = 0.01$ (outbound), $r(63) = -0.20$, $p = 0.1$ (return); **Supplementary Figure 9**]. Likely air speeds for the arctic terns ranged from 0.14 to 24.63 m.s^{-1} , with a mean (\pm standard deviation) of $9.04 (\pm 3.52) \text{ m.s}^{-1}$. However, these should be interpreted with caution because the temporal (hourly) and spatial ($\sim 10 \text{ km}$) resolution of the modelled wind data was much coarser than the bird data (every 15 min).

Use of Productive Areas: Net Primary Productivity and Overlap Between Arctic Terns and Fishing Vessels

Of the 3 years with available NPP data (2018–2020), the monthly average of NPP in June was greatest in 2019 (**Figures 3B,E,H**). In 2019 the most productive areas were toward the north and north east of the colony, whereas in 2020 the more productive areas were west and south west of the colony. Vessels fishing in pelagic waters surrounding the colony area (to the south west of the Reykjanes peninsula) generally remained within the Faxaflói bay area, with some fishing activity occurring to the south west of the Reykjanes peninsula (**Figures 3C,F,I,K**). Although the tracked arctic terns were recorded visiting different areas during the four study years, the vessels consistently targeted similar locations, and for the most part these did not overlap with the home ranges of the tracked arctic terns (**Figure 3**). There were fewer pelagic vessel locations recorded over the same time period and area in 2021 compared to the other three study years (2018: 8895 locations, 2019: 6675 locations, 2020: 9130 locations and 2021: 2100 locations). During the four study years, the percentage of arctic tern locations within close proximity to actively fishing pelagic vessels (within 1 km and 1 h) was 0, 0, 1, and 0%, respectively. This increased marginally if the spatio-temporal proximity was extended to 2 km and 6 h (0, 0.94, 10.4, and 0%). Based on the pelagic fishing activities identified through the AIS and VMS data, arctic terns appear to be for the most part, searching and foraging in different areas to fishing vessels.

DISCUSSION

This study provides the most comprehensive analysis of intra-breeding season foraging behaviours of arctic terns to date. Using biologging tags, we have been able to record arctic tern trips over multiple seasons and investigate the impact of wind conditions and fishing activity on their behaviour.

Foraging Behaviour

It is likely that the distances and home ranges that we report here reflect the space use of arctic terns breeding elsewhere in Iceland as Seward et al. (2020) reported that the home ranges of GPS tagged and non-GPS tagged arctic terns were comparable. Indeed, if there is an effect of carrying the device on the birds (Geen et al., 2019; Tomotani et al., 2019), we might expect other arctic terns to travel even further without the burden of a tracking tag. Additionally, with a resolution of a location every 900 s, the foraging distances that we report could be an underestimate of the actual distances travelled.

Mean foraging distances from the colony were 27–34 km, longer than the average distances reported in previous studies. The maximum displacement distances recorded in this study were also much greater; and the furthest distance any tern that did not abandon its breeding attempt travelled was 141 km, with nineteen terns travelling more than 40 km from the colony to forage. The shorter foraging distances reported elsewhere could be related to the ability of prior observers to physically follow terns so far offshore. Black and Diamond (2005) and Rock et al. (2007) both recorded trips with radio telemetry and limited searches to within 20–30 km from the colony, whilst Perrow et al. (2011) visually tracked foraging arctic terns and reported a maximum of 29 km from the colony. Although we only report the distances travelled during incubation in this study, this is unlikely to account for the differences in trip distances reported in previous studies as terns were tracked at a variety of incubation stages, from unknown breeding stages to during both incubation and chick rearing. During egg incubation most seabirds generally have larger foraging ranges compared to during chick rearing (Oppel et al., 2018). For example, red-billed tropicbird *Phaethon aethereus* foraging trips were longer and further during incubation compared to chick rearing, when adults likely fed in less profitable areas closer to the nest (Diop et al., 2018). Although the distance and duration of trips by brown skuas *Stercorarius lonnbergi* did not vary during brooding stage, they made fewer foraging trips whilst incubating, and whilst chick rearing skuas fed in areas with more varied prey resources (Carneiro et al., 2014). Thus, it is possible that Icelandic arctic terns may forage over a smaller range during chick rearing, but it was not possible to investigate this during the present study, as recapture of tags once the chicks hatched and moved away from the nests was not possible at this colony.

The total area across which arctic terns foraged (average 95% isopleth area) was 16–218 times larger than reported by Robertson et al. (2014b) who tracked terns visually. Visually tracking arctic terns in boats appears to lead to smaller utilisation distributions than studies using tracking devices (Seward et al., 2020). However, arctic terns carrying GPS tracking devices in the Skerries, Wales also had smaller mean estimated home ranges (half to one fortieth of those recorded in this study) (Seward et al., 2020). The smaller home ranges reported in Wales compared to those we recorded in Iceland could be a result of tracking terns during chick rearing, restrictions by land masses, or interspecific competition with other tern species reducing foraging areas due to resource or niche partitioning (Robertson et al., 2014b).

Many species of foraging seabirds associate with shelf breaks due to a concentration of prey at these upwelling or front regions (e.g., Freeman et al., 2010; Amelineau et al., 2016). However, there are no obvious differences in the shelf depth or extent between arctic tern colonies from which birds have been tracked so far, suggesting in this case bathymetry is not likely to be the major explanatory variable for the far greater foraging trip distances reported here. Alternatively, prey abundance and distribution may differ between these colonies. For example, the duration of foraging trips recorded for breeding kittiwakes *Rissa tridactyla* using GPS tags were double the length compared to those recorded 11–49 years earlier using activity loggers or field observations, possibly linked to changes in food availability (Redfern and Bevan, 2014). Electronic tracking of arctic terns from the aforementioned colonies may reveal if foraging ranges are truly smaller than arctic terns in Iceland, or if differences in methodology could explain the difference.

Regardless of the underlying causes of these greater reported foraging ranges, there are notable conservation and management implications across arctic tern breeding ranges. Incorporating available movement ecology data into policy and management strategies is an important conservation measure (e.g., Allen and Singh, 2016; McGowan et al., 2017; Oppel et al., 2018). Any protection measures around arctic tern colonies must consider the larger spatial scale that they use during the breeding season. For example, although some European offshore wind farms are within previously reported arctic tern foraging ranges, the average distance to shore of wind farms under construction in 2020 was 44 km (Wind Europe, 2021), a distance previously thought to be outside arctic tern foraging ranges. The data in the present study suggests this may not always be the case.

Contrary to previous suggestions that arctic terns are exclusively diurnal foragers (McKnight et al., 2013), we recorded arctic terns making foraging trips at the breeding colony throughout the 24 h cycle, but with fewer trips in the 2 h preceding sunset at 01:00. However, we note that during the breeding period, there is just 154–161 min between sunrise and sunset, meaning that the terns nesting in southwest Iceland never experience complete darkness. Indeed, arctic terns experience some of the greatest periods of light exposure, as they annually migrate between the boreal and austral summers (Sockman and Hurlbert, 2020). Flexibility in foraging behaviour has been recorded in other visual predators. For example, common guillemots *Uria aalge* will forage at night using moon or star light to locate prey, with shallower dives in the latter when the light levels are lower (Regular et al., 2011). Across their range Cory's shearwaters *Calonectris diomedea* display either diurnal or nocturnal foraging behaviours depending on the water temperature and depths, with diurnal foraging in warmer and shallower waters (Dias et al., 2012). Phenotypic plasticity in various aspects of foraging behaviour, such as prey switching or temporal changes, improve population resilience to global changes (e.g., Grémillet et al., 2012).

We found no relationship between individual size or sex and the distances travelled during foraging trips, suggesting that extrinsic rather than intrinsic factors are more likely to impact arctic tern foraging behaviour. This is further supported by

the generally lower mass of individuals in 2021 compared to 2019 and 2020. If, for example, prey were less abundant, had lower profitability, or the distribution had shifted in 2021, then foraging arctic terns may have had to travel further to reach their daily energy intake requirements. However, to investigate this we would require detailed information on the prey captured or record the mass change at the start and end of a foraging trip, but it was not possible to collect these data during this study. It is also possible that a combination of extrinsic and intrinsic factors affect arctic tern foraging trip metrics, but these were not detected due to the small sample size of tracked individuals (which was biased toward heavier individuals), and that foraging behaviours were only monitored during the egg incubation stage. Foraging conditions prior to egg laying or during incubation affect breeding success (such as reduced clutch size, or even increased adult mortality; Suddaby and Ratcliffe, 1997) and it is therefore likely that in years with low prey abundance only individuals with greater body condition were tracked, as tags were deployed on birds with eggs at least one third through incubation. Additionally, differences in the foraging behaviours of sexually monomorphic seabird species have been reported in multiple seabird families (e.g., Lewis et al., 2002; Thaxter et al., 2009; Welcker et al., 2009; Hedd et al., 2014; Clark et al., 2021) but can vary with the breeding stage. Foraging niche segregation by sex may therefore exist in arctic terns during other breeding stages, but currently we were only able to collect data during incubation as terns can only be reliably recaptured (to remove biologging tags at the conclusion of the study) on their nest. It is also possible that other intrinsic and extrinsic variables that did not affect foraging behaviours during incubation may alter behaviour during later breeding stages when the adults may travel shorter distances from the colony (e.g., Weimerskirch et al., 1993; Barlow and Croxall, 2002; Robertson et al., 2014a), and are limited to carrying one prey item at once (Hatch, 2002).

Impact of Wind Conditions on Foraging Behaviour

During the breeding season arctic terns are central place foragers and need to return to their nest after every trip, meaning that any deviations caused by winds need to be countered with adjustments to flight speeds and heading, which is likely to occur through visual cues as the terns are close to the colony (Hedenström and Åkesson, 2016). However, in this study we found limited effects of wind conditions impacting arctic tern flights during foraging trips. This might have been because terns were compensating in other ways that we were unable to detect with the temporal resolution of the tracking tags. For example, by altering pre-dive flight behaviours in strong winds (e.g., Forster's terns *Sterna forsteri* change from hovering to undulating flights; Salt and Willard, 1971), by increasing wing beat strength and air speed when flying into headwinds (e.g., European shags *Phalacrocorax aristotelis*; Kogure et al., 2016), or by spending longer foraging and diving more frequently in stronger winds due to altered prey visibility (e.g., Northern gannets *Morus bassanus*; Lane et al., 2019). Higher resolution tracking in the future, or

use of alternative devices such as accelerometers to determine wing beat frequency could determine how arctic terns may adjust flight behaviours in response to wind conditions. Alternatively, wind conditions that the tracked arctic terns encountered during the breeding season are much weaker compared to the winds they experience during the non-breeding season in the Southern Ocean (**Supplementary Figure 10**) and may therefore pose little relative challenge.

Our results indicate that arctic terns foraged in different areas in 2019, 2020, and 2021. They foraged more to the north-west and west in 2019 when the winds were stronger and in a westerly direction, they foraged toward the south-east in 2020 when the winds were weaker and more south to south westerly, and foraged far greater distances in 2021 to the west, south west, south and south east when the winds were strong and north westerly to westerly. Although the wind conditions did not appear to affect the arctic tern flights, the difference in foraging areas between the three years suggests that wind may still act indirectly on terns, perhaps as a driver of coastal circulation patterns affecting upwelling. Thus, the speed, direction and duration of wind could impact prey species distribution and abundance, particularly in the shallowest surface waters where arctic terns feed (e.g., Sætre et al., 2002; Mills et al., 2008; Bakun et al., 2015; Wilson and Laman, 2021). Additionally, there could be other extrinsic factors that we did not record that could influence foraging locations. Collins et al. (2020) reported that prey availability was more likely to affect black-legged kittiwake *Rissa tridactyla* foraging trip timing and direction than the wind conditions, and during short foraging trips any benefit gained from tailwind support will be countered by travelling into headwinds during the reverse journey.

Use of Productive Areas: Net Primary Productivity and Overlap Between Arctic Terns, and Fishing Vessels

Arctic terns are not thought to be susceptible to fisheries bycatch (Żydelis et al., 2013) and are generally not observed following fishing vessels (e.g., Garthe and Hüppop, 1994; Weimerskirch et al., 2000), although they have been recorded scavenging shrimp discards (Walter and Becker, 1998). In Iceland however, the practice of discarding by-catch is banned (Condie et al., 2014) so any overlap between pelagic fishing vessels and foraging arctic terns should be due to targeting the same productive areas, rather than the terns following vessels for discard. We found very little overlap between the areas that pelagic vessels were fishing and the areas that the breeding arctic terns were foraging, and further while the vessels consistently foraged in the same locations between the four study years, the terns changed their foraging locations, perhaps indicating that they are able to adapt to moving prey resources and locate areas with higher NPP levels. In 2019, the study year with the greatest monthly average NPP levels, tracked arctic terns had the smallest home ranges. This suggests that their foraging ranges may be likely to increase in years with lower productivity, although this is based on a small number of years with tracking data so may warrant further investigation.

Whilst in southwest Iceland there doesn't appear to be an overlap between fishing vessels and the breeding arctic terns, future monitoring of seabirds during the breeding season can be used to inform fisheries management (Einoder, 2009) and identify areas that are important for marine predators like seabirds. Additionally, further investigations of prey patch dynamics and any between year variations are warranted to better understand the energy landscape for arctic terns and other species foraging in this region.

CONCLUSION

In this study we have demonstrated that during the egg incubation stage, arctic terns travel much further out to sea to forage than previously recorded. They are still bound within 220 km of their breeding site, with average foraging trip distances of 36 km. During later breeding stages they are likely to be even further restricted in the distances that they travel, so local prey availability will have a profound impact on their success or the choice to abandon the breeding attempt. Vigfúsdóttir et al. (2013) concluded that a key issue causing low fledging success in arctic terns breeding in Iceland was food shortages and if this is the case, we have demonstrated that poor fledging rates are likely not as a result of directly competing for prey with commercial fisheries, but could, however, be due to changes in climatic forcing factors altering ocean structuring and overturning, with knock-on effects for ocean productivity and subsequent prey distribution (Hoegh-Guldberg and Bruno, 2010; Doney et al., 2012; Sydeman et al., 2015; Edwards et al., 2021). We also show that changes in wind strength and direction are unlikely to directly affect arctic terns, but further investigations are warranted both in Iceland and other areas where the breeding successes of arctic terns are poor in order to establish the underlying causes of population declines. With the continual developments of tracking technologies, it is vital to continue unravelling the foraging behaviours of arctic terns at colonies, prioritising the chick-rearing and post-fledging behaviours that are still little understood.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

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ETHICS STATEMENT

The animal study was reviewed and approved by the University of Exeter Ethics Committee (ethics ID eCLESBio000180).

AUTHOR CONTRIBUTIONS

LH, SM, and FV conceived the study. JM, LC, SM, E-JM, NP, FV, MW, and LH contributed to data collection. JB provided fisheries data. WT, MW, and LH supervised the research. JM analysed the data and prepared the first draft. All authors revised the first draft and worked on the final version of the article.

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SUPPLEMENTARY MATERIAL

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Western Gull Foraging Behavior as an Ecosystem State Indicator in Coastal California

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With accelerating climate variability and change, novel approaches are needed to warn managers of changing ecosystem state and to identify appropriate management actions. One strategy is using indicator species—like seabirds as ecosystem sentinels—to monitor changes in marine environments. Here, we explore the utility of western gulls (*Larus occidentalis*) breeding on Southeast Farallon Island as a proxy of ecosystem state in coastal California by investigating the interannual variability in gull foraging behavior from 2013 to 2019 in relation to upwelling conditions, prey abundances, and overlap with humpback whales (*Megaptera novaeangliae*) as gulls frequently feed in association with whales. Western gulls have a flexible diet and forage on land and at-sea. We combined gull GPS tracking data during the incubation phase, ecosystem survey data on multiple predator and prey species, and derived oceanographic upwelling products. When foraging at sea, gulls overlapped with cool upwelled waters. During 2015–2017, 25% more gull foraging trips visited land than in other years, where land trips were on average ~8 h longer and 40% further than sea trips, which coincided with high compression of coastally upwelled waters (habitat compression) in 2015–2016. Gull foraging behavior was related to local prey abundances, where more foraging occurred near shore or on land when prey abundances were low. However, visual surveys indicated that ~70% of humpback whale observations co-occurred with gulls, and the year with the most foraging on land (2017) corresponded to regionally low relative whale abundances, suggesting gull movement patterns could be an indicator of whale presence. Further, both whales and gulls forage near-shore under high upwelling habitat compression and low krill abundance. Hence, the deployment of year-round tags on gulls with the capability of near real-time data accessibility could provide important fine-scale metrics for conservation and management of the threatened yet recovering eastern Pacific humpback whale population between infrequent and coarse surveys. Entanglement in fishing gear and ship strikes are major inhibitors to whale recovery and

have increased concomitantly with human use of ocean resources. Moreover, as climate variability and change increase, novel indicators should be explored and implemented to inform marine spatial planning and protect species across multiple scales from new risks.

Keywords: ecosystem indicator, predator-prey, foraging ecology, humpback whale, biologging, entanglement, upwelling, marine heatwave

INTRODUCTION

Ecological indicators can be used to assess ecosystem state, such as indicator species that are easy to monitor, respond to a stressor in a predictable way, and can be used to guide management actions (Dale and Beyeler, 2001; Siddig et al., 2016; Samhouri et al., 2017). Seabirds are near the apex of most marine food chains and thus, many are well known as ecosystem sentinels to monitor changes in marine environments (Durant et al., 2009; Hazen et al., 2019; Grémillet et al., 2020; Sydeman et al., 2021). For example, seabird foraging behavior, breeding phenology, breeding success, diet, population, and body condition can be indicative of the productive capacity of ecosystem states (Durant et al., 2009; Sydeman et al., 2021). Long-term monitoring of seabirds can be accomplished using different methodologies: demographic monitoring at breeding colonies, biologging as a means to characterize movement and distribution, and at-sea visual surveys. Each approach provides different, but often complementary information on the annual status of a population. Analyzed separately, demographic monitoring provides no information of at sea distributions, biologging distribution data is often limited to a small number of individuals, and at-sea surveys provide population-level distribution data but are only a snapshot in time. However, when evaluating the utility and potential effectiveness of a seabird species indicator, the power of compiling information from different monitoring approaches may provide a more holistic ecosystem view.

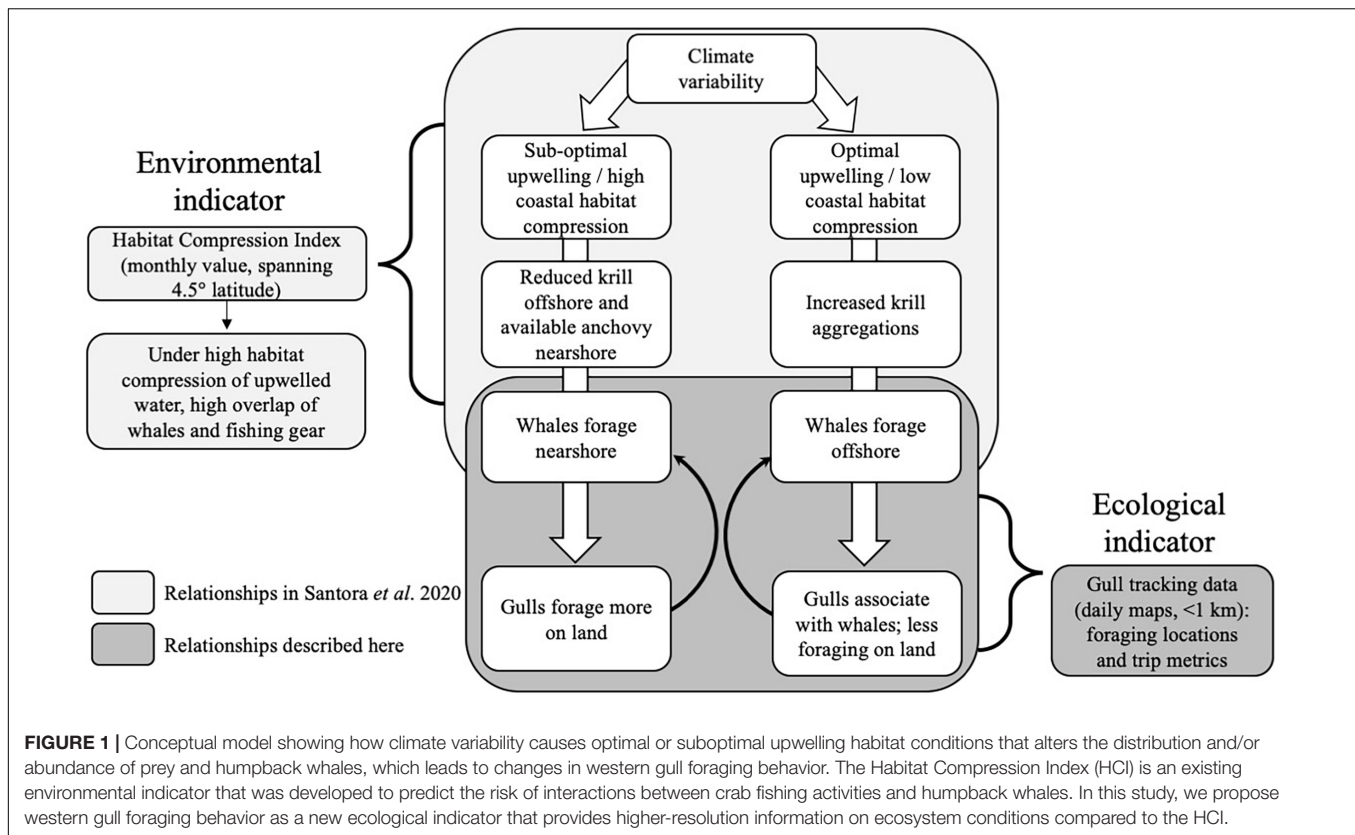
Novel ecosystem-based management approaches such as indicators and dynamic ocean management tools are increasing in use in the California Current region to understand various interacting factors that threaten species survival. For example, through the California Current Integrated Ecosystem Assessment (CCIEA¹), a variety of environmental, biological, economic, and social indicators are publicly available (Harvey et al., 2020). In addition, there are operational dynamic ocean management tools [e.g., EcoCast (Hazen et al., 2018; Welch et al., 2020), WhaleWatch (Hazen et al., 2017; Abrahms et al., 2019), and TOTAL (Welch et al., 2019)], aimed at protecting key species from human activity or other ecosystem stressors. Many of these tools provide either an annual index, or the resolution of the mapped data is limited by satellites or models (days to months, 10–25 km). As climate change and variability are amplified, indicators at higher spatiotemporal scales that improve predictability are increasingly necessary (e.g., days to weeks, ≤ 10 km). The foraging locations and trip characteristics of tracked animals, such as seabirds, can

resolve key fine-scale oceanographic or predator-prey dynamics that, in conjunction with current ecosystem indicators, can improve our understanding of ecosystem state for management. For example, seabird hotspots from multispecies tracking data can inform marine protected area design (Davies et al., 2021). Thus, considering additional indicators is critical as increased variability in ecosystem conditions has led to surprises in ecological interactions and a recognition that new approaches are needed for effective management (Santora et al., 2020).

A particularly concerning issue in the California Current system is severe whale injury or mortality as a result of entanglements in fishing gear and ship strikes (Williams and O'Hara, 2010; Redfern et al., 2013; Rockwood et al., 2021). With the urgent need to utilize ecosystem data to advise marine resource management, working groups were established to develop mitigation strategies and understand drivers of increased whale entanglement (Santora et al., 2020; Feist et al., 2021; Ingman et al., 2021) and ship strikes (Hazen et al., 2017; Abrahms et al., 2019; Blondin et al., 2020; Rockwood et al., 2020). Specifically, humpback whales (*Megaptera novaeangliae*) can shift between onshore and offshore foraging habitats depending on prey availability driven by upwelling conditions (see Figure 1). Shoreward upwelling habitat compression can lead to nearshore foraging and intensify the overlap between whales and nearshore crab fishing gear (Santora et al., 2020). Thus, a monthly habitat compression index (HCI), the areal extent of cool upwelled water, aids in understanding the risk of interactions between fishing activities and humpback whales. However, the HCI was not designed to capture the fine-scale spatiotemporal dynamics of whale distributions given it is calculated monthly integrated over 4.5° latitude, suggesting the development of other high-resolution indicators would be useful.

Seabirds and cetaceans often associate at sea, either through overlapping spatial distributions when targeting the same foraging habitats (Yen et al., 2004; Cox et al., 2018; Sutton et al., 2019), or by maximizing foraging efficiency when feeding together (Harrison, 1979; Ballance et al., 1997; Maxwell and Morgan, 2013). In these feeding associations, seabirds are the likely beneficiaries as cetaceans make food more accessible by driving prey that is typically out of reach toward the surface and sometimes concentrating prey into tight groups (Evans, 1982). Gulls are one species known to benefit from associating with whales (e.g., Harrison, 1979; Haynes et al., 2011; García-Cegarra et al., 2020) because they are only capable of shallow plunge dives (Henkel, 2009). In particular, western gulls (*Larus occidentalis*) are regionally abundant throughout coastal California and Oregon, spanning the range of biologically productive waters known for high cetacean biodiversity and are anecdotally known

¹ <https://www.integratedecosystemassessment.noaa.gov/regions/california-current>



to associate with whales. When breeding, western gulls are central place foragers with high repeatability in foraging locations, a capacity to respond quickly to changing conditions due to relatively high flight speeds, and they often feed in aggregations when attracted by social facilitation (Shaffer et al., 2017). Their adaptability is also related to being a generalist carnivore, feeding on a diversity of forage species while at sea and exploiting human refuse when feeding at landfills and urban centers (Annett and Pierotti, 1989; Annett and Pierotti, 1999; Cassell, 2016; Shaffer et al., 2017). Conservation strategies building upon seabird-cetacean feeding associations have been suggested (Veit and Harrison, 2017), but these common multi-species associations have not been explored as an ecological indicator.

Here, we examined the movement patterns and distribution of western gulls to evaluate their utility as an indicator of ecosystem state and specifically humpback whale presence in coastal central California. Humpback whales migrate through central California to feed on krill and forage fish historically during the late summer/fall upwelling season (Calambokidis et al., 2000) but currently arrive in the Farallon Island region in May/June, nearly 4 months earlier than during the early 1990s (Ingman et al., 2021). This time period overlaps with the incubation and chick rearing phases of western gulls breeding at the Farallon Islands. Using multiple years of high-resolution tracking data from incubating western gulls, we characterized interannual variability in foraging behavior (e.g., foraging at sea vs. on land, trip distance and duration) in relation to: (1) upwelling conditions, (2) prey abundances, and (3) humpback whale presence. We combined

gull tracking data with ecosystem assessment surveys that monitor predator and prey species abundances and upwelling conditions derived from an oceanographic model. Ultimately, the ecosystem relationship between predator-prey-oceanographic interactions (see Figure 1) allowed us to test whether western gull foraging movements and distributions could serve as an indicator of ecosystem conditions and humpback whale feeding aggregations in an effort to minimize negative human impacts on this threatened species. We aim to show that gull foraging behavior can provide a high-resolution, near-real time indicator of where and when whales may be foraging or switching their distributions to nearshore regions (indicating a shift in ecosystem state, see Figure 1) where entanglement or ship collision is more likely to occur. Combining multiple data streams leads to a better understanding of indicators, and more robust conservation and planning approaches.

MATERIALS AND METHODS

Western Gull Tracking and Data Processing

Western gulls were studied at Southeast Farallon Island (37.697N, -123.001W), within the Farallon Islands National Wildlife Refuge, located 45 km from the coast of San Francisco, California, United States. Southeast Farallon Island is one of the largest seabird breeding colonies in the Eastern Pacific and has the largest breeding population of western gulls in California (Ainley,

1990). In addition to this region containing important seabird habitat, the San Francisco Bay area contains a large port with high shipping and fishing traffic, high humpback whale density, and is a hotspot for the commercial Dungeness crab (*Metacarcinus magister*) fishery—the largest fixed-gear fishery in central California (Feist et al., 2021).

Birds were captured using noose mats or a single foot snare during the incubation phase of breeding between mid-May and early June of each year in 2013–2019 (see Shaffer et al., 2017; **Table 1**). Their breeding phenology at this colony is remarkably consistent (Sydeman et al., 1991). Western gull pairs exchange incubation duties where one individual forages, while the mate remains at the nest to incubate and protect the eggs. Each gull was captured twice at their nest, once to deploy a GPS logger and again 2–6 days later for logger recovery. A total of 133 adults (**Table 1**) were equipped with a GPS data logger (20-g iGotU GT-120 or 32-g GT-600, Mobile Action Technology, Taiwan) that recorded location data at 1–2 min intervals (spatial accuracy 3–4 m, manufacturer specifications). GPS loggers were encased in adhesive-line heat shrink tubing and attached to the base of 4–5 central tail feathers using Tesa tape for a total package that was < 3% of body mass (Shaffer et al., 2017). Only large (1,100 g) male gulls were tracked using the 32-g GPS loggers.

GPS location data were filtered using a speed algorithm to remove erroneous positions (<0.01% of data) based on a maximum flying speed of 70 km h⁻¹ (Shaffer et al., 2017), and tracks were linearly interpolated to a standardized 2-min interval. We processed the data into individual trips using the R package *track2KBA* (Lascelles et al., 2016; Beal et al., 2020) and we only considered complete trips that started and returned to the colony, were >30 min in duration, and >1 km away from the colony because gulls can make short trips offshore to drink or rest.

Foraging trip metrics included the maximum linear distance from the colony, total travel distance over a trip, and trip duration measured as the total time outside of a 1 km buffer from the colony (Shaffer et al., 2017). Within trip activity patterns were categorized into periods of transiting (travel speeds >6 km h⁻¹ between consecutive locations) and stationary (travel speeds <6 km h⁻¹ between consecutive locations) where stationary periods that were ≥4 min (two GPS fixes or interpolated locations) were assumed to be foraging events (following Shaffer et al., 2017). For each foraging event within a trip, we calculated the mean location and duration of event. In addition, we determined whether foraging events occurred at sea or on land by matching all foraging events to bathymetry/elevation data. Ocean trips were classified as any trip that did not overlap with land. A “land trip” was classified as any trip where a gull overlapped with land (elevation ≥0 m). We also determined whether gulls foraged within 5 km of the shoreline (i.e., relatively “nearshore”) or within 3 km of a landfill—reflecting the average size of landfills² at ~2.5 km². These trip characteristics were all used as potential gull foraging indicators. All analyses in this study were performed in R (R Core Team, 2020).

Tracking data were summarized by year to investigate interannual variability in gull behavior including trip duration, total distance traveled, maximum linear distance from colony,

and the proportion of foraging events by trip at sea, nearshore, and near a landfill (means ± SD were calculated by individual and then year); and the distribution of the proportion of foraging events on land by trip was determined to show the spread of the data. To determine if there were statistically significant differences in trip characteristics between years, we used linear mixed-effects models (for trip duration, total distance, and maximum linear distance) and generalized linear mixed-effects models with a binomial error distribution (for presence/absence of foraging events on land/at sea, nearshore, or at a landfill) using the *lme4* R package (Bates et al., 2015) with year as the fixed effect and individual as the random effect. While western gulls are generally sexually size dimorphic (Pierotti and Annett, 1995), there was some overlap in size measurements for both sexes and thus, data for both sexes were combined in this study. The response variables (trip duration and maximum trip distance) were log₁₀ transformed. For *post hoc* comparisons between years, we used the “glht” function in the *multcomp* R package (Hothorn et al., 2008) with Tukey’s honestly significant difference pairwise multiple comparisons of means (Bretz et al., 2016) and adjusted *p*-values using the Bonferroni correction to account for multiple comparisons. Results were considered statistically significant at *p*-value (*p*) < 0.05 and marginally significant at 0.05 < *p* < 0.10.

The spatial region encompassing gull foraging events each year and all years collectively was determined using two-dimensional kernel density estimations with an axis-aligned bivariate normal kernel in R following past work (Venables and Ripley, 2002; Pickett et al., 2018). To highlight the dominant areas utilized each year, we showed the 75 and 50% (core) foraging regions.

Environmental Data

We obtained medium resolution shoreline data from the National Oceanic and Atmospheric Administration (NOAA) nautical charts, shipping lanes from the NOAA Office of Coast Survey electronic navigational charts, National Marine Sanctuary boundaries from the NOAA Sanctuaries geographic information system database, and 1 arc-minute bathymetry/elevation data from the ETOPO1 Global Relief Model. Landfill locations were downloaded from the California Office of Environmental Health Hazard Assessment and included two Recology recycling center locations that western gulls are known to visit (Shaffer et al., 2017). Distance to the shoreline and landfills/recycling centers within our study area were calculated over a 1 km × 1 km grid.

The California Current system is characterized by wind-driven coastal upwelling that delivers deep, cool nutrient-rich waters to the surface, which supports a diversity of primary producers up to top predators (Huyer, 1983; Checkley and Barth, 2009; Jacox et al., 2018). The HCI evaluates the monthly area of coastal upwelling habitat and is considered a regional indicator of the likelihood of ecosystem shifts coinciding with the shoreward distribution and increased aggregation intensity of top predators (**Figure 1**; Santora et al., 2020). The HCI is the area covered by surface waters below a monthly sea surface temperature (SST; derived from data assimilative Regional Ocean Modeling System analysis of the California Current system) over the domain between latitudes 37.3–38.5°N and extending from the shore out

²https://www.waste360.com/mag/waste_mapping_landfill_space

TABLE 1 | Summary of western gull tracking dates, sample size of individuals tracked before and after speed and quality filters were applied, the mean deployment duration, the total number of trips and foraging events by year.

Year	Tracking period	Sample size of individuals tracked (sample size after filter)	Deployment length (days)	Number of trips (At-sea/On land)	Number of presumed foraging events
2013	26–30 May	9 (5)	2.62 ± 0.86	12 (8/4)	87
2014	1–12 June	20 (20)	3.3 ± 1.05	66 (54/12)	396
2015	24 May–3 June	15 (14)	4.77 ± 1.96	51 (28/23)	475
2016	29 May–11 June	23 (23)	4.43 ± 1.12	68 (34/34)	645
2017	28 May–4 June	15 (14)	4.16 ± 0.76	39 (16/23)	249
2018	20–31 May	28 (28)	5.76 ± 1.62	169 (124/45)	1,019
2019	20–31 May	23 (21)	5.66 ± 1.43	139 (110/29)	891
Summary		133 (125)	4.39 ± 1.16	77.71 ± 56.05	537.4 ± 336.3

It should be noted that the tracking effort was lower in 2013 (first year of study), but the data still provided valuable information. For summary statistics, the total number of logger deployments and mean ± standard deviation for the other metrics are shown.

to 150 km from land. The monthly SST thresholds were the long-term (1980–2010) SST spatial average for a given month over the same latitude range (37.3–38.5°N) and over 75 km from shore (11.5°C in May and 12.0°C for June). We computed monthly HCI for May and June from 2013 to 2019, corresponding to the period when western gulls were tracked and ecosystem surveys occurred. We evaluated the spatial areas that fall below the thresholds during May and June in relation to western gull habitat use each year.

Prey Data and Predator Sightings From Ecosystem Surveys

The NOAA-NMFS Rockfish Recruitment and Ecosystem Assessment Survey (RREAS) occurs predominately during May and often into early June each year (Sakuma et al., 2016) and spans most of coastal California. Prey abundance indices were obtained from 15-min net tows using a modified Cobb midwater trawl with a 9.5 mm cod-end liner with a headrope depth of 30 m (Sakuma et al., 2006; Ralston et al., 2013). Individuals from the net hauls were sorted to species and the total number per haul and species were estimated by extrapolating the species subsample to the total species volume. Abundance was estimated as log-transformed catch-per-unit-effort [$\ln(\text{CPUE} + 1)$]. Prey taxa included krill (Euphausiids), market squid (*Doryteuthis opalescens*), northern anchovy (*Engraulis mordax*) adults and young-of-the-year (YOY), Pacific sanddab (*Citharichthys sordidus*) YOY, and rockfish (*Sebastes*) YOY based on past studies (Cassell, 2016; Santora et al., 2017). For each year, we mapped the proportional abundance of each species at each sampling station within our study region. To examine interannual variability near the gull colony, CPUE across the five or six stations (not all stations were sampled each year) directly around the Farallon Islands were averaged to give a single annual abundance value for each prey species. Because tracked western gulls overlapped considerably with these selected stations, these stations likely provide the best information on the available prey field in the region.

Daytime seabird and whale sighting observations were made using standardized survey methods (Tasker et al., 1984; Yen et al., 2004) where an observer counted seabirds and mammals from

the ship's bridge at vessel speeds above 5 kts. All mammals out to 3 km and seabirds within a 300 m arc from the bow and 300 m off the side were counted. Because visual surveys do not occur in the same location each year, we calculated how much of the study region (box in **Figure 2**) was covered by the survey each year. These calculations showed the survey covered 25% of the study region in 2013–2014, < 10% in 2015, 20% in 2016–2017, ~12% in 2018, and 30% in 2019. In 2018, the small area that was surveyed (**Supplementary Figure 1**) missed the main gull foraging region to the northwest of the Farallon Islands, and similarly, 2015 had the lowest survey coverage. In contrast, in 2019, the survey covered the largest area with the most nearshore observations overlapping with the gull foraging region to the north of the Farallon Islands. We also determined the total area of overlap between the survey and the tracking data (shown on **Supplementary Figure 1**). The tracking data was integrated on a 5 km × 5 km grid where 0 indicated the absence of foraging events and 1 indicated the presence of at least one foraging event for each year (**Supplementary Figure 1**).

Using this survey data, the number of western gulls and humpback whales were summed within the same 5 km × 5 km grid cells each year (see **Supplementary Figure 1**). Further, to investigate associations between the two species each year, we determined the grid cells where humpback whales were present and retaining only those cells, we determined the number of western gulls and humpback whales within those grid cells. The proportion of those grid cells where both species were present was determined to understand the likelihood of associations in the two species distributions. It was inappropriate to do the comparison by first determining where gulls were present because gulls spend most of their time at-sea transiting compared to foraging and we only expected their foraging locations to overlap with whales.

Statistical Analyses

We computed Pearson's correlations between prey abundance indices, gull foraging characteristics, and the HCI. We also calculated correlations between the gridded number of gulls and number of whales from the survey including each grid cell and all years. These correlations provide a simple metric of association among the many investigated time series.

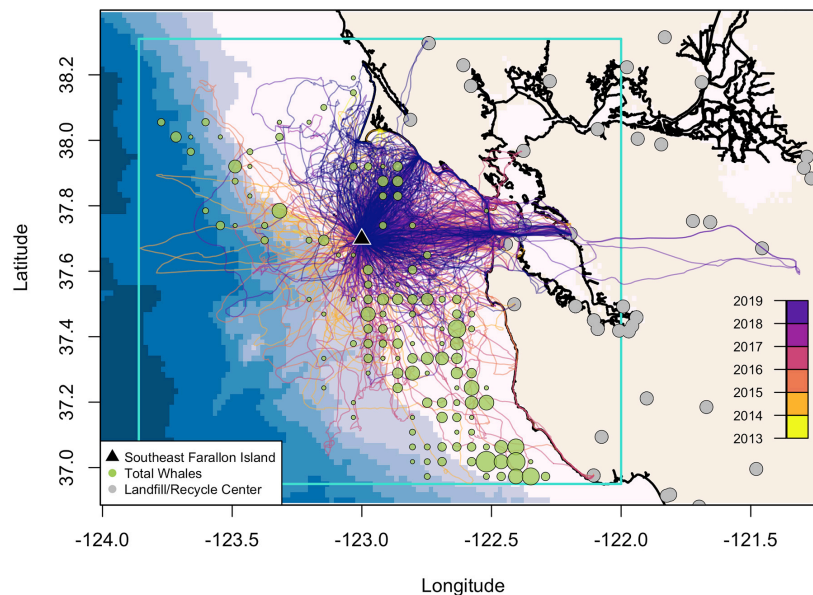


FIGURE 2 | Map of western gull tracks from 2013 to 2019 from their breeding colony on Southeast Farallon Island, east of the San Francisco Bay, California, United States (inset). The blue box is the study region. The total number of humpback whale sightings (summed on a 5 km × 5 km grid) from 2013 to 2019 from the Rockfish Recruitment and Ecosystem Assessment Survey where the size of the circle is scaled from 1 to 23 individuals. Note, the survey did not equally cover our entire study area. Landfill or recycling center locations are denoted in gray and bathymetry is shown in the background from 0 to 3,800 m depth in ~600 m increments.

To investigate overlap between whales, gulls and cool upwelled waters, we computed a range overlap metric. Range overlap measures the proportion of a species' range where another species or habitat condition co-occurs, and is the area occupied by both species or conditions divided by the area occupied by one species (Araújo et al., 2011; Carroll et al., 2019). We computed range overlap for each year between: (a) foraging gull locations from tracking data and cool SST (gulls were the denominator), (b) whales and gulls from survey data (whales were the denominator), and (c) the co-occurrence of whales and gulls from survey data and cool SST (whale and gull co-occurrence was the denominator). Cool SST thresholds were 11.5°C in May and 12.0°C for June (as described in section "Environmental Data"). For *a*, we computed range overlap separately for May and June in all years while for *c*, we used only May cool SST as the majority of the RREAS survey occurs in May. Range overlap has values from zero to one, where one indicates high overlap. We report the mean and standard deviation of all years.

We tested whether the proportion of foraging events at specific locations (e.g., near shore and on land) were related to the HCI and prey abundances. We tested 12 models in total for each proportional dataset, six models with May HCI and the abundance of each prey species and six models with June HCI and the abundance of each prey species. We used generalized additive models (GAMs) fit using the "mgcv" package in R (R Core Team, 2020), using the "betar" family that is appropriate for proportional data and logit-link function. GAMs can fit complex non-linear relationships using a smoothness parameter estimated by generalized cross-validation. In cases where a non-linear

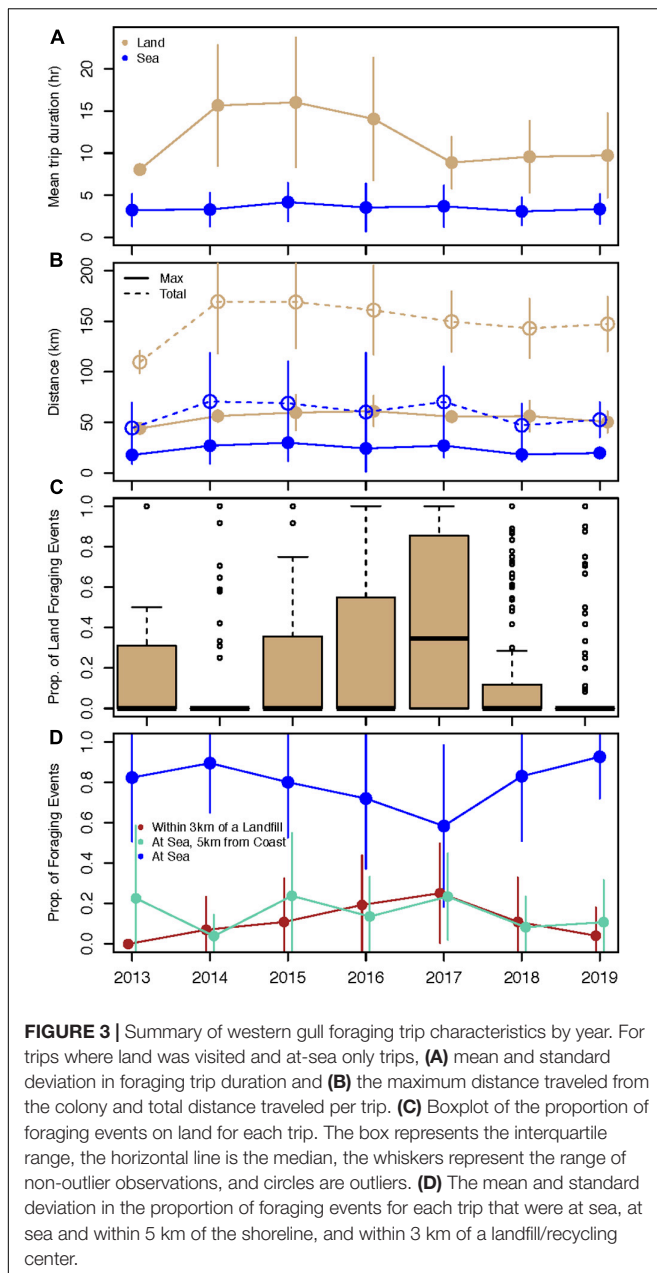
relationship did not exist and a linear relationship was more appropriate, we did not use the smoothness parameter. We tested for multicollinearity between predictor variables using variance inflation factors, which we found was not a problem as all values were <4 (O'Brien, 2007). We calculated variable importance using the "caret" R package. Akaike information criterion corrected for small sample size (AIC_c) was used to rank model performance, where models with a $\Delta AIC_c < 2$ were considered to have substantial support and > 10 had no support (Burnham and Anderson, 2002). We removed models that had negative R^2 -values, which indicated the model fit was worse than a horizontal line. We report the R^2 , deviance explained and Akaike weight as an indicator of model performance for all models with a $\Delta AIC_c < 10$.

RESULTS

Western Gull Foraging Patterns

After applying our filtering criteria, there were foraging tracks from 125 gulls yielding a total of 544 complete foraging trips. Of these, 516 foraging trips included at least one foraging event, with a total of 3,762 foraging events across all trips (Table 1). Gull foraging trips were concentrated along the continental slope or shelf where whales typically aggregate (Figure 2 and Supplementary Figure 1), along the shoreline, and to specific landfill/recycling center locations in urban areas (Figure 2).

There was interannual variability in foraging trip characteristics. The highest percentage of land trips out of the total number of trips were in 2015 (45%), 2016 (50%), and



2017 (59%), and the lowest percentage of land trips were in 2014 (19%), 2018 (27%), and 2019 (21%, **Table 1**). Mean trip duration ranged from 8 to 15 h for land trips and ~3–4 h for sea trips (**Figure 3A**). There were no significant differences between the duration of land trips across years or the duration of sea trips across years ($p > 0.05$) but the durations of land trips were significantly longer than sea trips in all years (z -statistic(z) = -3.7 to -11.9 , $p < 0.001$). The mean maximum trip distance from the breeding colony was 45–60 km for land trips and 17–30 km for sea trips, and the mean total distance traveled was 110–170 km for land trips and 45–70 km for sea trips (**Figure 3B**). There were no significant differences between the maximum distance or total distance traveled for land trips

across years or the maximum distance or total distance traveled for sea trips across years ($p > 0.05$). In all years, the maximum distances of land trips were significantly farther than sea trips ($z = -2.8$ to -12.6 , $p < 0.001$), and the total distances of land trips were significantly farther than sea trips ($z = -2.6$ to -11.8 , $p < 0.001$). On average, land trips were 8.2 h longer, 31.4 km farther from the colony, and the total distance of the trip was 90.7 km farther.

Gulls foraged at sea but also at a variety of sites on land, including landfills, parks, cemeteries, fast food, and other restaurants. The proportion of foraging events that were on land for each trip was generally low but there were always a few trips that solely or partially had foraging events on land (**Figure 3C**). On average, ~80% of foraging events were at sea while ~20% were near shore or a landfill (**Figure 3D**). There were significantly more foraging events at sea in 2019 compared to 2015 ($z = 2.91$, $p = 0.07$), 2016 ($z = 3.41$, $p = 0.01$), and 2017 ($z = 4.27$, $p < 0.001$) as well as less foraging at sea in 2017 compared to 2014 ($z = -2.96$, $p = 0.06$). There were significantly fewer foraging events near landfills in 2019 compared to 2015 ($z = -3.08$, $p = 0.04$), 2016 ($z = -4.11$, $p < 0.001$), 2017 ($z = -4.39$, $p < 0.001$), and marginal significance in 2018 ($z = -2.83$, $p = 0.09$). Similarly, there was less foraging near the shore in 2014 compared to 2015 ($z = 4.00$, $p = 0.001$) and 2017 ($z = 4.04$, $p = 0.001$); and marginally less foraging near the shore in 2018 compared to 2015 ($z = -2.87$, $p = 0.09$) and 2017 ($z = -2.95$, $p = 0.07$). Some of the annual foraging characteristics (e.g., distance and duration) were significantly related to each other (see **Supplementary Figure 2**).

Gull Habitat Space in Relation to Coastal Upwelling and Prey Abundance

Western gull foraging habitat space varied by year as did the area with cool upwelled waters and regional prey abundances. Core foraging areas (within the 50% contour of the kernel densities of foraging locations) generally encompassed an area adjacent to the colony but oriented in different directions each year (**Figure 4**). In 2013, 2014, 2018, and 2019, foraging occurred predominantly to the north of the colony, and in 2014–2017, foraging also occurred to the west and there were larger hotspots over landfill locations over the mainland. The location and area of cool surface waters varied, with the greatest compression shoreward and to the north occurring in 2015–2016 and 2019. The spatial footprint of cool waters was generally similar in May and June but with a greater southward extension during May in 2014–2017 and during June in 2018–2019. Despite the variability in location of cool waters, gulls often foraged within these areas. The range overlap between foraging locations from gull tracking data and cool SST generally showed high overlap (0.73 ± 0.33 , see annual values for May and June on **Figure 4**). However, 2019 had low overlap due to the small area of cool waters in the north but it should be noted that gulls foraged to the north of the Farallon Islands toward the region with cool waters.

Interannual variability in prey distribution and abundance was observed, including latitudinal and onshore-offshore patterns (**Supplementary Figure 3**). Focusing on trawl data around the

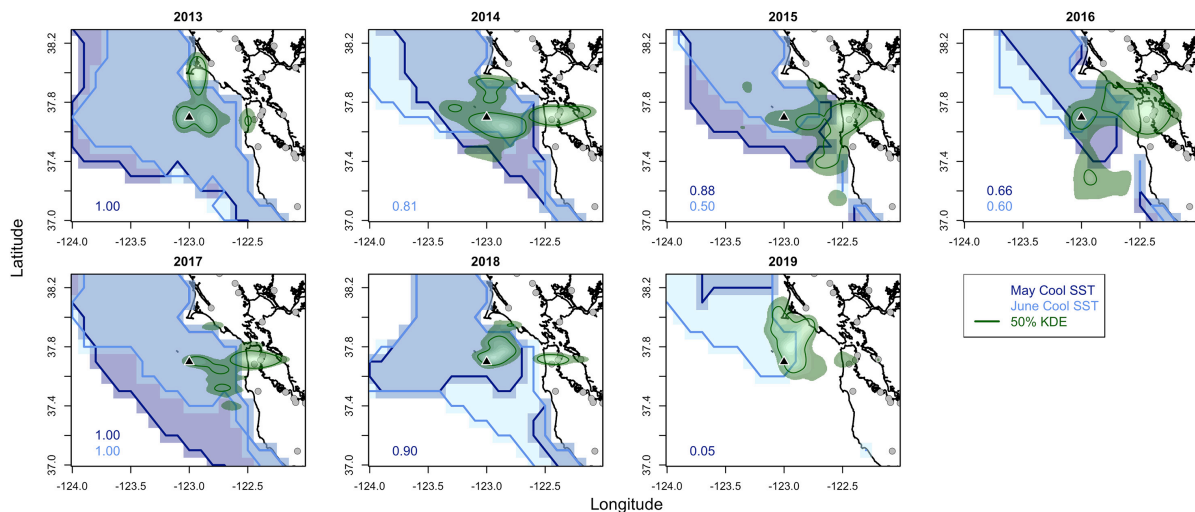


FIGURE 4 | Western gull kernel density estimates (KDE, green) for foraging locations for each year with the outer area being the 75% KDE and the inner 50% KDE line representing the core foraging area. The area with cool sea surface temperature (SST) in May (SST below 11.5°C) and June (SST below 12°C) is shown with the numbers indicating the range overlap between gull foraging locations and cool SST for each month. Southeast Farallon Island is the black triangle and landfills/recycling centers are the gray circles.

Farallon Islands, the most abundant prey item was krill (mean CPUE 7.91), which had dips in abundance in 2015–2016 and 2019 (**Figure 5A**). Market squid had a mean abundance of 2.88 CPUE with a dip in 2016. Rockfish YOY peaked in 2015 (4.85 CPUE) and declined from 2016 to 2019 to 0.85 CPUE. Pacific sanddab YOY followed a somewhat similar trend to rockfish, peaking in 2014 and declining from 2015 to 2019 (0 CPUE) with a small peak in 2018. Comparatively, northern anchovy YOY were least abundant with small peaks in 2015 (1.18 CPUE) and 2019 (0.60 CPUE) while adult anchovy CPUE increased in 2018–2019 to 3.42 from 0. Annual prey abundances were not correlated to each other except for a marginal relationship between rockfish YOY and anchovy adults ($r = 0.70$, $p = 0.08$; **Supplementary Figure 2**).

Given significant interannual variability in the proportion of foraging events that were on land, at sea, near shore or a landfill, we tested for drivers of this interannual variability focusing on the proportion of foraging events on land and near shore given the high correlations between these proportional datasets (**Supplementary Figure 2**). The proportion of foraging events on land was related to the HCI during May (variable importance 63.3%) and Pacific sanddab YOY abundance (variable importance 36.7%, **Table 2** and **Supplementary Table 1**). Gulls foraged over land more frequently when the HCI was high (i.e., high shoreward compression of upwelled water) and when sanddab abundance was low (**Supplementary Figure 4A**). The proportion of foraging events near shore was also related to the HCI during May (variable importance 58.2%) and krill abundance (variable importance 41.8%, **Table 2** and **Supplementary Table 1**). Gulls had more foraging events near shore when the HCI was high and krill abundance was low (**Supplementary Figure 4B**). The two best performing models only explained 50–60% of the deviance (**Table 2**).

TABLE 2 | Generalized additive models relating the proportion of foraging events on land and near shore to the Habitat Compression Index (HCI) and prey abundances.

Model	R^2	Deviance Explained	AIC _c	Δ AIC _c	Akaike weight
Proportion of foraging events on land~					
MayHCI + PacificSanddabYOY	0.40	53.8	10.4	0.0	0.32
Proportion of foraging events near shore~					
MayHCI + TotalKrill	0.59	61.6	5.5	0.0	0.44
MayHCI + NorthernAnchovyYOY	0.36	48.1	7.6	2.1	0.15
MayHCI + PacificSanddabYOY	0.17	47.0	7.8	2.3	0.14
MayHCI + MarketSquid	0.02	27.0	9.8	4.3	0.05
MayHCI + NorthernAnchovyAdults	0.06	24.3	10.0	4.5	0.05
MayHCI + TotalRockfishYOY	0.00	20.9	10.3	4.8	0.04

For each model, we report the R^2 , deviance explained, AIC_c for small sample size, the amount of information lost using AIC_c (difference from the lowest AIC_c value), and model support using Akaike weight. Models with Δ AIC_c < 2 have substantial support and only models with a Δ AIC_c < 10 are shown. Only one model for the proportion of foraging events on land had a positive R^2 -value.

Ecosystem Survey Informs Overlap of Humpback Whales and Gulls

The ecosystem survey coverage varied each year but in general, spatial patterns in visual sightings revealed that western gulls were likely to be present near the Farallon Islands and that humpback whales were more abundant south of the island (**Figure 2** and **Supplementary Figure 1**). Across years, there were a total of 9–44 grid cells per year where humpback whales were observed (see the size of circle in **Figure 5B**). The total number of whales within those grid cells ranged from 13 to 133 and the total number of gulls ranged from 12 to 342. A higher abundance of whales within a grid cell was weakly, but positively correlated to gull abundance (Spearman's Rank $\rho = 0.18$, $p = 0.02$). During

all years except 2018, 65–82% (mean 71%) of grid cells had both whales and gulls present. In 2018, despite a moderate number of whales observed (101 whales in 26 grid cells), there were few gulls sighted resulting in only 35% of grid cells with both species, which is likely related to the small area surveyed outside of the gull foraging region (**Supplementary Figure 1**). In 2017, the survey reported the fewest number of whales observed (13 whales) concomitant with the second lowest number of gull sightings in 2018. Range overlap indicated a high degree of overlap between whales and gulls from the survey data (0.71 ± 0.13), and where whales and gulls co-occurred, there was often high range overlap with cool SST (0.82 ± 0.16 for 2013–2018, with no overlap in 2019 as the footprint of cool SST was small, **Figure 4**).

DISCUSSION

We examined the drivers of interannual variability in western gull foraging behaviors at the Farallon Islands and the utility of western gulls as an ecological indicator by combining animal tracking data, ecosystem survey data on multiple predator and prey species, and oceanographic data on upwelling. Our analysis suggests that western gulls can serve as a valuable ecosystem sentinel and more specifically as a fine-scale indicator of humpback whale presence. Specifically, our results indicate that gull foraging behavior can differ between years, where this behavioral plasticity combined with the capacity to exploit resources in both marine and terrestrial habitats may allow gulls to buffer more extreme oceanic events (e.g., marine heatwaves) compared to other seabird species with less flexible diets and behavior. Gull foraging patterns were coincident with regions of cool upwelled waters, foraging closer to shore and on land in years when there was higher compression of upwelled water and lower prey abundances. Evidence that gull at-sea distributions were associated with humpback whales suggests prey accessibility may be more important than prey-abundance alone. However, continued sampling that increases this short time window within a season and tagging outside the breeding period could be key factors that may strengthen these relationships.

Gull Foraging Patterns in Relation to Environmental Variability

Although seabird foraging behavior often relates to ecosystem state, including variables such as productive waters, prey distribution, abundance and accessibility (reviewed by Durant et al., 2009), the utility of western gulls as an ecosystem indicator was unknown. Many gull species employ a dual-habitat foraging strategy alternating between marine and terrestrial habitats (e.g., Schwemmer and Garthe, 2008; Garthe et al., 2016; Navarro et al., 2017). The most striking patterns in gull foraging behavior were interannual shifts in foraging locations between landscapes and seascapes. When conducting land trips, the gulls mainly followed and foraged along the shoreline or visited specific landfills/recycling centers (as previously identified by Shaffer et al., 2017). A flexible diet and plasticity in foraging dynamics may allow gulls to adapt to a changing environment, and

terrestrial habitats with predictable food sources may provide a buffer in years when food at sea is harder to acquire (Garthe et al., 2016; Navarro et al., 2017).

The interannual variability in gull behavior and habitat use appears somewhat related to environmental conditions as more near shore and land foraging occurred during years with high upwelling habitat compression. During our study, marine heatwaves caused unprecedented ocean warming, altered upwelling and impacted ecosystem dynamics (e.g., Cavole et al., 2016; McCabe et al., 2016; Ryan et al., 2017; Santora et al., 2020). Marine heatwaves cause a shoreward compression of cool surface waters (e.g., 2015) whereas strong upwelling conditions often result in cool surface waters extending further offshore (e.g., 2013, Checkley and Barth, 2009; Bograd et al., 2019). The 2015 marine heatwave (Bond et al., 2015) was followed by a moderate El Niño in late 2015/early 2016, which coincided with shoreward habitat compression. During 2015–2017, a higher proportion of foraging occurred nearshore and on land. While upwelling conditions and habitat compression may have influenced gull foraging dynamics in 2015–2016, gull foraging behavior in 2017 (the year with the most foraging on land) cannot solely be explained by oceanographic anomalies. To establish more robust climate connections, we acknowledge that a longer time series is necessary.

Gull Foraging Behavior in Relation to Prey Species During Incubation

Gull food consumption and foraging strategies can vary with food availability, breeding stage, and intraspecific competition (Annett and Pierotti, 1989; Belant et al., 1998; Camphuysen et al., 2015; Corman et al., 2016; Isaksson et al., 2016; Navarro et al., 2017). The variability in prey communities and shifts in gull foraging dynamics suggests that the prey species consumed varied both intra- and interannually. We found that there were more gull foraging events on land and near shore when Pacific sanddab and krill abundance was low, respectively. These models explained 50–60% of the deviance, with prey abundances contributing 35–40% to the models. Apart from these relationships, we did not find evidence that prey abundance around the Farallon Islands was related to other gull foraging dynamics but more complex and finer-scale comparisons between the prey field and foraging behavior may be needed as the spatial structure of prey communities are convoluted (see **Supplementary Figure 3**). It is also possible that stronger relationships between gull foraging dynamics and prey exist during the chick-rearing period, when gulls prey switch from human refuse to marine resources (Spaans, 1971; Ward and Zahavi, 1973; Annett and Pierotti, 1989). Food found on land can be of lower quality leading to reduced breeding success (Isaksson et al., 2016) but adults may initially forage on land due to the predictability and abundance of food. Therefore, foraging at landfills could provide a buffer for adults during incubation when prey availability at sea is low, but this may not provide a buffer for chicks who either reject items from landfills or do not get adequate nutrition (Annett and Pierotti, 1989; Isaksson et al., 2016).

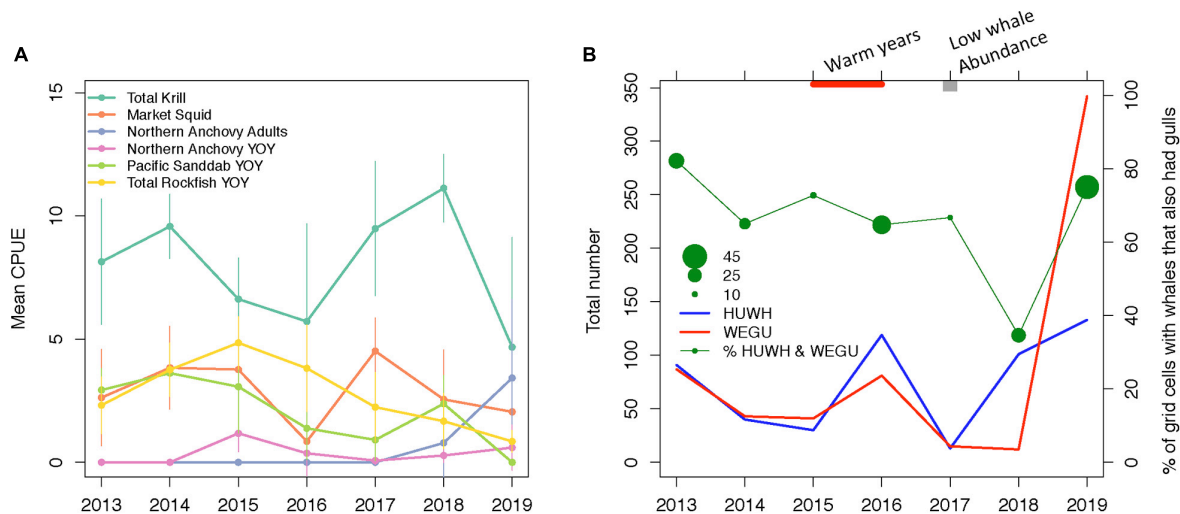


FIGURE 5 | Prey indices and predator overlap from the ecosystem survey. **(A)** Mean and standard deviation in Catch-Per-Unit-Effort [$\ln(\text{CPUE} + 1)$] of prey species within the 5 or 6 trawl stations surrounding the Farallon Islands (see **Supplementary Figure 3**). For taxa with multiple species, the “total” abundance of all species was used. **(B)** The number of humpback whales (HUWH, blue line) within 5 km \times 5 km grid cells within the gull foraging domain (blue box in **Figure 1**) and the number of western gulls (WEGU, red line) in grid cells where humpback whales were observed from 2013 to 2019. The percentage of grid cells with whales that also had gulls (green line) with the size of the circle indicating the number of grid cells where at least 1 whale was present. During 2015 and 2016, there were marine heatwave impacts on our study area, and in 2017, there were regionally low humpback whale abundances.

Gull Foraging Behavior as an Indicator of Humpback Whales

Another critical factor to consider when characterizing gull foraging behavior and prey availability is gull feeding associations with humpback whales. From visual sighting data, ~70% of humpback whale observations coincided with gulls, which is also supported by high range overlap (0.71). While present in central California, humpback whales prey switch from krill to anchovy when krill are less available, which results in changes in feeding locations from offshore to onshore habitats (Ainley and Hyrenbach, 2010; Santora et al., 2018, 2020; **Figure 1**). In 2015–2016, onshore shifts of whales due to prey availability was also driven by upwelling habitat compression. This same relationship was seen in the gull tracking data, where there was a higher proportion of foraging locations near shore under high habitat compression and low krill abundance. There were also more foraging events on land during high compression, suggesting gulls take advantage of predictable terrestrial feeding hotspots. Further, when whales and gulls co-occurred, it was often within cool upwelled waters. As noted above, 2017 was the year with the most foraging on land, which could not be explained by environmental characteristics alone. Whale abundance in the region was low in 2017, with the second lowest encounter rate from 1996 to 2019 (Wells et al., 2017; Thompson, 2019), and distributed shoreward likely feeding on anchovy (Wells et al., 2017), which aligned with gull foraging locations (**Figure 4**). If whales were a key factor in making prey available to gulls and whales were not highly abundant, gulls likely shifted their foraging locations to regions with predictable sources of food (such as landfills). Further, if whales aid in making prey available, it is not surprising that prey abundances

were not the main driver of gull foraging behavior as gulls are capable of switching among many species of krill, fish and squid when available within surface waters. Overall, whales respond to prey and oceanographic dynamics in a predictable manner (Santora et al., 2020; Ingman et al., 2021; **Figure 1**), and our findings suggest gulls respond in the same way. Given that gull distributions were related to humpback whale presence, gulls could perform as an informative indicator of ecosystem state.

Using Gulls for Marine Spatial Planning and Conservation

Fishery and vessel interactions with protected species pose a risk to populations and are a global conservation issue (Read, 2008). Entanglement in trap fisheries is thought to be the most common source of human-related injury or mortality to humpback whales followed by ship strike (Carretta et al., 2015). With whale protections under the Marine Mammal Protection Act, entanglements and ship strikes generate public concern and many agencies are actively working to recover these populations. To reduce risks to whales, it is critical to identify where and when threats occur. While ship strikes often occur in the vicinity of large ports (especially off San Francisco for humpbacks) with peaks in high traffic summer months (Rockwood et al., 2017; Keen et al., 2019), the Dungeness crab fishery is usually open from mid-November to the end of June with the highest activity from mid-November to February (Carretta et al., 2015; **Figure 6**). Indicators that provide actionable high-resolution information are critical as more decision support tools are needed (Santora et al., 2020), especially given that earlier arrivals, longer residency and higher concentrations of whales in central California could lead to increased risks (Ingman et al., 2021).

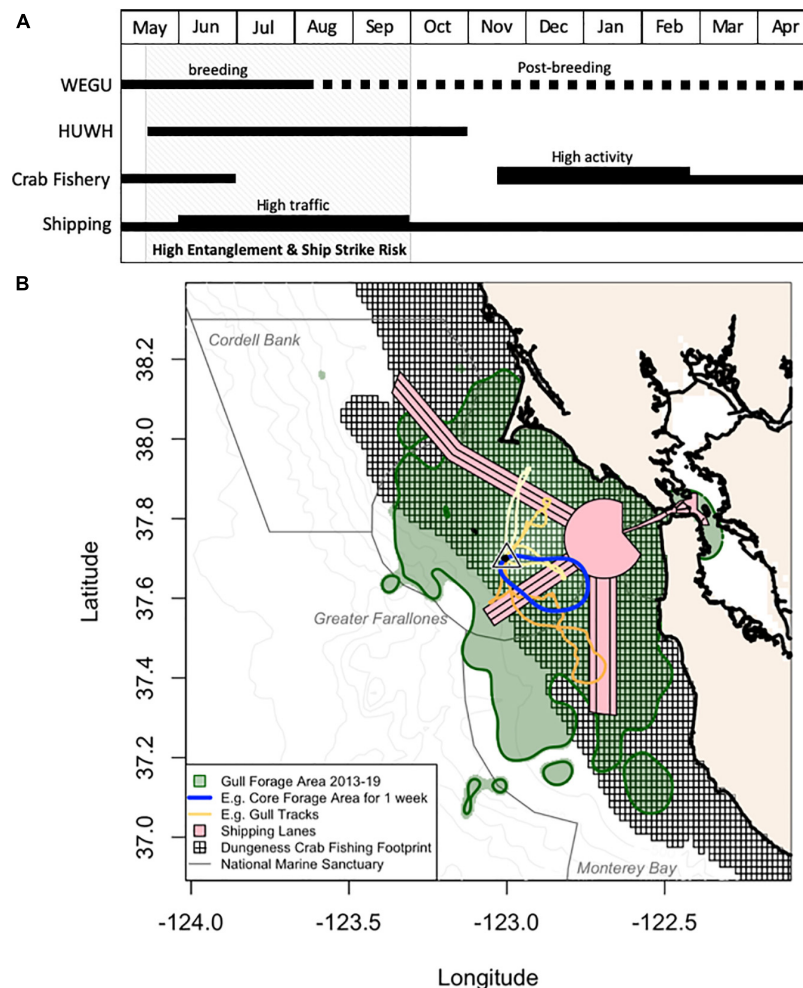


FIGURE 6 | Temporal and spatial overlap of western gulls (WEGU), humpback whales (HUWH), the Dungeness crab fishery, and shipping traffic in central California. **(A)** Phenology of the WEGU annual cycle at Southeast Farallon Island (black triangle) and HUWH presence in central California. After the gull breeding period, many birds remain in the Greater Farallones region occasionally visiting their colony. The Dungeness crab fishery operates from November to June with a peak in November–February. Shipping traffic outside of the San Francisco Bay is present year-round with a peak in the summer (June–September). Whale entanglement and ship strike risk occurs roughly from May to November (depending on whale arrival and departure dates), with the highest risk period between May and September (gray shading). **(B)** An example of a gull tracking visualization that could exist on an indicator dashboard highlighting: shipping lanes, the footprint of the crab fishery (<180 m), and gull foraging metrics including habitat use over 2013–2019 [95% kernel density estimate (KDE)], core habitat space over a 1-week period (50% KDE), and four examples of foraging trips. Also shown are three National Marine Sanctuary borders and bathymetry contours.

By using animal tracking data and known seabird-cetaceans feeding associations, we can obtain information on where humpback whales face threats from fisheries or large vessels. Western gulls occupy their Farallon Island breeding colony during a critical period when shipping traffic is high, crab fishing is ending, and humpback whales arrive in the region (Figure 6). Although the gull breeding period ends in late July/early August, many individuals remain nearby until the majority of the population returns in October–November (Spear, 1988; Ainley, 1990). Thus, the population has the capacity to provide clues about how the ecosystem and humpback whale distributions shift over the summer–fall entanglement and ship strike period (Figure 6). Such generalist predators also offer a different view on the state of an ecosystem than would a

habitat specialist, suggesting that combining a few indicator species could give a more complete assessment of ecosystem response (Hazen et al., 2019). Outfitting a small portion of the gull population with year-round transmitters that are capable of near real-time, remote offload could benefit dynamic ocean management. Successful long-term deployments of tags on birds are also higher than whales due to reduced tag shedding, increased transmissions as birds largely remain above the surface, and reduced tag/labor costs.

The Gulf of Farallones–Monterey Bay area accounts for a high percentage of humpback strike mortality and entanglements, and should be a high priority area for mitigation efforts (Rockwood et al., 2017, 2020). Based on the results presented here, we suggest a few strategies for using gulls to inform ecosystem management.

First, from continuous gull tracking datasets, indices on foraging characteristics (e.g., **Figure 3**) could be produced on daily to weekly scales. A threshold (e.g., >20%) for the proportion of foraging events on land indicates low whale abundances or suboptimal at sea foraging habitats. Second, gull tracking data could be mapped and viewed in relation to crab pot/fishing vessel locations or shipping lanes (e.g., **Figure 6**), and alerts can be set up to provide an early warning system of potential human-wildlife conflicts. For example, when the gull core foraging area overlaps with a shipping lane, vessel speed reductions could be implemented until that region is no longer highly utilized by gulls likened to a Seasonal Management Area with the designation of temporary “Areas to be Avoided.” Keen et al. (2019) found a 2–3 kt reduction significantly reduces ship strike risk by 20–50%. Core foraging areas could also indicate risky crab pot deployment locations, or signal fishers to retrieve deployed gear. Third, more simply, notifying ship captains of these predictable seabird-cetacean relationships could mitigate ship strike risk as it is easier to spot a gull aggregation above the water and adjust course than a whale on the sea surface.

Visualizations or metrics derived from the tracking data could feed into existing ocean observing dashboards and provide information to the public, fishers, fisheries managers, scientists and other teams who consider the tradeoffs between economic needs and the risk to protected resources. Tracking data yields cost-effective information on fine time and space scales, complementing and improving upon existing coarse resolution indicators used in central California. The tracking and monitoring of new indicator species in addition to existing indicators can provide critical information for identifying and establishing management tools and arming managers with the best information to protect species from climate and anthropogenic threats.

DATA AVAILABILITY STATEMENT

The datasets used in this study are available in publicly accessible websites or repositories, or included in the **Supplementary Material**: shoreline data (<https://shoreline.noaa.gov/data/datasheets/medres.html>), bathymetry/elevation data (<https://www.ngdc.noaa.gov/mgg/global/global.html>), landfill locations (<https://oehha.ca.gov/calenviroscreen/indicator/solid-waste-sites-and-facilities>), sea surface temperature is provided as supplementary dataset with access from the UC Santa Cruz Ocean Modeling and Data Assimilation group (<https://oceanmodeling.ucsc.edu/ccsnrt/#txtOutput>), habitat compression index (<https://www.integratedecosystemassessment.noaa.gov/regions/california-current/cc-projects-whale-entanglement>), RREAS data (<https://data.noaa.gov/dataset/>

[dataset/rockfish-recruitment-and-ecosystem-assessment-survey-catch-data1](https://data.noaa.gov/dataset/rockfish-recruitment-and-ecosystem-assessment-survey-catch-data1)), and gull tracking data is deposited in the Animal Telemetry Network data portal (<https://portal.atn.ioos.us/#metadata/20adbe37-d59b-4bf6-a2e0-db725ecbd29c/project>).

ETHICS STATEMENT

The western gull tracking study was reviewed and approved by the Institutional Animal Care and Use Committee at San Jose State University (protocol #979) and approved by USFWS Special Use Permits (SUP 81640 and 81641) issued to S.A. Shaffer for research activities at the Farallon Island National Wildlife Refuge.

AUTHOR CONTRIBUTIONS

SS and MC conceived of the study. SS, PW, and JS collected the data. MC, HW, SS, JS, and IS analyzed the data. MC made the manuscript figures. MC wrote the initial manuscript with contributions from all authors. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2021.790559/full#supplementary-material>

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Foraging Paths of Breeding Leach's Storm-Petrels in Relation to Offshore Oil Platforms, Breeding Stage, and Year

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The global population of Leach's Storm-Petrels (*Hydrobates leucorhous*), the smallest and most abundant breeding seabird species in eastern Canada, has declined substantially in recent decades. The species is listed as "Threatened" by the Committee On the Status of Endangered Wildlife in Canada (COSEWIC) and as "Vulnerable" by the International Union for Conservation of Nature (IUCN). Fatal attraction to anthropogenic light is a major risk for Leach's Storm-Petrels and many other nocturnal seabirds. From May to September each year, Leach's Storm-Petrels in eastern Canada breed in island colonies and travel many hundreds of kilometers to obtain prey for themselves and their chick. At the species' largest colonies in eastern Newfoundland, brightly illuminated oil production platforms intersect breeding storm-petrels' foraging paths. The level of risk posed by these platforms is poorly understood. GPS tracking from 2016 to 2021 at one of the world's largest colonies revealed considerable similarity in foraging trip distance, location, and behavior (inferred from Hidden Markov Models) among years, and a decrease in trip distance and duration between incubation and chick-rearing. Leach's Storm-Petrels flew within the light catch-basin of an oil platform in 17.5% of trips, and the birds tended to transit rapidly past platforms during the day when light attraction is minimal. Exposure to oil platforms at night occurred in only 1.1% of trips. Despite our findings, Leach's Storm-Petrels are known to strand on oil platforms in large numbers, especially during the fledging period. In addition, storm-petrels migrate over great distances and are likely exposed to brightly illuminated oceanic oil platforms outside the breeding season. Our results emphasize the need to focus conservation research on risks during migration and winter, and on juveniles and immature birds.

Keywords: foraging, risk, tracking, oil platform, light attraction, *Hydrobates leucorhous*

INTRODUCTION

Globally, seabirds are declining, with nearly 50% of species classified as Near Threatened or worse, and 50% of the at-risk species having earned this classification due to recent rapid declines (Croxall et al., 2012; Dias et al., 2019). Brightly lit offshore oil production platforms are a known risk to many seabird species (Wiese et al., 2001; Burke et al., 2012; Montevecchi et al., 2012; Ronconi et al., 2015),

which may be at risk from attraction (positive phototaxis, see Reed et al., 1985; Miles et al., 2010; Rodríguez et al., 2014) to these structures and the flares they produce. In Atlantic Canada, where large populations of seabirds breed, episodic mortality events are ongoing at oil platforms (Davis et al., 2017; Gjerdrum et al., 2021) and can result from collisions, incineration in flares, oiling, injury by machinery, increased predation due to artificial reef attraction, or disorientation and excessive energy expenditure while circling the platform (Wiese et al., 2001; Montevecchi, 2006; Burke et al., 2012; Ronconi et al., 2015; Dierschke et al., 2016).

Procellariiformes, one of the most threatened groups of seabirds (Croxall et al., 2012), are particularly at risk because they aggregate around sources of anthropogenic light (Le Corre et al., 2002; Miles et al., 2010; Davis et al., 2017; Rodríguez et al., 2017b; COSEWIC, 2020; Gjerdrum et al., 2021). Leach's Storm-Petrels (*Hydrobates leucorhous*) are the most commonly observed species in stranding events on oil platforms in Atlantic Canada (Davis et al., 2017; COSEWIC, 2020; Gjerdrum et al., 2021). This species is listed as "Vulnerable" on the International Union for Conservation of Nature (IUCN) Red List and "Threatened" by the Committee On the Status of Endangered Wildlife In Canada (COSEWIC) as a result of a 54% decline in northwestern Atlantic colonies over three generations (approximately 44 years; BirdLife International, 2018; Bird et al., 2020; COSEWIC, 2020). The species' largest colonies, located in Atlantic Canada, are experiencing the most drastic declines (Montevecchi and McFarlane, 2019; Duda et al., 2020; d'Entremont et al., 2020; Wilhelm et al., 2020), with lower estimated annual survival than conspecifics in the Pacific Ocean (Fife et al., 2015; Rennie et al., 2020). These birds are highly pelagic and spend the non-breeding period on the open ocean (Pollet et al., 2021). During the breeding season, Leach's Storm-Petrels are central place foragers (Halpin et al., 2018) and often travel more than 2,000 km during a single foraging trip to feed over deep off-shelf waters (Pollet et al., 2014b; Hedd et al., 2018). The core foraging areas of birds from several Atlantic Canadian colonies intersect offshore oil production platforms (Hedd et al., 2018), so it is vital to better understand the risks platforms pose.

While previous studies using geolocation devices have detailed the colony-level intersection of storm-petrel foraging areas with platforms, the coarse nature of these data precluded detailed investigation of exposure risk. Leach's Storm-Petrels depart and return to the colony almost exclusively at night (Collins, 2021; Pollet et al., 2021), and their primary prey, myctophid fishes, occur in mesopelagic waters beyond the continental shelf and are only available to surface feeding storm-petrels at night owing to their diel vertical migration (Hedd and Montevecchi, 2006; Hedd et al., 2009; Watanuki and Thiebot, 2018; Pollet et al., 2021). Hence, the behavior of these birds, particularly the location and timing of their foraging and nest attendance, appears to be temporally constrained. Bird timing and behavior near platforms is also a determinant of the level of exposure and risk. These factors, as well as other aspects of foraging trip structure (duration, total distance, and location), may also vary within and among years. Annual differences in foraging location

or behavior may reflect attraction to or avoidance of lit structures (e.g., Dierschke et al., 2016; Syposz et al., 2021), or could reflect shifts in prey distribution or availability (e.g., Burke and Montevecchi, 2009; Garthe et al., 2011). Within-year differences could result from changing energetic demands through offspring development.

Dietary changes, adult energetic requirements, and the frequency at which they return to the burrow likely influence the duration, distance, and location of foraging trips. Adults usually incubate in 3–4 day shifts but can incubate for up to 6 days (Gross, 1935; Pollet et al., 2021). Once chicks have hatched, adults rarely stay in the burrow during the day, but individual parents return to the burrow nocturnally to feed their chick every one to four nights (Ricklefs et al., 1985), and the chick-feeding interval increases as chicks age (Pollet et al., 2021). During chick-rearing, adult mass is less, and metabolic rate is higher than during incubation (Montevecchi et al., 1992; Niizuma and Watanuki, 1997; Niizuma et al., 2001). Adults also consume more pelagic fishes and crustaceans during chick-rearing (Watanuki, 1985; Vermeer et al., 1988). These dietary and energetic changes may influence trip structure and area use within a breeding season. Previous studies have found consistent foraging area use by incubating Leach's Storm-Petrels among years (Pollet et al., 2014b; Hedd et al., 2018). Foraging information for Leach's Storm-Petrels during chick-rearing is limited, but differences in the foraging strategies of other Procellariiformes are informative. European Storm-Petrels (*H. pelagicus*), Mediterranean Storm-Petrels (*H. pelagicus melitensis*), and Wandering Albatrosses (*Diomedea exulans*) reduce the total distance traveled, area covered, and duration of foraging trips during chick-rearing (Weimerskirch et al., 1993; Bolton, 2021; De Pascalis et al., 2021), while Antarctic Prions (*Pachyptila desolata*) and Blue Petrels (*Halobaena caerulea*) alternate between long and short trips while raising young (Chaurand and Weimerskirch, 1994; Weimerskirch et al., 1999). Because other Procellariiformes, and storm-petrels in particular, reduce trip metrics during chick-rearing, Leach's Storm-Petrels might be expected to do the same.

Here, we use a global positioning system (GPS) tracking dataset spanning 2016–2021 from the population of Leach's Storm-Petrels nesting on Gull Island, Witless Bay, Newfoundland and Labrador, Canada to investigate light exposure from oil production platforms occurring within their foraging range on the Grand Bank. The number and location of oil platforms remained constant throughout the study period. As foraging behavior can vary both within and among years, we investigate temporal differences in foraging trip structure to better understand risk exposure. We predict that (1) foraging adult Leach's Storm-Petrels will pass near oil platforms on the Grand Bank (as in Hedd et al., 2018), (2) foraging trip structure will remain consistent among years (as in Pollet et al., 2014b; Hedd et al., 2018), and (3a) foraging trip structure will change during the breeding season with storm-petrels making shorter trips during chick-rearing than during incubation (based on observations of other Procellariiformes; Weimerskirch et al., 1993; Bolton, 2021; De Pascalis et al., 2021), (3b) resulting in differences in risk exposure. We also predict that, owing to obligate nocturnality at the colony and on the foraging ground

(Collins, 2021; Pollet et al., 2021), (4) storm-petrels will pass by oil platforms mostly during the day.

MATERIALS AND METHODS

Field Methods

Study Site

We studied the Leach's Storm-Petrel population on Gull Island (47.26265, -52.77187) in the Witless Bay Ecological Reserve, Newfoundland and Labrador, Canada. The island is approximately 0.74 km² in area and Leach's Storm-Petrel burrows cover more than 60% of the island. The most recent population estimate for this colony (2017) is 179 743 pairs, down from a 2001 estimate of 351 866 pairs (Robertson et al., 2006; Wilhelm, 2017). This colony has been monitored for more than 10 years for dietary trends, foraging and migratory behavior, survival, and reproductive success. The island is mostly forested, with open fern areas and grassy slopes around the perimeter.

GPS Deployment and Retrieval

GPS devices (Pathtrack nanoFix GEO-Mini devices, 1.31–2.74% body mass, **Figure 1**) were deployed on breeding adult Leach's Storm-Petrels to track and map foraging area use. GPS device deployments (2016–2021, $n = 127$, **Table 1**) occurred within an area of approximately 200 m radius within the colony. These archival devices can log a maximum of 160–300 data points (depending on the year of production). The sampling interval for all GPS devices was 2 h (except 3 h in 2019, $n = 7$). When attempting to determine a location, the GPS devices searched for satellite signals for up to 12 s (10 s in 2016 and 2018).

Incubating Leach's Storm-Petrels were captured in burrows by hand during the day. During chick-rearing, when adults only make brief night-time provisioning visits to the burrow, one-way trap doors were inserted into burrow entrances to retain birds until GPS device deployment or retrieval, which occurred either the same night or the following morning. GPS devices were sutured to the back of the birds (as described in Pollet et al., 2014a,b; **Figure 1**). GPS devices were deployed in late June/early July to record foraging trips during incubation in all study years and different adults were equipped in mid-August to record foraging during chick-rearing in 2016, 2020, and 2021 (**Table 1**). Two birds were tracked in multiple years. GPS devices were recovered 6–29 days (average 9.4 days during incubation and 15.1 days during chick-rearing) after deployment and recorded one or more foraging trips. For incubation trips, two chicks hatched before GPS device recovery (both during 2021) but were likely < 5 days old as adults were still brooding them. Each tracked adult bird was weighed in a cloth bag (100 g Pesola scale in 2016 and 2018 and Starfruit High Precision Pocket Scale, resolution = 0.1 g in 2019–2021) then returned to the burrow following deployment and recapture of the GPS device. To determine device effects, we conducted a paired *t*-test for bird mass before deployment and after recapture for all tagged birds. All analyses were performed in R version 4.0.1 (R Core Team, 2020).



FIGURE 1 | Adult Leach's Storm-Petrel with a GPS sutured to its back (photo taken by Sydney M. Collins).

Analysis of GPS Data

Trip Delineation

GPS tracks were partitioned into foraging trips (**Table 1**) using the “track2KBA” package, and the “tripSummary” function in particular (Beal et al., 2020). Trips were delineated based on the proximity of points to the colony, with a “trip” being defined as having a minimum travel distance of 68 km and a minimum duration of 8 h. These values were based on manual examination of a sample of GPS tracks and on return and departure data from Passive Integrated Transponder (PIT) tags (borne by birds that did not have a GPS device) on Gull Island (DE, unpublished data). Trips were classified as complete if the captured GPS points started and ended within approximately 100 km of the colony (based on the observed step lengths in our data, it is possible that a bird could have traveled this far within the 2-h interval). Incomplete trips resulted from our program setup (delayed start times), battery running out, full memory, or damage to the device. We forced each complete trip to start and end at the colony by assigning the start/end times to be 1 h (i.e., half the GPS sampling interval) before/after the first/last recorded trip points. We did not calculate trip distance, duration, or platform proximity for incomplete trips and these trips were not used in the statistical models (see below).

TABLE 1 | Summary of GPS tags deployed, birds (GPS) recaptured, and useable tracks downloaded for each year of the study on Gull Island, Witless Bay, Newfoundland and Labrador, Canada.

Year	Breeding phase	GPS deployed	Birds (GPS) recaptured	GPS downloaded	Number of trips (complete)
2016	Incubation	23	19	18	20 (12)
2016	Chick-rearing	13	8	8	31 (24)
2018	Incubation	19	16	16	29 (28)
2018	Chick-rearing	0	0	0	0 (0)
2019	Incubation	10	7	7	9 (5)
2019	Chick-rearing	0	0	0	0 (0)
2020	Incubation	10	4	4	4 (1)
2020	Chick-rearing	17	14	13	59 (52)
2021	Incubation	14	8	6	12 (12)
2021	Chick-rearing	20	15	13	48 (48)
Total	Incubation	77	54	51	74 (58)
Total	Chick-rearing	50	37	34	138 (124)
Total	Total	127	91	85	212 (182)

Failed GPS fixes and the variable delay in achieving successful fixes (10–12 s max) result in inconsistent inter-point timing that is unusable for behavioral classification (see below; Patterson et al., 2008). Hence, trip points were interpolated to achieve consistent inter-point intervals of 2 h (3 h in 2019) by mathematically approximating the longitude and latitude of each point at these standardized times, given the assumption of a straight path between each GPS point (as in Raine et al., 2021). These interpolated data were used for all statistics, except for the calculations of total trip distance and trip duration, as the raw data gave more accurate estimations of these values.

Behavioral Classifications

As delineating behavior may inform the level of risk, we assessed bird behavior for each point in a trip and explored differences within and among years. For example, birds spend considerably more time in areas where they are resting or feeding than in areas through which they transit, so their exposure times to any associated risks may vary. The time spent in an area may not be the only factor affecting risk, however. There are numerous ways that oil platforms may pose risk to storm-petrels, and the risk from these factors may differ depending on behavioral state. For example, a transiting bird may be more likely to collide with a platform than a foraging bird, and a foraging or resting bird may be more at risk from increased predation than a transiting bird. Because we do not have a high temporal resolution for our data and it is unknown exactly how and in what proportion different factors may negatively affect birds around oil platforms, we do not attempt to interpret risk from behavioral state beyond exposure time.

Hidden Markov Models (HMMs) are commonly used to categorize points in a GPS track into different states, allowing researchers to infer behavior at sea based on properties of the state (Boyd et al., 2014; Bennison et al., 2018; McClintock and Michelot, 2018). This method first calculates the step length (distance in km) and turning angle between each point. The mean step length and turning angle is then calculated for groups within the data, the number of which is predetermined. Each

group represents a distinct behavior known as a “behavioral state.” The chosen number of groups is the number of behaviors that the researchers expect to observe, and can be chosen based on previous studies, and/or by running the model several times with different numbers of groups and comparing the models using AIC.

We constructed all HMMs using the “*momentuHMM*” package in R (McClintock and Michelot, 2018). This package allows the addition of covariates to account for variations in turning angle within a behavioral state, and for variations in the probability of transitioning between states. We chose to classify the data into three states to align with previous studies (e.g., Boyd et al., 2014; Torres et al., 2017; Bennison et al., 2018), and because a three-state model fit better than a two-state model. We fit models with different combinations of *Hour* (of day) and *Bathymetry* (depth of ocean floor) as covariates. Bathymetric data were obtained from the package “*marmap*” (Pante and Simon-Bouhet, 2013). The HMM with both turning angle and state transition probabilities varying with hour was the best model for the main dataset (**Supplementary Figures 1, 2**, respectively). For the 2019 dataset, the HMM with hour covarying with transition probabilities was the best model, though it was only marginally better than the same model used for the larger dataset. So, the same model was used for all datasets to ensure consistency. The models showed little deviation from the assumptions involved (no obvious patterns in the pseudoresiduals, no skewness in the normal q-q plot, and no evidence of autocorrelation; **Supplementary Figure 3**). Three behavioral states were categorized. State 1 is characterized by short step lengths and tighter turning angles (**Figure 2**). State 2 has intermediate step lengths and turning angles that are wider than state 1 (**Figure 2**). State 3 is characterized by much longer step lengths and turning angles closer to zero (**Figure 2**), indicating that the bird was traveling over long distances in a relatively straight path. We therefore consider state 3 as “Transiting.” Because state 1 shows birds spending the most time in a concentrated area, they may be resting or actively feeding, but it is impossible to differentiate between

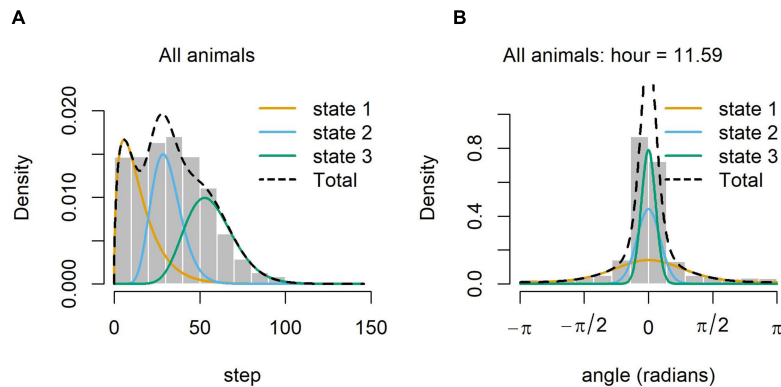


FIGURE 2 | Distributions of step lengths (km) and turning angles (degrees) for each behavioral state. Within each behavioral state, there is a range of step lengths and turning angles that can be associated with each point where the mean is the highest point of the smooth curve in both plots. Gray bars are histograms of the data. Plot **(A)** shows that the step lengths associated with state 1 are, on average, the shortest and the step lengths associated with state 3 are, on average, the longest. Step lengths associated with state 2 are usually between those of states 1 and 3. In **(B)**, the distributions of turning angles are shown for each state. Although the mean turning angle for all states was around 0, the distribution curve for state 3 is much steeper and tighter around 0 than those of states 1 and 2, which means that the turning angles associated with each state 3 point are most likely to be close to 0. The much flatter curve of state 1 means that sharper turning angles are more likely in this state. Again, the distribution of state 2 is between that of states 1 and 3.

these two behaviors with the 2-h sampling interval. We refer to state 1 as “Intensive Search.” State 2 will be referred to as “Extensive Search,” because birds slow their movement compared to transiting, likely in response to location of a food source or recognition of a feeding area, but cover a wider area compared to intensive search. Because the fit of the model can be improved with covariates and because other studies have deemed the HMM to be one of the best methods for modeling behavioral states in foraging seabirds (Bennison et al., 2018), we use the states produced by the HMM in our analyses.

Calculating Distance to Oil Platforms

We calculated the closest distance of each trip (assuming a straight line between each point; hereafter “platform proximity”) to an oil platform, noting both the time and behavioral state at the closest point (determined using the “spDistsN1” function of package “sp”; Pebesma and Bivand, 2005; Bivand et al., 2013). For each trip, sunrise and sunset times were obtained with the package “suncalc” (Thieurmel and Elmarhraoui, 2019), allowing us to determine if birds were closest to the platform at night or during the day. A light catch basin is the area around a lit structure within which light can presumably be seen by an animal and therefore could result in attraction to the structure. We calculated the number of birds that flew within the annual average (average radius = 5.33 km) and maximum (average maximum radius = 10.70 km) light catch basin of the oil platforms on the Grand Bank. These radius values were calculated using the average catch basin areas for platforms on the Grand Bank determined by Gjerdrum et al. (2021), and based on a light radiance cut-off value of $0.75 \text{ nW}\cdot\text{cm}^{-2}\cdot\text{sr}^{-1}$, determined from the maximum light radiance in areas distant from any light source and thus considered dark. We chose to use the same radius value for all platforms because the catch basin radius varies between platforms but also for each individual platform based on time, date, and weather factors (Gjerdrum et al., 2021).

To characterize the overlap with and potential risk of oil platform light attraction for breeding Leach’s Storm-Petrels, we calculated the average platform proximity and the proportion of trips in which an individual flew within the light catch-basin. The proportion of trips in which individuals were transiting when closest to an oil platform and the proportion of trips in which individuals were closest to the platform during the night (when the risk of light attraction is assumed to be highest) were also calculated. We estimated the time per trip that individuals spent within the average and maximum light catch basins by calculating the distance traveled within the catch basin and dividing by the average flight speed. Because Leach’s Storm-Petrels travel at different speeds depending on their behavior at sea, we calculated exposure duration with multiple possible flight speeds.

Kernel Home Range Analysis

To determine consistency in area use for Leach’s Storm-Petrels, we used Kernel Home Range Analysis to quantify spatial overlap among behavioral states, individuals, breeding phases, and years. Kernel Home Range analyses (Worton, 1989) were conducted using “adehabitatHR” (Calenge, 2006). We utilized the reference bandwidth smoothing parameter (Worton, 1989), as opposed to the bandwidth that minimizes the least square cross validation score (Worton, 1995; Seaman et al., 1999) as the latter can result in highly fragmented and under-smoothed utilization distributions (UDs) for large datasets with frequent (multiple per day) points (Kie, 2013). The UD provides a probability estimate of finding a storm-petrel within an area, so we also calculated the minimum utilization distribution that contains all four oil platforms. The 50, 64, and 95% Utilization Distributions (UDs) were constructed for the entire dataset; the 64% UD being the minimum % UD that overlapped with all four oil platforms on the Grand Bank. We used the 50% UD to estimate consistency in area use, and these were constructed for each year, for the breeding phases (using all incubation and chick-rearing trips), for

individuals, and for the behavioral states (Worton, 1989; Fieberg and Kochanny, 2005; Oppel et al., 2018).

Utilization Distributions Overlap

Overlap of 50% UD were conducted using the “kerneloverlap” function of the “adehabitatHR” package (Calenge, 2006). As recommended by Fieberg and Kochanny (2005), we used the Bhattacharyya Affinity Index (BAI) to measure similarity between UD. The BAI ranges from zero (no similarity) to one (completely similar). We also report the average percent overlap as these values complement the presented maps of the UD. We first calculated the overlap among behavioral states. Because the behavioral states occurred in distinct regions, we calculated the overlap for individuals, years, and breeding phase separately for transiting and foraging areas. Some individuals were only tracked for a single trip whereas others had up to nine total trips, so for calculations of overlap among individuals, we compared only the UD of individuals from their first trip to minimize behavioral bias from acclimation to the GPS device. We made annual comparisons of area use separately for each breeding phase, and we compared the breeding phases only in 2016, 2020, and 2021 (no tracking data were collected in 2017, and no chick-rearing data were collected in 2018 or 2019).

Statistical Models

The difference between chick-rearing and incubation in the proportion of time spent in each behavioral state was calculated with a test of equality of proportions. We fit three models to examine the sources of variation in total (1) trip distance, (2) trip duration, and (3) risk exposure (binary) using the package “lme4” (Bates et al., 2015). All regression models were created and assessed following the steps of Zuur and Ieno (2016), and all assumptions were checked according to Zuur et al. (2010). For all models, the trip, not the individual, was the unit of replication.

We looked at the variation of trip distance and trip duration with Year and Breeding Phase and included the individual bird ID as a random intercept (Equations 1 and 2). Although there were low outliers ($n = 8$) in the data for both models that caused violation of the normality assumption, removal of these points did not change the inference, so the final models included all points. The models of trip distance and trip duration did not violate the other assumptions of Gaussian distributed residuals.

$$\text{Total Trip Distance}_{ij} \sim N(\mu_{ij}, \sigma^2)$$

$$E(\text{Total Trip Distance}_{ij}) = \mu_{ij} \text{ and } \text{var}(\text{Total Trip Distance}_{ij}) = \sigma^2$$

$$\mu_i = \alpha + \beta_1 \cdot \text{Year}_{ij} + \beta_2 \cdot \text{Breeding Phase}_{ij} + ID_j + \varepsilon_{ij}$$

$$ID_j \sim N(0, \sigma_{ID}^2)$$

$$\varepsilon_{ij} \sim N(0, \sigma^2)$$

Equation 1. The general linear mixed model relating Total Trip Distance to Year (categorical) and Breeding Phase (categorical), where Total Trip Distance_{ij} is the distance in km for the *i*th

foraging trip of bird *j*, μ_{ij} is the mean and σ^2 is the variance of Total Trip Distance_{ij}, α is the intercept, βx are the computed regression coefficients, ID_j is the random intercept for each bird, ε_{ij} is the error term, $i = 1, \dots, 182$, and $j = 1, \dots, 70$.

$$\text{Total Trip Duration}_{ij} \sim N(\mu_{ij}, \sigma^2)$$

$$E(\text{Total Trip Duration}_{ij}) = \mu_{ij} \text{ and } \text{var}(\text{Total Trip Duration}_{ij}) = \sigma^2$$

$$\mu_i = \alpha + \beta_1 \cdot \text{Year}_{ij} + \beta_2 \cdot \text{Breeding Phase}_{ij} + ID_j + \varepsilon_{ij}$$

$$ID_j \sim N(0, \sigma_{ID}^2)$$

$$\varepsilon_{ij} \sim N(0, \sigma^2)$$

Equation 2. The general linear mixed model relating Total Trip Duration to Year (categorical) and Breeding Phase (categorical), where Total Trip Duration_{ij} is the time in hours for the *i*th foraging trip of bird *j*, μ_{ij} is the mean and σ^2 is the variance of Total Trip Duration_{ij}, α is the intercept, βx are the computed regression coefficients, ID_j is the random intercept for each bird, ε_{ij} is the error term, $i = 1, \dots, 182$, and $j = 1, \dots, 70$.

We used logistic regression to model variation in risk exposure (binary response: 1—flew within the light catch basin, 0—did not fly within the light catch basin) with Year, Breeding Phase, and Time of Approach (day or night), and included the individual bird ID as a random intercept (Equation 3). The model did not violate the assumptions of logistic regression.

$$\text{Risk}_{ij} \sim B(1, \pi_{ij})$$

$$E(\text{Risk}_{ij}) = \pi_{ij} \text{ and } \text{var}(\text{Risk}_{ij}) = \pi_{ij} \cdot (1 - \pi_{ij})$$

$$\text{logit}(\pi_{ij}) = \alpha + \beta_1 \cdot \text{Year}_{ij} +$$

$$\beta_2 \cdot \text{Breeding Phase}_{ij} + \beta_3 \cdot \text{Time of Approach}_{ij} + ID_j$$

$$ID_j \sim N(0, \sigma_{ID}^2)$$

Equation 3. The logistic mixed model relating risk exposure to light catch-basin around an oil platform (binary) to Year (categorical), Breeding Phase (categorical), and Time of Approach (categorical, day or night), where Risk_{ij} is the binary qualification of whether bird *j* flew within the average light catch-basin of an oil platform during the *i*th foraging trip, π_{ij} is the probability of success (bird flies within catch basin), α is the intercept, βx are the computed regression coefficients, ID_j is the random intercept for each bird, $i = 1, \dots, 182$, and $j = 1, \dots, 70$.

RESULTS

Recapture Rates and Device Effects

Our overall recapture rate was 72%, and data were retrieved from 92% of recaptured devices (Table 1). All recaptured birds had

the GPS attached. Devices that did not collect data were likely damaged while being worn by the bird, resulting in water ingress or antenna damage that prevented the device from picking up a satellite signal. Over 5 years, we captured the foraging tracks of 85 individual Leach's Storm-Petrels from Gull Island, resulting in 212 total trips (182 complete; **Table 1**). Most complete trips (69%) were during the chick-rearing phase (31% during incubation; **Table 1**). Bird mass did not change significantly during the deployment period ($t = -1.59$, $df = 86$, $p = 0.12$), indicating that carrying a GPS did not negatively affect the birds' condition.

Area Use and Utilization Distributions Overlap

Leach's Storm-Petrels breeding at Gull Island were found across most of the Grand Bank as well as adjacent deeper waters during the study period (**Figure 3**). Breeding storm-petrels tended to forage over deeper waters off the continental shelf edge (**Figure 4**). Some individuals also foraged closer to Gull Island, either after returning from a longer trip on which they foraged off-shelf, or on a shorter trip where they foraged exclusively in the area (**Figures 4, 5** and **Supplementary Figure 4**). Individual storm-petrels performed both short and long trips (**Figure 5**), but there was no obvious alternating pattern (**Supplementary Table 1**).

There was high similarity between the UD for intensive and extensive search behavioral states (together termed "foraging"), and the UD for transit and foraging behaviors were more dissimilar (**Supplementary Table 2**). Because birds did not tend to transit and forage in the same locations, we investigated the overlap of foraging areas and transiting areas separately to better understand consistency in area use. The average similarity between the UD of all individuals (as measured by the average of each calculated BAI or % overlap for every possible pair of individuals) was higher for transiting locations than for foraging locations (**Supplementary Table 2**). The average similarity in UD between incubation and chick-rearing was generally high and was higher for transiting areas than for foraging areas (**Supplementary Table 2** and **Figure 6**). Within incubation, foraging areas were more dissimilar than transiting areas among years (**Supplementary Table 2** and **Figures 6A,C**). This difference was less pronounced during chick-rearing (**Supplementary Table 2** and **Figures 6B,D**). Overall, the area used to transit was more consistent (higher overlap among individuals, breeding phases, and years) than the area used to forage (**Supplementary Table 2**).

Variation in Trip Structure and Platform Proximity

The proportion of time spent in each behavioral state was similar during incubation and chick-rearing (Intensive: $\text{prop}_{inc} = 0.38$, $\text{prop}_{chick} = 0.33$, $\chi^2 = 0.047$, $df = 1$, $p = 0.83$; Extensive: $\text{prop}_{inc} = 0.30$, $\text{prop}_{chick} = 0.30$, $\chi^2 < 0.001$, $df = 1$, $p = 1$; Transit: $\text{prop}_{inc} = 0.33$, $\text{prop}_{chick} = 0.37$, $\chi^2 = 0.045$, $df = 1$, $p = 0.83$). Total trip distance and trip duration did not vary between years (distance: $\chi^2 = 6.32$, $df = 4$, $p = 0.18$; duration: $\chi^2 = 3.99$, $df = 4$, $p = 0.41$), but trips during chick-rearing were

significantly shorter in both total distance and duration (distance: mean difference = 86.15 km, $\chi^2 = 4.39$, $df = 1$, $p = 0.036$; duration: mean difference = 7.78 h, $\chi^2 = 5.20$, $df = 1$, $p = 0.023$; **Table 2** and **Supplementary Tables 3, 4**).

The average platform proximity was 65 km (range: 0.3–287.5 km; **Figure 7**), and on 89.0% of all trips, Leach's Storm-Petrels passed closest by the oil platforms during the day. In 71.4% of all trips, birds were transiting when they flew closest to the oil platforms. Birds flew within the average light catch basin of an oil platform in 17.5% of trips and flew within the maximum average catch basin in 25.8% of trips. In just 1.1% of all trips, birds flew within the average light catch basin at night, while during the remainder of trips (16.4%), they traversed the average light catch basin during the day. Of birds that flew within the average catch basin of the platforms, 71.9% were transiting.

When considering the average flight speed of transiting storm-petrels (~30 km/h), birds spent an average of 21 min (60 min in maximum light catch basin) within the light catch basin of an oil platform (**Supplementary Table 5**). The exposure duration within the average light catch basin ranged from 6 min (minimum for transit flight speed) to 3.4 h (maximum for intensive search flight speed) depending on the flight speed (**Supplementary Table 5**). The exposure duration within the maximum light catch basin ranged from 2.7 h (minimum for transit flight speed) to 10.6 h (maximum for intensive search flight speed) depending on the flight speed (**Supplementary Table 5**). 25.0% of the birds that flew within the average light catch basin flew within the light catch basin of more than one oil platform (two maximum). 53.2% of birds exposed to the maximum light catch basin flew within multiple maximum light catch basins (one platform: 46.8%, two platforms: 42.6%, three platforms: 10.6%). The odds of a storm-petrel flying within an average light catch basin did not vary with year ($\chi^2 = 1.46$, $df = 4$, $p = 0.83$), breeding phase ($\chi^2 = 0.039$, $df = 1$, $p = 0.84$), or time of day (whether the bird flew within the catch basin during the day or at night; $\chi^2 = 1.35$, $df = 1$, $p = 0.25$; **Supplementary Table 6**).

DISCUSSION

The objective of this study was to examine the exposure of Leach's Storm-Petrels to brightly lit offshore oil platforms while foraging during the breeding season. To better understand exposure and risk, we examined variation in foraging trip structure, behavior near platforms, and the timing and duration of platform proximity within and between years. Likely owing to their dual temporal constraints involved with nocturnal colony visitation and nocturnal foraging off the shelf-edge, Leach's Storm-Petrels flew past oil platforms during the day in nearly 90% of trips. Leach's Storm-Petrels were no more likely to fly within a light catch basin if they passed closest by the platform during the day or at night (**Supplementary Table 6**). While attraction to artificial light during the day has been demonstrated for some animals (Baik et al., 2020), there is no evidence that storm-petrels are attracted to light during daylight. Still, studies of light attraction in different

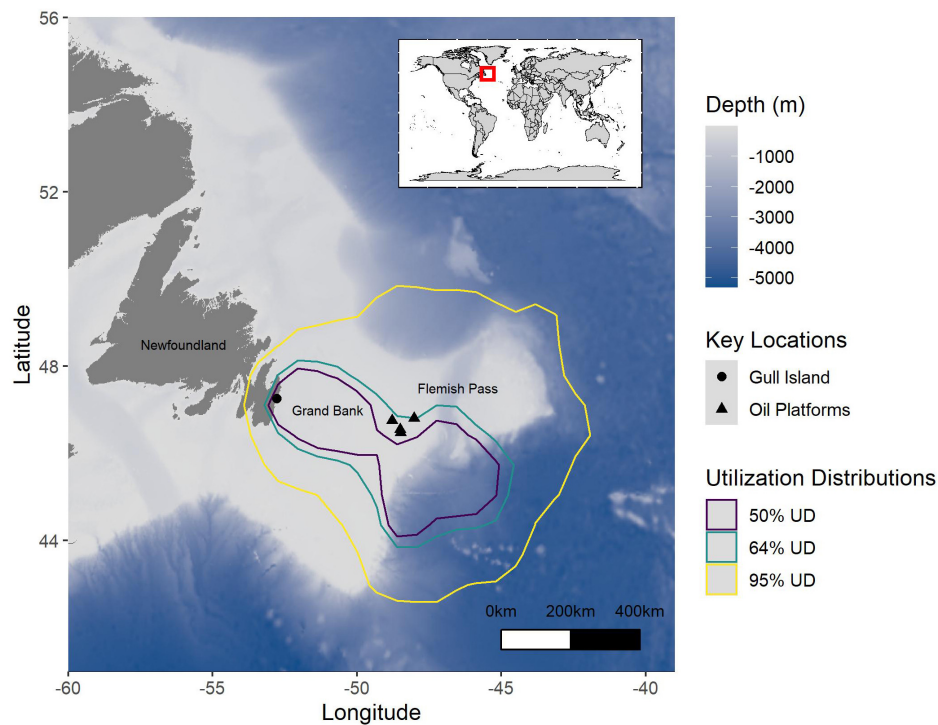


FIGURE 3 | The full Utilization Distributions (50%: purple, 64%: teal, 95%: yellow) for Leach's Storm-Petrels breeding on Gull Island, Witless Bay, Newfoundland and Labrador, Canada from 2016 to 2021. Note that the 64% Utilization Distribution includes all oil platforms. The large black triangles represent the oil platforms, and the large black circle represents Gull Island. The bathymetry is represented where darker blue indicates deeper water.

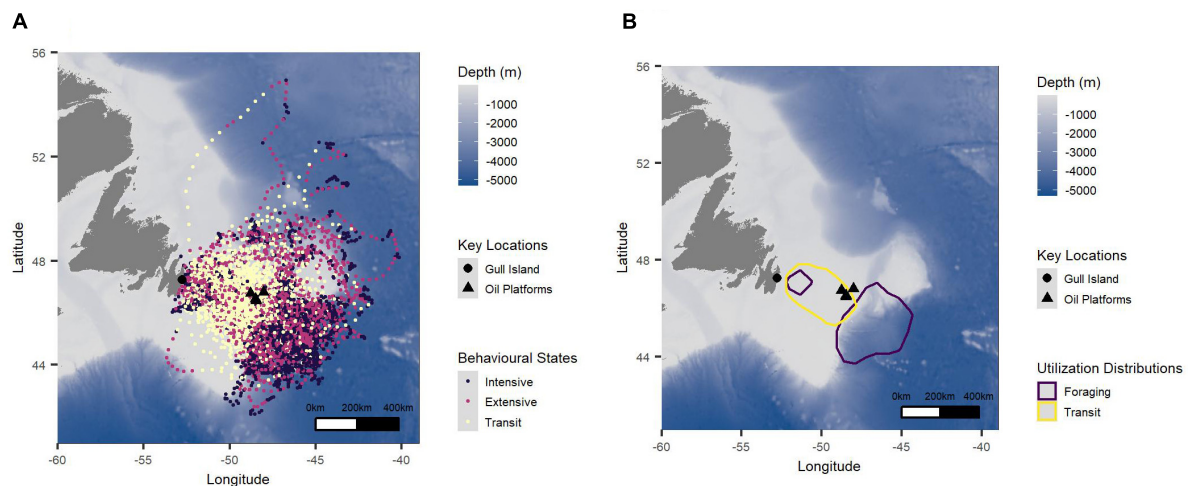


FIGURE 4 | (A) All tracking points colored by behavior (intensive search: black, extensive search: pink, transit: yellow) and **(B)** 50% utilization distributions of transiting (yellow) and foraging (intensive and extensive states combined; purple) locations for Leach's Storm-Petrels in the study sample from Gull Island, Witless Bay, Newfoundland and Labrador, Canada from 2016 to 2021. The large black triangles represent the oil platforms, and the large black circle represents Gull Island. The bathymetry is represented where darker blue indicates deeper water. Data from all years and breeding phases are included in these figures.

environmental lighting conditions should be conducted to better understand the risk to seabirds. This is particularly important on the Grand Bank where foggy conditions are common (Isaac et al., 2020). Light may disperse differently in fog, influencing the size of the light catch basin. Additionally, Leach's

Storm-Petrels may be attracted to oil platforms in other ways. For example, the artificial reef effect could be at play, and storm-petrels may navigate toward a potentially increased food source via olfaction or social cues (Nevitt and Haberman, 2003; Dierschke et al., 2016; COSEWIC, 2020). These mechanisms

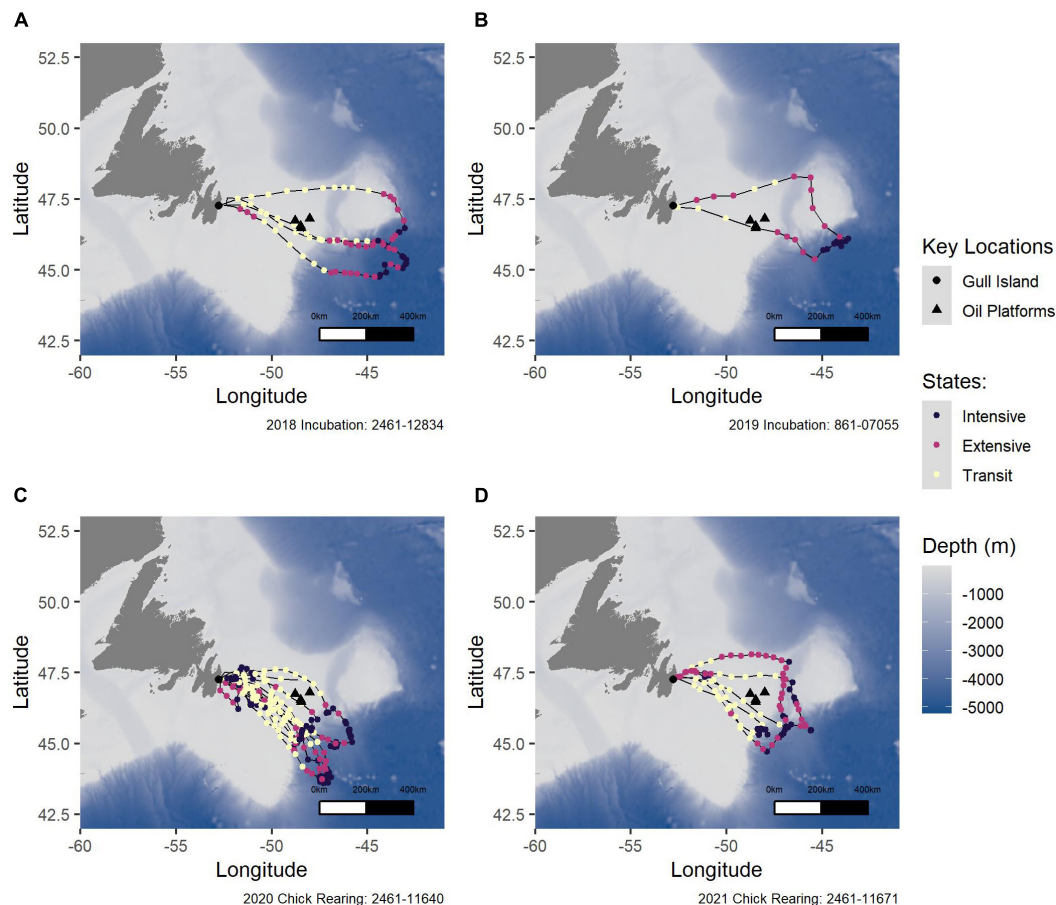


FIGURE 5 | A selection of tracks from individual Leach's Storm-Petrels in the study sample from incubation in (A) 2018, (B) 2019, and from chick-rearing in (C) 2020, and (D) 2021. Black points represent intensive search, pink points represent extensive search, and yellow points represent transiting. The large black triangles represent the oil platforms, and the large black circle represents Gull Island. The bathymetry is represented where darker blue indicates deeper water. The 8- or 9-digit numbers indicate the ID of each bird.

require further study to understand the extent and radius of attraction and risk.

At the population level, Leach's Storm-Petrels exhibited similar at-sea area use among years and between incubation and chick-rearing, although incubating birds tended to forage farther off the continental shelf than chick-rearing birds (Figure 6). The areas used for transiting were more consistent than those used for foraging (Supplementary Table 2 and Figure 6). This consistency may result from the fact that all tracked birds were from the same colony, as Leach's Storm-Petrels in Atlantic Canada tend to show colony-level consistency in area use but differences in area use among colonies (Hedd et al., 2018). Birds tended to transit over the Grand Bank, and intensively and extensively searched beyond the edge of the shelf, mainly within the Flemish Pass and east of the Grand Bank, though at times near the colony (Figures 4, 6). There was considerable overlap in the areas in which birds intensively and extensively searched, but lower overlap between foraging areas and transit areas (Supplementary Table 2 and Figure 4B). This suggests that, at the population level, storm-petrels breeding on Gull Island

likely do not forage to any great degree over the Grand Bank. The utilization distributions observed in this study are consistent geographically with previous tracking of Leach's Storm-Petrels from this colony (Hedd et al., 2018). At-sea surveys in the region conducted from 1966–1990 and 1998–1999 also indicate high use of shallow water habitats (near colonies) and deeper waters off the shelf (Hedd et al., 2009). Myctophids, mesopelagic fish that migrate to the surface at night, dominate the diets of Leach's Storm-Petrels in the region, suggesting why foraging effort is concentrated over deep waters off the continental shelf edge (Hedd and Montevecchi, 2006; Hedd et al., 2009).

At the individual level, there was generally low overlap in area use, and foraging areas tended to be less consistent than transiting areas (Supplementary Table 2). These findings concur with Oppel et al. (2018) who found low individual overlap for several wide-ranging seabird species, including storm-petrels. This result emphasizes that, at the population level, area use tends to be consistent among years and between breeding stages, but individual birds tend to use different foraging areas. This could mean that individuals may experience differing levels of risk, so

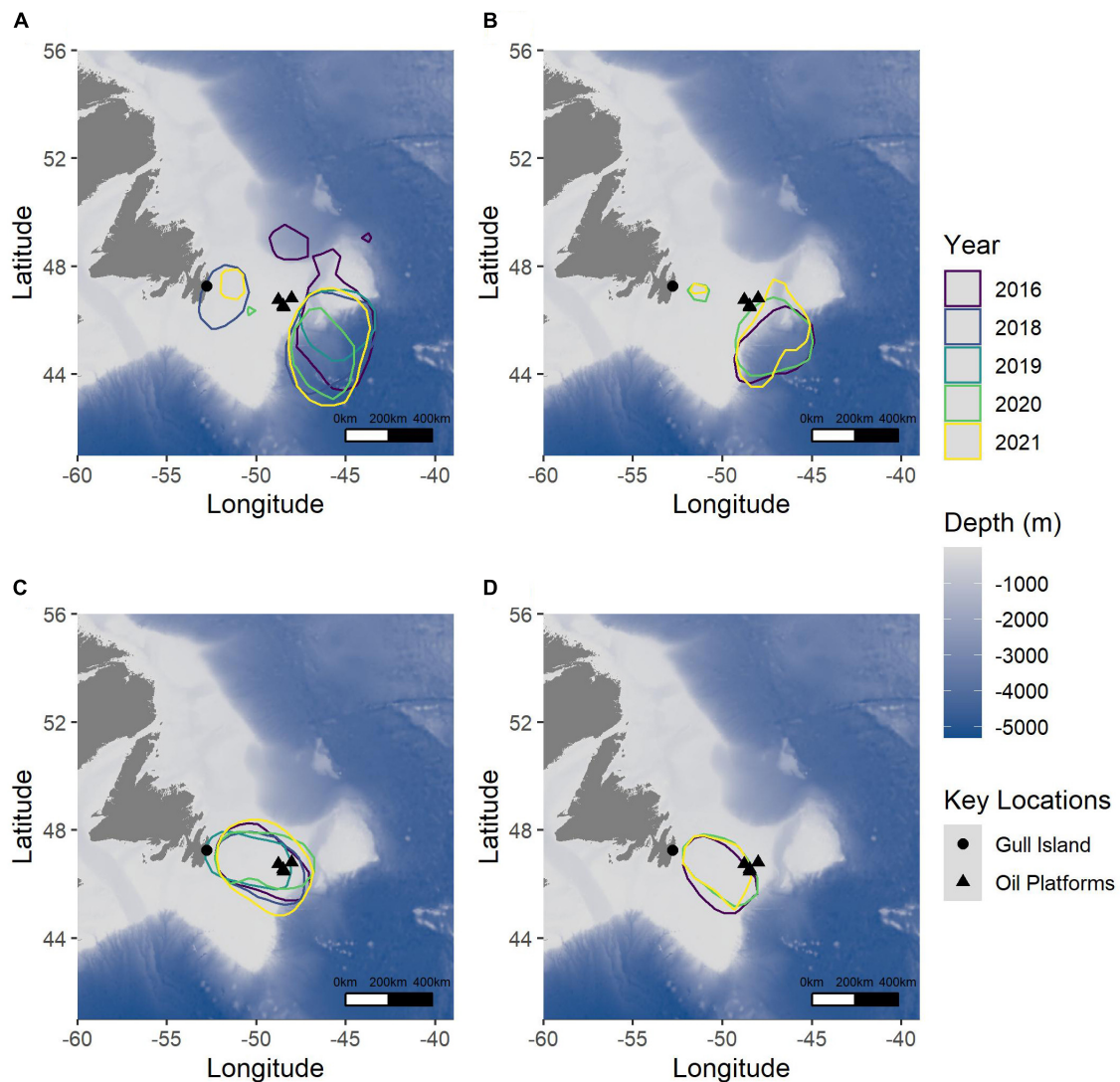
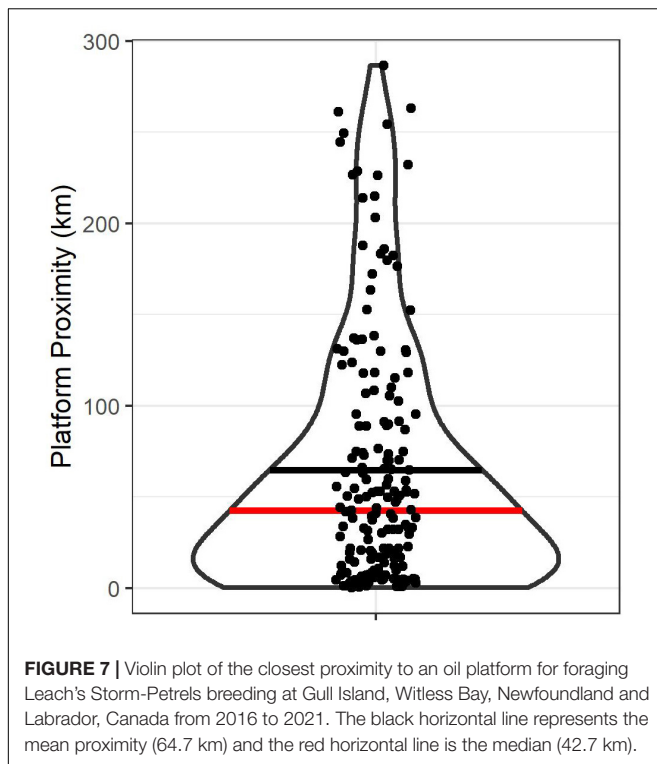


FIGURE 6 | 50% Utilization Distributions of Leach's Storm-Petrels breeding on Gull Island, Witless Bay, Newfoundland and Labrador, Canada, in 2016–2021 for foraging areas (intensive and extensive) during (A) incubation and (B) chick-rearing, showing reduced foraging areas which are closer to the edge of the Grand Bank during chick-rearing. Transiting areas were not modified between (C) incubation and (D) chick-rearing. The large black triangles represent the oil platforms, and the large black circle represents Gull Island. The bathymetry is represented where darker blue indicates deeper water.

TABLE 2 | Average trip distance \pm SD and duration \pm SD by year and breeding phase for Leach's Storm-Petrels breeding at Gull Island, Witless Bay, Newfoundland and Labrador, Canada from 2016–2021.

Year	Breeding phase	Average trip distance (km)	Average trip duration (days)
2016	Incubation	1,476.9 \pm 389	3.41 \pm 0.99
2016	Chick-rearing	1,352.9 \pm 438	2.99 \pm 0.98
2018	Incubation	1,241.6 \pm 561	2.93 \pm 1.33
2019	Incubation	1,680.2 \pm 63	3.76 \pm 0.46
2020	Incubation	1,645.3	5.00
2020	Chick-rearing	1,324.6 \pm 410	2.84 \pm 0.94
2021	Incubation	1,622.0 \pm 503	3.54 \pm 1.22
2021	Chick-rearing	1,318.2 \pm 287	3.01 \pm 0.88

No SD is given for 2020 incubation because only one complete trip was collected at this time.



further research into individual consistency in foraging area use, at-sea behavior, and risk exposure is needed.

Neither trip distance nor trip duration varied significantly among years (**Supplementary Tables 3, 4**). Within years, however, trips during chick-rearing tended to have shorter duration and total distance (**Supplementary Tables 3, 4**). This is consistent with our prediction and aligns with findings for other Procellariiformes (Weimerskirch et al., 1993; Hedd et al., 2014; Bolton, 2021; De Pascalis et al., 2021). The most likely explanation for this pattern is that breeding birds are reducing their foraging trips in response to the high energetic demands and need for frequent provisioning of the chick (Ricklefs et al., 1980). Storm-petrels took both short and long trips, but the occurrence of short trips cannot explain the shorter overall trip distance and duration we observed. Short and long trips occurred in no obvious pattern in our sample, and short trips were equally likely in incubation and chick-rearing (**Supplementary Table 1**). Short trips during chick-rearing likely function primarily to provision chicks (Chaurand and Weimerskirch, 1994), while short trips during incubation likely reflect mates not switching duties when the foraging partner returned to the nest (as in Shy Albatrosses *Thalassarche cauta*, Hedd and Gales, 2005). This result also cannot be explained by changes in behavioral patterns, as incubating and chick-rearing adults spent proportionally similar time foraging vs. transiting on their trips. Overall, the birds spent about a third of their time in each behavioral state, regardless of breeding stage. Because Leach's Storm-Petrels are central place foragers, they must optimize energy expenditure when foraging (Burke and Montevecchi, 2009; Elliott et al., 2009). They must spend enough time foraging to make a long trip

worthwhile. Digestion, which likely occurs when storm-petrels are in behavioral state 1 (intensive search) and is mutually exclusive from active foraging (Rosen et al., 2007), is also an important and time-consuming component of the foraging trip. Leach's Storm-Petrels reduce food volume by concentrating ingested prey as high-energy oils which are used by the adult or fed to chicks (Place et al., 1989). Rather than changing the proportion of time spent on specific behaviors, Leach's Storm-Petrels appear to compensate for increased energetic demands during chick-rearing in different ways. For example, body mass loss during early chick-rearing increases flight efficiency by 14% (Niizuma et al., 2001). While previous research has identified population-level consistency in the foraging locations of Leach's Storm-Petrels across years and throughout incubation (Hedd et al., 2009, 2018; Pollet et al., 2014b), this is, to our knowledge, the first study to compare foraging locations and behavior between incubation and chick-rearing.

The home range of Leach's Storm-Petrels overlapped with oil and gas production platforms on the Grand Bank (**Figure 3**; Hedd et al., 2018). They flew within 65 km of an oil platform on average throughout the breeding period. Overall, storm-petrels flew within the average light catch basin of oil platforms on almost 20% of foraging trips and within the maximum light catch basin on more than 25% of trips. The risk of flying within the light catch basin of an oil platform did not vary among years or between incubation and chick-rearing (**Supplementary Table 6**). Of birds that flew within the average light catch basin, most (72%) were transiting. When near a platform, storm-petrels are at risk of collision, oiling, incineration in the flare, predation, and exhaustion from flying around the illuminated structure (Wiese et al., 2001; Montevecchi, 2006; Burke et al., 2012; Ronconi et al., 2015; Dierschke et al., 2016). Prolonged exposure likely increases the likelihood of risk. Transiting Leach's Storm-Petrels spent an average of about 20 min within light catch basins of oil platforms on the Grand Bank, but exposure durations ranged from just a few minutes to more than 3 h, depending on a bird's behavior when near the platform. A quarter of the birds that flew within a light catch basin were exposed to multiple oil platforms on their foraging trips. Our analyses indicate that the duration of exposure to oil platforms may be minimal given that the birds are usually rapidly transiting to or from the foraging area when they pass.

Our calculations were based on the assumption that storm-petrels fly in a straight line between locations, though they may have flown closer or farther away from the platforms than we calculated. We used 5.33 km for the average light catch basin and 10.70 km for the maximum light catch basin, but the catch basin of gas flares can be much greater than the values found by Gjerdrum et al. (2021). We also used the average annual value, though the size of the catch basin can vary within the year, with flare heights that are higher when oil cannot be offloaded in poor weather, and with other weather conditions (e.g., fog; Gjerdrum et al., 2021). Importantly, we can only report results for the birds that we recaptured. The fate of birds that we did not recapture (about 30%, **Table 1**) is unknown. We could simply have missed their return, they may have abandoned their nest, or they may have died. Our recapture rates were similar to or better than those of other tracking studies of this species (Pollet et al., 2014b;

Hedd et al., 2018; Mohammad Fahmy, unpublished data). Given that strandings of adults on oil platforms during the breeding season are not uncommon (Gjerdrum et al., 2021), it is possible that some of these unrecovered birds died from interactions with oil platforms. Hence, it is possible that the percentage of trips in which storm-petrels from Gull Island fly within the light catch basin of oil platforms at night is higher than 1.1% and that the assumed risk is higher than reported here.

Considerable effort is being invested into risk assessment for Leach's Storm-Petrels across Atlantic Canada with a focus on breeding adults (e.g., Hedd et al., 2018; d'Entremont et al., 2020; Wilhelm et al., 2020; Collins, 2021; COSEWIC, 2020; Hoeg et al., 2021). Studies indicate that Leach's Storm-Petrels in the region strand on oil platforms, vessels, and at brightly illuminated coastal sites during the breeding season, but the greatest number of stranded birds are found during the fall when fledglings are departing colonies for the first time (Davis et al., 2017; Gjerdrum et al., 2021; Wilhelm et al., 2021; WM, unpublished data). These circumstances raise concern about risk posed by light attraction for adults and other age-classes outside the breeding period. Light pollution poses a major risk to seabirds globally, with tube-nosed seabirds being especially vulnerable (Reed et al., 1985; Wiese et al., 2001; Montevecchi, 2006; Poot et al., 2008; Burke et al., 2012; Day et al., 2015; Rodríguez et al., 2017a; Rebke et al., 2019). Based on the expansive area covered by Leach's Storm-Petrels during the non-breeding period (Pollet et al., 2014a, 2019), individuals from this and other populations will be exposed to oceanic sources of anthropogenic light such as boats, oil platforms, and drill rigs. Very little is known about juvenile survival, but the majority of seabirds that have been recovered from light-polluted areas are juveniles (Rodríguez et al., 2017b; Atchoi et al., 2020; Wilhelm et al., 2021). The visual system of Leach's Storm-Petrel chicks develops very slowly, and their eyes may not be fully developed until after fledging (Mitkus et al., 2018). Atchoi et al. (2020) proposed a connection between the slow development of the visual system and the increased level of juvenile attraction to light. Adults and juveniles could, therefore, differ in their level of vulnerability to light attraction, owing to differences in eye structure (Mitkus et al., 2018).

Mitigation efforts have been investigated regarding light sources. Different wavelengths of light appear to differ in their level of attractiveness (Montevecchi, 2006). There is, however, disagreement over the least attractive wavelengths to birds. Some studies have found that white and red light are the most attractive (Poot et al., 2008), whereas others have found that white, green, and blue light attract more migrating birds (Rebke et al., 2019; Syposz et al., 2021). The rapidly increasing use of bright LEDs, which are a major source of short blue wavelength light, is a problematic development (Rodríguez et al., 2017a; Hung et al., 2021). Mitigation strategies such as shielding light from unnecessary skyward projection (Reed et al., 1985), or changing the type of light source (i.e., LED vs. high-pressure sodium; Rodríguez et al., 2017a), have a range of efficacy that depends upon the species and, likely, the weather (Wilhelm et al., 2013).

Continued research on the risks of light attraction to Leach's Storm-Petrels is needed and should be broadened to include vessel and coastal lighting, to assess the risks at different times

of the year (e.g., Wilhelm et al., 2021), and to assess the risks for individuals of different age groups. Further research on the visual system of Leach's Storm-Petrels will inform best practices moving forward. Researchers and governments should work with corporations that produce oceanic light pollution to develop and implement mitigation strategies to reduce the attraction of marine birds.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by the Memorial University of Newfoundland Animal Care Committee and by Environment and Climate Change Canada's Eastern Wildlife Animal Care Committee.

AUTHOR CONTRIBUTIONS

This research was produced as a part of the Master of Science thesis of SC. SC: conceptualization, methodology, investigation, formal analysis, and writing (both original draft and review and editing). AH: conceptualization, methodology, investigation, formal analysis, and writing (reviews and editing). DF: methodology, investigation, formal analysis, and writing (review and editing). DW: writing (review and editing). WM: conceptualization, methodology, investigation, writing (both original draft and review and editing), and supervision. All authors contributed to the article and approved the submitted version.

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Space and Habitat Utilization of the Red King Crab (*Paralithodes camtschaticus*) in a Newly Invaded Fjord in Northern Norway

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The red king crab (RKC, *Paralithodes camtschaticus*) was introduced to the southern Barents Sea in the 1960s with the aim to develop a new, commercially attractive stock of the species. In the subsequent decades, the stock has indeed become abundant and widespread, but the species' presence also implies intense predation on benthic biota and thereby severe degradation of benthic ecosystems. Our capacity to monitor and harvest the species efficiently is therefore imperative. Yet, fishermen report highly variable catches despite little variation in the timing and location of fishing, possibly induced by the species' migratory behavior, which makes the search for crab aggregations time consuming and expensive. Previous studies have shown that the RKC is capable of conducting long-distance migrations, and suggest that the species conduct seasonal migrations between shallow (winter- and springtime) and deep waters (summer and autumn). Here, we applied telemetry to investigate the migratory behavior and habitat utilization of 37 adult individuals of the RKC in a relatively shallow fjord in northern Norway from late May until early November. Approximately half of the crabs ($n = 16$) left the study area early during the study period, but some individuals ($n = 3$) were recaptured between 53 and 147 km away from the study area, confirming that the RKC may conduct long-distance migrations. In contrast to expectations, most of the remaining individuals of RKC ($n = 16$) stayed for a prolonged summer and autumn period and used a limited portion of the fjord. These crabs responded quickly to changes in ambient water temperature, seeking deeper and colder waters masses when the temperature in shallower waters increased. Several individuals showed nearly identical spatio-temporal distributions, which supports earlier observations of crab aggregations. Our data indicates that the area utilization of the RKC is affected by trade-offs between biotic and abiotic factors, in which sub-optimal water temperatures may be tolerated provided appropriate access to food. Thus, our findings suggest that the current knowledge of RKC seasonal migration patterns may need to be revised, which in turn will have implications for managers and the fishing industry. This study demonstrates the high potential of telemetry studies to yield new, high-resolution data and knowledge of species' ecology.

Keywords: crustaceans, efficient fisheries, seasonal variation, migration, temperature, trade-offs

INTRODUCTION

The red king crab (RKC, *Paralithodes camtschaticus*) is indigenous to the northern Pacific Ocean, but was introduced at the Murman coast (Russia) of the Barents Sea in the 1960s (Orlov and Ivanov, 1978), and has since increased in abundance and expanded its spatial distribution. Dense occurrences of the RKC are currently found from Kolguyev Island (eastern Barents Sea, Russia) in the east to the city of Tromsø, Troms and Finnmark County (Norway) in the west, and the crabs are most numerous in coastal areas (Britayev et al., 2010; Windsland et al., 2014). In Norway, the RKC has high commercial value (first-hand value of catches in Norwegian waters in 2019: ~30,000,000 €).¹ In Norwegian waters, the RKC is managed according to two different approaches. In the areas east of 26°E (North Cape; **Figure 1A**), the fishery follows a conventional management regime in which both males and females above the minimum landing size of 130 CL can be exploited throughout the year (e.g., Anon, 2019). West of this border an eradication fishery is implemented (Anon, 2007). Accurate monitoring, management and effective harvesting rely on detailed knowledge of the species' distribution, population structure, and habitat use, features that are likely driven by trade-offs between crab density, food availability, and water temperature (Christiansen et al., 2015). Yet, these features are challenging to assess due to the species' migratory behavior.

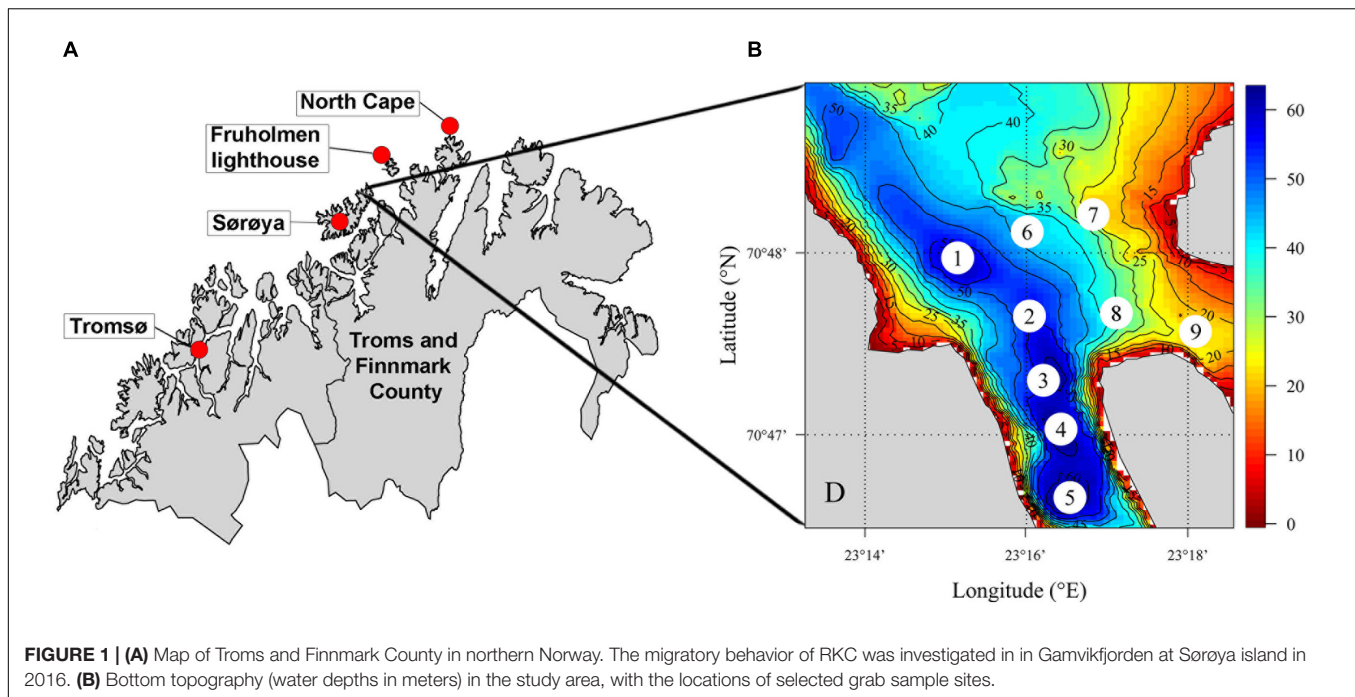
The RKC is highly mobile and exhibits both seasonal habitat shifts and considerable long-distance migration. In Northern Pacific waters, individuals of both genders were shown to move > 10 km day⁻¹ (Marukawa, 1933), whereas in Alaska, an average walking distance of nearly 1 km day⁻¹ was maintained for 200 days (Hayes and Montgomery, 1963). Similarly, tag-recapture investigations in Norwegian waters confirm that the RKC is capable of long-range (> 100 km) migrations (Windsland et al., 2014). However, most investigations indicate that the RKC largely operates at small spatial scales and avoids extensive migrations (Hayes and Montgomery, 1963; Stone et al., 1992; Windsland et al., 2014), typically residing in fjords and coastal waters (Pinchukov and Sundet, 2011). Within these local home ranges, the RKC is assumed to conduct seasonal migrations between shallow mating areas (during winter- and springtime) and deeper feeding areas (summer and autumn; Sundet and Hjelset, 2010). In another fjord in northern Norway, where the seasonal variation in the depth distribution of RKC was investigated using traps, catches of adult males were made in shallow waters (50 m) in the period between November to May (Sundet and Hjelset, 2010). On the other hand, the catches of adult females in shallow waters mainly occurred during the months January–March (Sundet and Hjelset, 2010). Furthermore, Sundet and Hjelset (2010) speculated that the poor catches of females in April and May were not due to an absence of individuals, but rather due to a reduced tendency to enter traps caused by a low feeding activity during reproductive activities. From June through September (males) or November (females), adult RKC were almost exclusively

caught in deeper waters (≥ 150 m; Sundet and Hjelset, 2010). Furthermore, although the RKC tolerates water temperatures of > 15°C (Rodin, 1989), laboratory studies indicate that the RKC prefers water temperatures between 2.5 and 3.5°C and avoid water temperatures > 4°C (Christiansen et al., 2015). As such, seasonal variation in ambient water temperatures plausibly promote migrations between shallow and deep waters. Nevertheless, divers frequently report observations of adult RKC in shallow waters during summertime (Aune, pers. obs.), which suggest that exceptions from the seasonal migration pattern are common. Observations from the Russian part of the Barents Sea suggest that the RKC prefers sandy and muddy sediments and topographies characterized by underwater slopes (Anisimova and Lubin, 2008). However, most data on RKC distributions have been obtained by means of trap fisheries (commercial and scientific) and are therefore biased by variation in the species' catchability. Indeed, low catchability of the RKC may occur due to life history events such as reproduction and molting (e.g., Sundet and Hjelset, 2010). Moreover, a combination of factors including aggregative behavior, high mobility and seasonal variation in habitat utilization suggest that it is challenging to predict the species' actual distributions in time and space. Consequently, fishermen report highly variable catches despite low variability in the timing and location of the fishery. Indeed, high-resolution data describing RKC habitat use and migratory and aggregative behavior are largely lacking, and the current knowledge of the species' general migrations is therefore uncertain.

The RKC is omnivorous, and ~100 prey species have been recorded in their stomachs, mostly including polychaetes, mollusks, crustaceans, echinoderms, fish, and algae (Britayev et al., 2010; Falk-Petersen et al., 2011; Fuhrmann et al., 2017). The diet in the southern Barents Sea is comparable to that in their home range in the northern Pacific Ocean (Falk-Petersen et al., 2011). Although the king crab is a generalist, it seems to prefer certain types of prey, such as polychaetes and bivalves (e.g., the scallop, *Chlamys islandica*; Jørgensen and Primicerio, 2007; Britayev et al., 2010). The RKC has been shown to effect the ecosystem structure and function in areas where it is abundant, causing bioturbation and abundance declines of taxa common in the northeast Atlantic including non-motile polychaetes, bivalves, and echinoderms (Falk-Petersen et al., 2011; Oug et al., 2011, 2018). This fact, and the recognition that it is an introduced alien species, requires authorities to enact policies to limit the species' footprint. To facilitate such efforts, detailed knowledge of the species' seasonal variation in migratory behavior and habitat utilization is required.

In this study, we applied acoustic telemetry to investigate the summer and autumn migratory behavior of the RKC in Gamvikfjorden, a fjord in northern Norway recently invaded by the species. As a consequence of the high but strongly variable catches of the RKC in the fjord and adjacent areas during recent years, the fishermen spent considerable amounts of time and fuel searching for crab aggregations. This issue motivated the implementation of a field study aiming to shed light on drivers of the species' spatio-temporal distribution patterns. Focusing on a period of > 5 months (the 24th of May to the 1st of November 2016), we integrated triangulated telemetry data from 37 adult

¹ www.ssb.no/fiskeri



(CL = 15.5–20.5 cm) RKC individuals with high-resolution data on bathymetry and water temperature. Our overall aim for the study was to obtain detailed data and knowledge on RKC environmental preferences, migratory behavior, and activity level (e.g., walking speed), to facilitate effective monitoring, management and harvesting of this introduced species.

Aiming to assess how telemetry data correspond with our current understanding of RKC seasonal migrations, we hypothesized that

1. A proportion of the tagged RKC individuals would reside in the study area for a prolonged period.
2. The crabs would show seasonal variation in behavior, including area utilization and habitat choice (e.g., bottom depth and water temperature).

MATERIALS AND METHODS

Study Area

Gamvikfjorden is located at the north-western side of the island Sørøya in northern Norway (Figures 1A,B). The study area extended across most of the fjord (Figure 1), with direct access to the climatic and oceanographic conditions of the Barents Sea to the north. The fjord is deeper (maximum depth is ~63 m) than the area in the 5 km radius outside the fjord mouth (20–50 m), and the fjord bathymetry and topography is steep on the western side and in the inner parts, whereas flatter and partially sandy on the eastern side. The study area included the inner and central parts of the fjord (Figure 1), with water depths ranging between 1 and 63 m (mean depth of study area ~35 m).

Investigations of Seafloor Topography, Sediments, and Benthic Fauna

High-resolution seabed topography data were obtained from the Norwegian Mapping Authority and aggregated to a raster grid with a spatial resolution of 35 m × 35 m (Figure 1B).

Sediment sampling using a grab (0.1 m² van Veen grab equipped with 2 × 5 kg lead weights) was conducted at 9 locations within the study area to collect data on sediment quality (texture, chemistry) as well as composition and density of benthic fauna (macrofauna and infauna known to be consumed by RKC). The sediment sampling was conducted on the 12th of October 2019. The sediment sample sites were located along gradients of bottom depth and distance from the fjord mouth (Figure 1B and Supplementary Table 1). Sediments from the upper 5 cm were selected from one sediment sample per location for common chemical and sediment analyses [total organic carbon (TOC), total nitrogen (TN), and the TOC/TN (C/N) ratio]. The coarseness of the sediments was defined as the percentage of the sediment grains being < 0.063 mm (i.e., % pelite), where a high pelite percentage indicates fine sediments. The remaining sediments in the grab were sieved through 1 mm sieve, and the composition of the benthos assemblage was identified to major taxonomic groups and counted on site (Supplementary Table 2).

Tagging, Tracking, and Positioning

Baited square pots were used to catch 37 adult RKC individuals (24 males and 13 females) in Gamvikfjorden on the 24th of May 2016 (Table 1). The crabs were in the body weight (BW) range 1.2–3.5 kg, carapace width (CW) range 13–20 cm and carapace length (CL) range 15.5–20.5 cm. The CL values implies that all crabs were sexually mature (Hjelset et al., 2009). Each crab was tagged with an acoustic transmitter (tag types ATID-MP-13 or

TABLE 1 | Overview of acoustically tagged RKC included in a telemetry study in Gamvikfjorden, northern Norway, in 2016.

ID	Sex	BW	CL	CW	RESTIME	NREG
#749	Male	2.6	18.5	18	1	16
#239	Female	1.9	18	16.5	1	25
#241	Female	1.6	17	15	1	17
#748	Male	3	18.5	20	2	52
#766	Male	1.6	15.5	15	2	32
#236	Male	2.9	18	18	2	47
#237	Male	2.2	17.5	17	2	16
#238	Male	1.3	16	14	2	29
#750	Male	2.1	17	17	3	151
#762	Male	2.9	19.5	19	3	86
#768	Female	1.5	16	14.5	3	117
#234	Male	2.9	19	20	3	112
#754	Female	1.2	16	13	7	389
#235	Male	3.2	20.5	19.5	9	132
#243	Female	1.6	16.5	14.5	10	1,083
#759	Male	2.9	19	18	11	230
#765	Male	1.7	16	15.5	51	778
#240	Female	1.9	18	15	73	1,112
#233	Male	2.6	17	17.5	97	5,368
#242	Female	1.7	18	15.5	121	3,945
#756	Female	1.3	16	14	134	2,092
#746	Male	1.9	16	15.5	156	1,869
#757	Female	1.4	16	15	160	10,489
#758	Male	1.7	17	16	160	2,026
#231	Male	2.7	20	19	160	4,633
#747	Male	3.4	19.5	20	162	5,034
#751	Female	1.7	18.5	14.5	162	3,643
#752	Female	1.3	16	13	162	4,430
#753	Female	1.3	16	14	162	4,784
#760	Male	3	19.5	19.5	162	9,751
#761	Male	3.5	20	20	162	9,828
#763	Male	2.6	17	17.5	162	1,624
#764	Male	2.3	17	17.5	162	11,501
#767	Male	1.9	15.5	15	162	2,678
#232	Male	2.7	19	18.5	162	1,058
#244	Female	1.4	18	14	162	6,081
#245	Male	1.8	16	15	162	10,226

The table shows the biological measurements: body weight (BW, kg), carapace length (CL, cm), carapace width (CW, cm), residence time in Gamvikfjorden (RESTIME, the number of days from the first until the last registration), and number of recorded acoustic positions (NREG). The RKC individuals were tagged and released the 24th of May 2016.

ADT-MP-13, transmission rate: 240–360 s random interval, mass with attachment in water ~ 8.5 g, Thelma Biotel AS, Norway)² attached to the fourth pereopod, and the crabs were then carefully released back into the water at the same location where they were captured. Tag to body weight ratio was $< 0.8\%$, i.e., well below the general rule of thumb of 2% of the study object (e.g., Cooke et al., 2004).

Acoustic receivers ($n = 54$) equipped with temperature sensors (type TBR-700, Thelma Biotel AS) were deployed close

to the seabed throughout the inner part of Gamvikfjorden on the 25th of April 2016 (Figure 2). These receivers were located according to a pre-defined grid system, which allowed for detailed triangulation of the crabs' positions during the period from the 24th of May until the 1st of November 2016. Harsh weather conditions caused the loss of 16 receivers, and the acoustic coverage was therefore limited in some parts of the fjord (in particular in the inner part of the study area; Figure 2). Data obtained by the 38 remaining receivers (Supplementary Table 3) resulted in a position dataset consisting of 105,484 pairs of accurate spatial coordinates and associated time indications, describing the seasonal movements of the 37 tagged crabs within the study area. These recordings constituted the basis for further numerical analyses. An exhaustive description of the methodology is provided in Aune et al. (2022).

Numerical Analyses

To assess the seasonal variability of water temperature in the study area, the temperature recordings from the acoustic receivers were assessed as a function of time for each receiver position. Also, to explicitly assess daily range and difference in temperature within the study area, we calculated daily mean temperatures at each receiver position.

Fjord oceanography is known to be affected by meteorological conditions such as strong winds (Inall and Gillibrand, 2010). In order to investigate whether the seasonal variation in water temperature could be related to wind conditions, we obtained data on daily maximum wind speed recorded at the closest weather station, located at Fruholmen lighthouse, located 42 km northeast of Gamvikfjorden (Figure 1A). These data were freely available from <https://seklima.met.no/observations>.

To assess the relationships between benthic faunal composition and associated covariates (data on bottom depths and sediment properties), a canonical correspondence analysis (CCA; ter Braak, 1986) was conducted using the R package *vegan* (Oksanen et al., 2020).

Sex-specific seasonal variation in migratory behavior and habitat utilization was assessed by means of the latitude and water depth that the crabs used, as well as the water temperature they experienced during the study period. Water depths associated with crab locations were obtained from the gridded bottom topography data. As the study area lies approximately along a north-south gradient, crab movements in and out of the fjord were assessed by means of the latitude of each recording. For each individual, estimates of the minimum walking speed were calculated as the distance between two successive recordings divided by the time difference between these two recordings, and the daily averages of these estimates were calculated. The seasonal progression of these daily minimum walking speed estimates was assessed by means of a linear regression model.

For each recorded crab location, the temperature experienced by the crab was obtained from the closest acoustic receiver. Monthly individual space use for each crab was estimated as the central location occupied by each individual (not taking into account depth). Total monthly space use by all tagged crabs in

²www.thelmabiotel.com

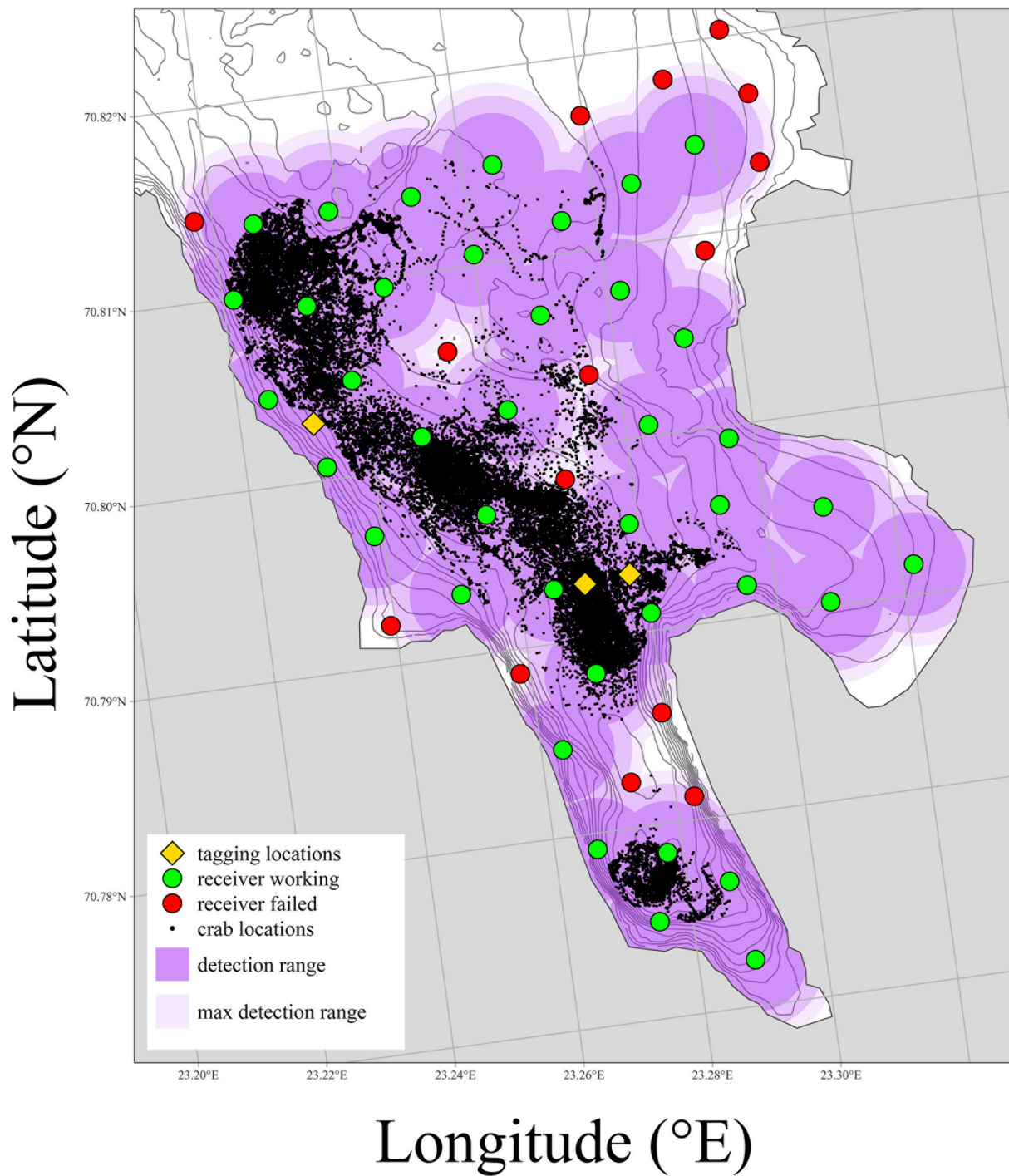


FIGURE 2 | Overview map showing the study fjord, locations of receivers (both working and failed), locations where tagged individuals were released and all estimated locations of tagged red king crab (*Paralithodes camtschaticus*). Additionally, estimated detection ranges for each working receiver have been overlayed in three levels. These correspond to—in decreasing color intensity—minimum, mean and maximum distance all crab locations had to their nearest working receiver. See **Supplementary Table 3** for positions of acoustic receivers.

turn was calculated using minimum convex polygons (MCP) encompassing all recorded locations each month. Individual home ranges were estimated as 100% MCP of all relocations

recorded by each respective crab. This analysis was only conducted for individuals with at least 9 days of data. All analyses were carried out in R 4.0.0 (R Core Team, 2020).

RESULTS

Seafloor Samples

Grab sample data from selected locations along gradients of latitude and water depth indicate spatial variation in sediment properties and benthic community structure (both composition and abundance) (**Supplementary Tables 1, 2**). In the CCA, axis 1 accounted for 81.0% of the variation, characterized by a gradient in depth and bottom substrate (**Figure 3**). Indeed, pelite, TOC and TN values increased with increasing water depth, and showed the highest values at > 45 m water depth (**Supplementary Tables 1, 2**). Polychaetes constituted the most abundant benthos group at most of the grab sample stations. Bivalves were only present in the stations shallower than 45 m. Crustaceans and the echinoderms were also generally more abundant at shallow than deeper stations.

Water Temperature Regime

Strong spatial and seasonal variation in bottom water temperature was observed, and the seasonal water temperature variability largely depended on the water depth (**Figure 4A** and **Supplementary Figure 1**). When the acoustic receivers were deployed (i.e., 25th of April), relatively homogeneous water temperatures were recorded, ranging from 3.8 to 4.2°C (not

shown in the figures). One month later, when the tagged crabs were released into the study area (i.e., 24th of May), the water masses had started to heat up, but with a stronger temperature increase in shallow than in deeper water masses, resulting in an increased temperature range (4.8–6.5°C). The largest difference in water temperature within the study area was observed on the 14th of July (range: 7.3–10.8°C), after which the water temperature at the shallowest stations started to decrease. In the beginning of October, the water temperatures at the deepest stations started to decline from a maximum of 9.0°C, after which the temperature difference between shallow and deep parts of the fjord was never greater than 0.9°C. At the last day of the study period (the 1st of November), the water temperatures ranged from 7.7 to 8.4°C.

With one exception (i.e., at acoustic receiver #124, located at a water depth of 46 m), the average bottom water temperature over the entire study period was lower in areas deeper than 45 m as compared to shallower areas. Shallow parts of the fjord (< 45 m water depth) showed a relatively continuous increase in water temperature, whereas temperature increases in deeper parts of the fjord (> 45 m water depth) largely depended on episodic water exchange with the surrounding oceanic water masses. We identified six prominent water exchange events, occurring on the 4th of June, 23rd of June, 8th of August, 29th of August, 6th of September, 3rd of October and 18th of October. An

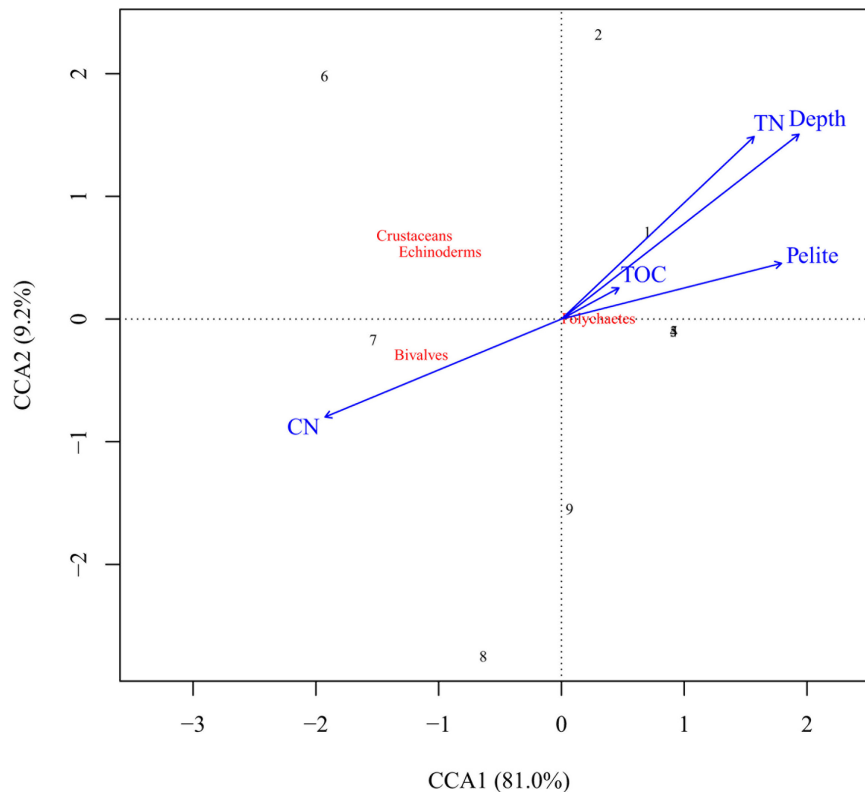
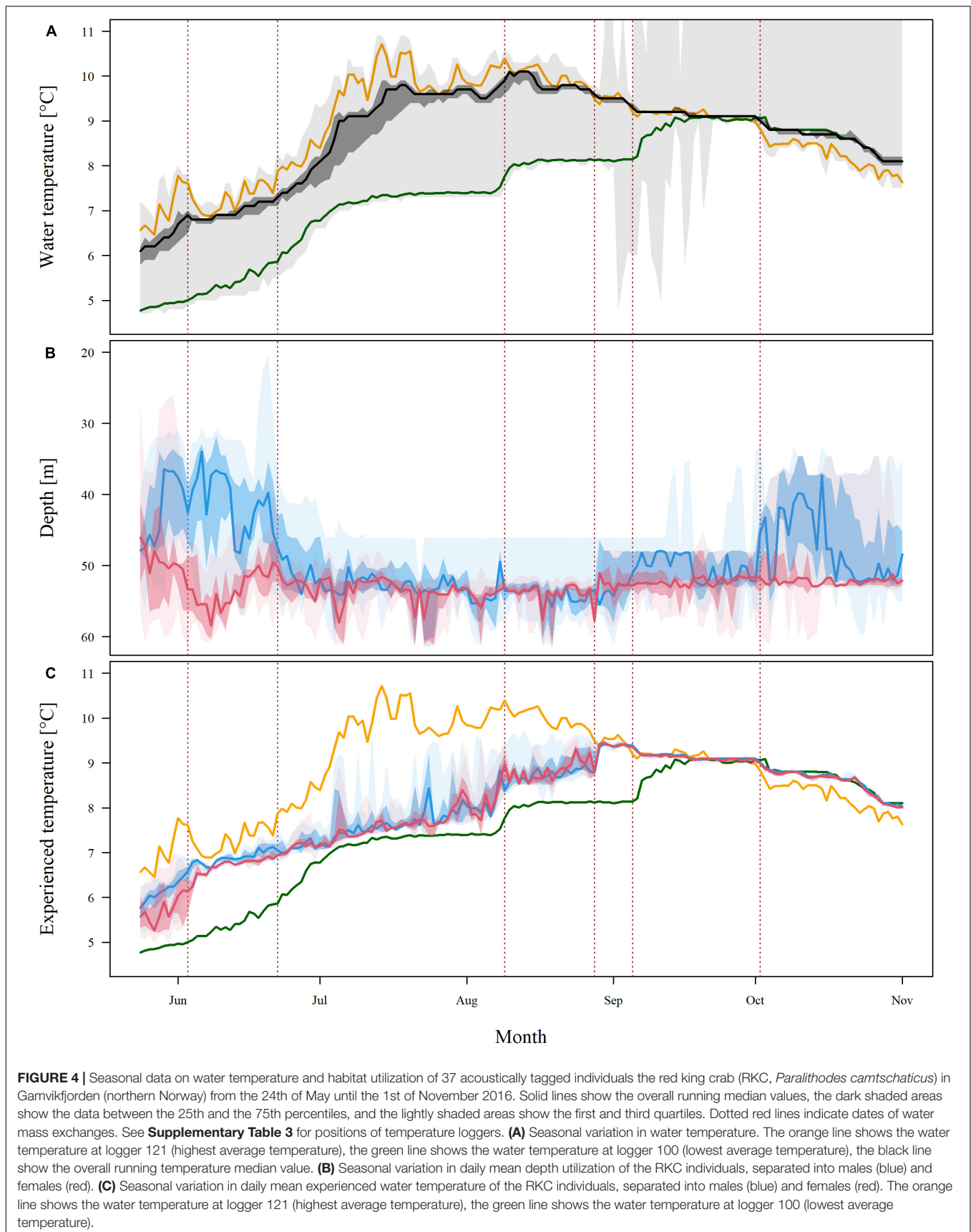


FIGURE 3 | CCA plot of benthic taxa composition as function of selected environmental variables, based on grab samples collected from the seabed in Gamvikfjorden the 12th of October 2019. TOC, total organic carbon; TN, total nitrogen; Pelite = fine fraction of the sediment (% < 0.063 mm); CN, the C:N ratio (i.e., TOC:TN). The numbers refer to the grab sample sites (**Supplementary Table 1**).



examination of historic weather data revealed that the important water exchange events coincided with distinct events of strong winds ($> 19 \text{ ms}^{-1}$; **Supplementary Figure 2**). Specifically, on average, the six episodes of water exchange identified were associated with maximum daily wind speeds of $22.4 \pm 1.9 \text{ ms}^{-1}$. In contrast, the average of the daily maximum wind speed over the entire study period was $13.6 \pm 4.4 \text{ ms}^{-1}$.

General Migration Behavior

The detection range estimated as the maximum distance of each crab location to the nearest working receiver was on average 400 m up to a maximum of 476 m (**Figure 2**). The residence time of the crabs (i.e., the number of days from the first until the last registration) varied from 1 to 162 days (mean: 80 days). Whereas 16 crabs left the study area during the first 11 days, 5 crabs stayed in the study area for between 51 and 134 days, and the remaining 16 crabs stayed in the study area for at least 156 days. Harsh weather conditions caused the loss of several acoustic receivers during the study period, and therefore some parts of study area were poorly covered, which in turn made individual crabs “disappear” from the study area during certain days (**Supplementary Figures 3, 4**). The average number of crabs recorded per day was 12.5 ± 3.8 crabs. Depending on the residence time and the time spent in poorly covered parts of the fjord, the number of records per crab during the entire study period varied from 16 to 11,501 (mean number of records per crab: 2,851).

Position data revealed that the crabs mostly resided in the central, deep trench and largely avoided the shallower parts of the fjord (examples given in **Figure 5**). The crabs that left the study area shortly after the release typically followed remarkably straight lines toward the fjord mouth (**Figures 5A,B**). On the other hand, those crabs that stayed in the study area for an extended period of time typically made several movements between the northern and southern parts of the fjord, largely (but not always) following the central deep trench (**Figures 5C,D**).

Seasonal Variation in Depth, Latitude, and Experienced Temperature

The crabs displayed strong seasonal variation in water depth, latitude, and experienced temperature (**Figures 4B,C** and **Supplementary Figure 5**). From the end of June until the beginning of October, the crabs were largely found in > 50 m water depth, whereas also shallower waters (~ 30 – 50 m) were utilized by male crabs earlier and later than this period (**Figure 4B**). With one exception (i.e., 8th of August, a date when only three crabs were registered because they moved into areas with limited acoustic coverage due to the loss of acoustic receivers; **Figure 2** and **Supplementary Figures 3, 4**), the crabs were found significantly deeper during the period 23rd of June to the 7th of September (both dates associated with water mass exchange) compared to at the beginning of the study period ($p < 0.05$). Males showed a tendency to utilize shallower parts of the fjord more than the females, and displayed a stronger seasonal variation in depth “preference.”

From the beginning of the study period until the middle of July, the crabs were largely found in the central and northern part of the study area (north of 70.79°N ; **Figure 6** and **Supplementary Figure 5**). In July, some crabs moved into the southernmost (innermost) parts of the fjord, whereas others stayed in the outer part of the fjord, resulting in the most widespread crab distribution observed during the study period. From mid-August onward, the crabs were mostly recorded in the mid-latitudes of the study area (70.79 – 70.80°N).

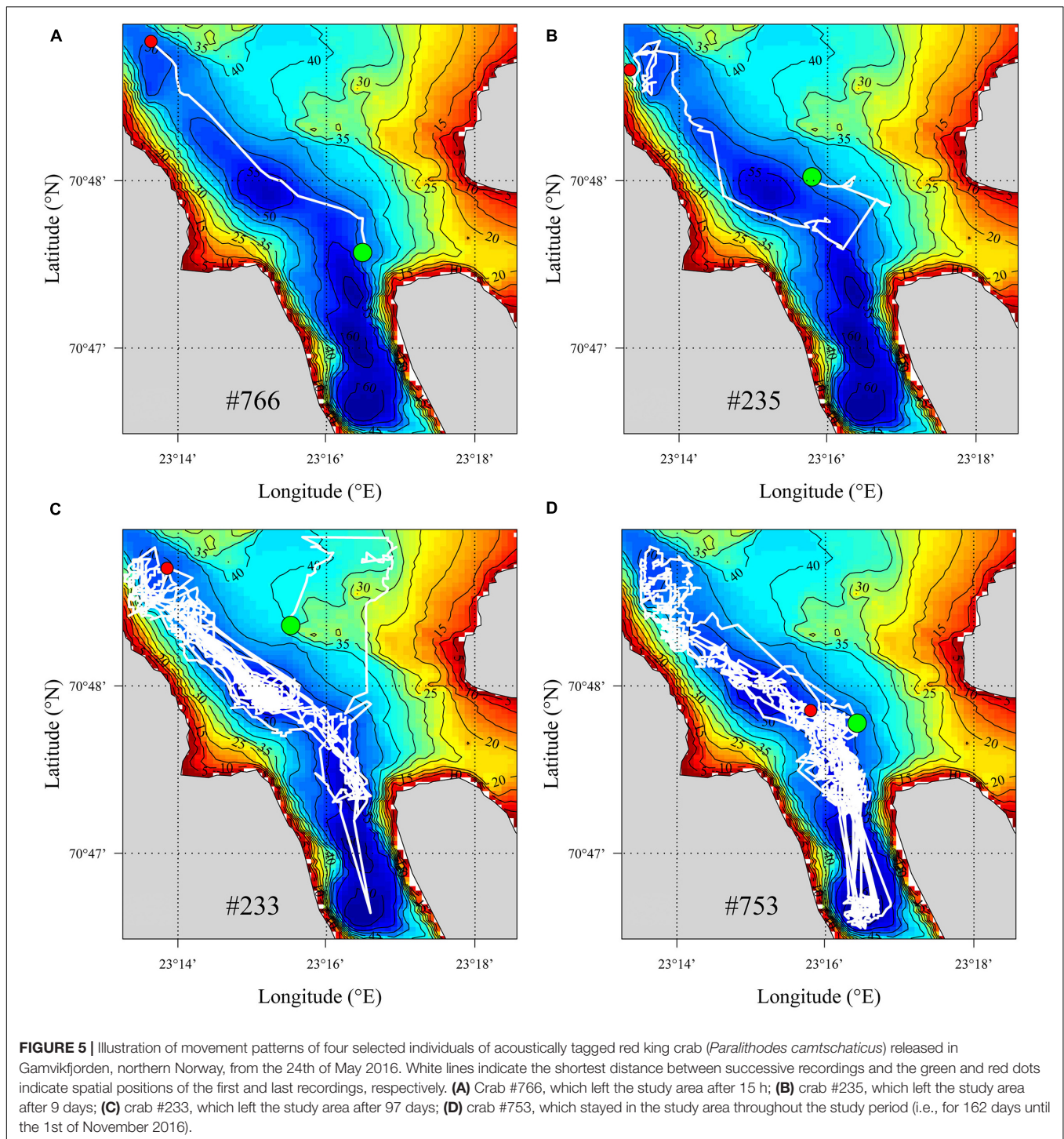
The crabs experienced water temperatures that were slowly increasing from ~ 5.5 to 6.5°C in the beginning of the study period to $\sim 8^\circ\text{C}$ in the beginning of August (**Figure 4C**). On the 8th of August, the experienced temperature rose quickly from ~ 8.0 to 8.5°C , followed by 3 weeks of slow increase and a new rapid increase to maximum values of $> 9^\circ\text{C}$ on the 29th of August. From this date and to the end of the study period, there was minimal variation among crabs with respect to the water temperature that they experienced, which declined to $\sim 8^\circ\text{C}$ in the end of the study period. Several of the tagged crabs (i.e., crab #245, #757, and #760) showed nearly identical profiles of depth, latitude and experienced temperature.

From May until late August, the crabs appeared to counteract the effect of increasing ambient water temperatures on their experienced temperatures by gradually moving deeper and further into the fjord. Consequently, the area that they utilized contracted as the water masses got warmer. Rapid movements were mostly associated with accelerated increases in ambient water temperature due to water mass exchange events (i.e., quickly rising water temperatures at the locations where they were found just before the movement; see vertical green lines in **Figure 6** for dates of important water exchange events). As such, a change in temperature in shallow waters did not necessarily affect the crabs, which were mostly found in deeper waters. Although the lowest water temperatures were found in the innermost part of the fjord, the crabs preferred the area where the second coldest water masses were found (i.e., in the central deep trench; **Figures 4C, 6**). The median distance from the tagging location was 1,200 m across individual crabs (1st–3rd quartile, 90–1,775 m). Among those individuals that left the study area early in the study period ($n = 16$), the maximum distance from the tagging location was 1,482 m (1st–3rd quartile, 1,313–2,697 m). Median home ranges used by male and female RKC during the study period were 230 m^2 (range: 28–507 m^2) and 221 m^2 (range: 45–385 m^2), respectively.

Walking Speed

The daily mean walking speed of the crabs ranged from 0.35 to 3.08 m min^{-1} within the study area (mean 1.14 m min^{-1} ; **Supplementary Figure 6**). There was a weak, yet significant ($r^2 = 0.12$, $p < 0.001$) decline in daily mean walking speed throughout the study period.

Fishermen recaptured three of the tagged crabs (#234, #237, and #238), all of which left the study area early in the study period. Crab #234 was recaptured close to Vannøya, $\sim 147 \text{ km}$ southwest of Gamvikfjorden in the beginning of April 2017, which accounts for a minimum walking distance of 490 m day^{-1} . Crab #237 was



recaptured ~25 km northwest of Gamvikfjorden, but since the date of recapture of this crab is unknown, it was not feasible to estimate its daily walking speed. The exoskeleton of Crab #238 was recovered in a fishing net deployed east of Rolfsøy, ~53 km northeast of Gamvikfjorden on the 5th of February. This implies a minimum walking distance of 208 m day^{-1} , followed by molting after being caught in a fishing pot.

DISCUSSION

This study successfully combined acoustic telemetry on RKC migratory behavior with environmental recordings and benthic investigations to reveal the species' movements in relation to its surroundings. The findings reveal the RKC as a aggregative, highly opportunistic species capable of long-distance migrations,

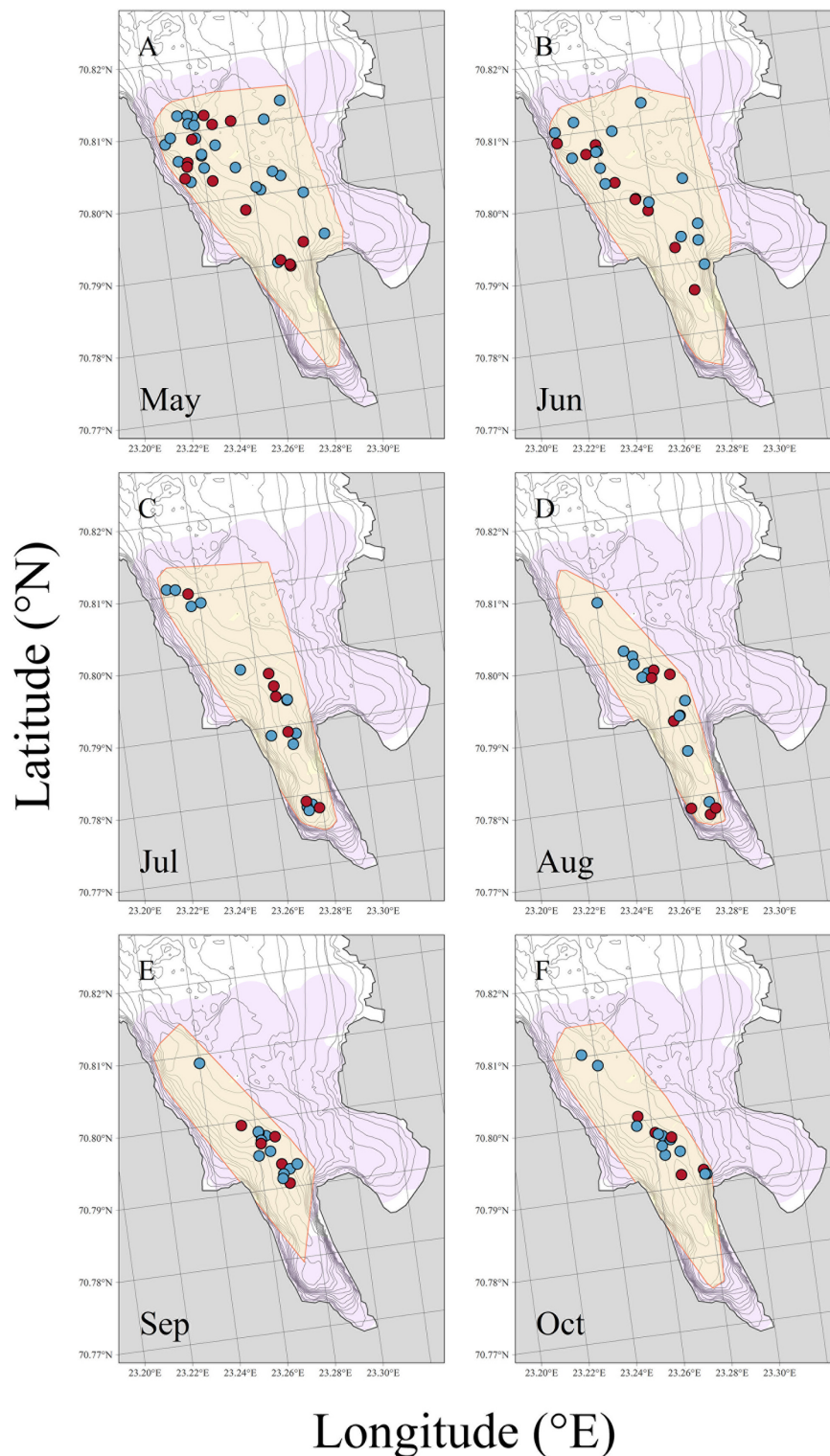


FIGURE 6 | Monthly (May–October) sex-specific space use of each tagged individuals of the red king crab (*Paralithodes camtschaticus*) released in Gamvikfjorden, northern Norway, the 24th of May 2016. Each symbol corresponds to monthly individual space use for each crab estimated as the central location occupied by each individual in given month. Males and females are displayed in blue and red, respectively. Yellow shapes in each panel illustrate the entire area occupied by both sexes in a given month (as 100% MCP). The purple shape in each panel delimits the area where crab locations could be detected (details in “Materials and Methods” section). **(A)** May, **(B)** June, **(C)** July, **(D)** August, **(E)** September, and **(F)** October.

that is capable of withstanding large temperature fluctuations. Furthermore, our results indicate that the RKC can reside far outside its assumed temperature preference (e.g., Christiansen et al., 2015).

What Does the Atlantic Coastal Red King Crab Habitat Look Like?

The grab sample data from Gamvikfjorden revealed several interesting patterns that are probably typical for many Norwegian fjords newly invaded by RKC. For instance, shallow locations (<45 m water depth) showed relatively coarse sediments (low pelite values) and low values of total nitrogen (TN), whereas progressively finer sediments coupled with increasing values of TN were observed at deeper locations. As anticipated, the spatial variation in sediment texture within the study area was reflected in benthic community composition. Polychaetes dominated at most stations and showed the highest numbers in the deep trench, whereas bivalves, echinoderms and crustaceans were almost exclusively found in the shallower parts of the fjord. These findings may indicate that the seabed in the study area can be divided into two distinct categories: “shallow” and “deep,” characterized by different benthic faunas which are both appropriate as food for the RKC (Britayev et al., 2010; Falk-Petersen et al., 2011; Fuhrmann et al., 2017).

The environmental conditions within fjords varies greatly and are dependent on numerous parameters such as thresholds, depth, water exchange and freshwater runoff. In Gamvikfjorden, the deep, inner basin had the highest TOC values, similar to e.g., fjords at Svalbard. This is likely explained by a regular supply of terrestrial, organic material due to e.g., river runoff (Koziorowska et al., 2016). As the inner basin of Gamvikfjorden also showed the highest C/N ratio, a metric suggestive of organic material of terrestrial origin (Koziorowska et al., 2016), we argue that the supply of organic carbon from land (i.e., Sørøya) may have contributed to the high TOC values in the area. Indeed, field notes revealed that the grab sample taken from the inner, deep basin contained substantial amounts of organic material such as small branches. Similarly, a recent study of a river-impacted fjord in northern Norway showed the highest C/N ratio in the innermost part of the fjord (i.e., closest to the river outlet) and the highest TOC further out in the deeper parts of the fjord (McGovern et al., 2020). A few smaller creeks flow into the inner part of the study area, and the location close to the open ocean probably causes transportation of terrestrial material by wind. Our bottom-water temperature data suggest that the bottom water masses of the deep, inner basin are seldomly exchanged during the summer season, and this part of the fjord may thus function as a sedimentation basin for terrestrial organic material. The infrequent water exchange in the deep, inner basin may also cause O₂ limitation close to the seabed in this part of the fjord, which is supported by the field team registering the smell of sulfur at the two innermost grab sample locations. Lack of oxygen points toward less favorable conditions for benthos. Indeed, we observed few macrofauna in this part of the fjord. However, early during the study period (July), the deep, inner basin was relatively frequently visited by

tagged crabs. It is therefore also possible that predation from RKC contributed to the impoverishment of the benthos community in the small, inner fjord basin, as observed locally in adjacent fjords in northern Norway (Oug et al., 2011, 2018). Despite low water temperatures, generally poor food availability apparently made the deep, inner basin of Gamvikfjorden unfavorable as habitat for the RKC.

Movement Patterns

In contrast to the tagged individuals remaining in the study area for a prolonged period, which typically resided within ~1.2 km from the tagging locations, recaptures of three tagged crabs (i.e., ~8% of the studied crabs) up to 147 km from the study area confirm that the RKC is also capable of long-distance migrations. Such migrations have previously been observed in the Barents Sea and in the species' native areas in the Pacific Ocean (e.g., Marukawa, 1933; Hayes and Montgomery, 1963; Windsland et al., 2014). We cannot demonstrate that additional individuals among the early emigrating crabs made subsequent, long-distance migrations beyond the maximum distance of ~1,500 m from the tagging locations. Nevertheless, provided the low likelihood of recaptures, these numbers suggest that such migrations are a common feature of the red king crab. The crabs presently studied by use of acoustic telemetry typically displayed walking speeds of up to 3 m min⁻¹ between successive registrations (therefore capable of > 4,000 m d⁻¹), which largely agrees with previous studies (e.g., Jørgensen et al., 2007). Several of the crabs in our study left the fjord along straight paths, yet others moved in seemingly random patterns (as observed in Jørgensen et al., 2007), presumably searching for food. Thus, we observed two modes of movement, likely corresponding with long-distance migration and foraging behaviors, where at least the latter may imply seasonal migrations between shallow and deep waters. It is unclear, however, what prompts an individual crab to choose one mode at any time, or how often and under what circumstances a crab may shift modes. Further telemetry and mark-recapture studies can be correlated with potential food resources and environmental characteristics in future studies. With regard to the recaptured crabs, we therefore assume that the actual walking distances between the study area and the sites of recapture, and consequently the walking speeds, were greater than initially estimated.

Although more than half of the tagged crabs stayed in the study area for several months, 16 of the crabs left the study area within the first 11 days (i.e., before the 4th of June), after which no crabs left the study area for another 40 days. This departure from the shallow study area was not surprising given the general expectation that the RKC move to deeper water masses before June (e.g., Sundet and Hjelset, 2010). Most of the early emigrating crabs followed a consistent and a directed migratory path: following the central, deep trench northwards toward the outer part of the fjord. This suggest that the RKC display a spatial understanding, perhaps prompted by cues from the water mass, and that they may follow specific migratory routes, e.g., along topographic features such as slopes. Indeed, the RKC is often caught in slope areas (Anisimova and Lubin, 2008). Moreover, evidence from Alaskan waters suggest that the RKC conduct

long-distance migrations as groups of individuals (Stone et al., 1993), which suggest a means of aggregative behavior. Indeed, several of the tagged crabs showed nearly identical profiles of depth, latitude and, consequently, experienced temperature, and it can certainly not be ruled out that these three individuals co-occurred in time and space with individuals that were not acoustically monitored. Although the formation of dense aggregations is thought to be most common among juvenile RKC (i.e., “podding”), the behavior has also been observed among adult individuals (Jewett and Powell, 1981; Stone et al., 1993). In sum, various observations suggest that RKC individuals co-occur and move collectively, which would facilitate the identification of potential migratory routes. Detailed knowledge of such migratory routes would, if they exist, support effective management and exploitation of this RKC stock.

Interestingly, we note that the 16 early emigrating specimens left the study area before the first major water exchange, which occurred from the 4th of June. A movement northward from the study area into deeper offshore areas implies that the crabs must transit a broad area of 35–50 m water depth. A closer examination of the temperature data from this depth interval revealed water temperatures of ~ 5.9 – 6.6°C the 1st of June (i.e., before the first major water exchange), whereas higher and less variable water temperatures (~ 6.6 – 6.8°C) were observed 5 days later (i.e., after the water exchange event). Although Christiansen et al. (2015) showed that mature RKC prefers temperatures lower than 4°C , they also utilized the 4 – 6°C temperature range and to a lesser degree water masses warmer than 6°C . We therefore hypothesize that the shift to warmer water masses in the shallower areas north of the study area, largely caused by discrete water exchange events, may have imposed a thermal barrier of $\sim 6^{\circ}\text{C}$ that trapped the remaining crabs inside the deeper parts of the study area, preventing migrations to colder offshore areas. Alternatively, our data questions our current knowledge of seasonal migrations between deep and shallow waters. We expected crabs to be present in Gamvikfjorden in May, when the tagging was conducted. Yet the proportion of tagged individuals remaining in the study area for several months was surprisingly high given the assumption that they would reside in deeper waters from June onward (e.g., Sundet and Hjelset, 2010). This may indicate that the crabs remaining in Gamvikfjorden were not hindered from conducting a feeding migration to deeper waters, but on the contrary stayed in the fjord despite sub-optimal water temperatures, possibly due to favorable feeding conditions there. Likewise, it is assumed that mature males that have recently molted may skip spawning and stay in deeper waters throughout the spawning season (Powell et al., 1973; Sundet and Hjelset, 2010). These observations combined point toward a seasonal migration regime that is more flexible or complex than previously thought, which may point toward a means of dispersive migration pattern (e.g., Fayet et al., 2016). Nevertheless, the ectothermic RKC is sensitive to changes in water temperature, as its food conversion efficiency as well as its ability to bind oxygen (i.e., the hemocyanin oxygenation) severely decreases in response to increased water temperature (Decker et al., 2007; Siikavuopio and James, 2015). Thus, a general avoidance of high ($> 4^{\circ}\text{C}$) temperature waters

is expected (Christiansen et al., 2015). However, in a previous study, no relationship between quick, synchronous movements of the RKC and water temperature could be detected (Stone et al., 1992). Contrary, our combined data on crab movements and water temperature variability in the current study area show a tendency for crabs to respond quickly to changes in ambient water temperature. For instance, water exchange events occurring in springtime (as shown by quick changes in water temperature) apparently caused the presently studied crabs to move quickly into deeper, colder water masses. In turn, these water exchange events were largely associated with strong winds at the surface. Surface wind conditions were also shown to be decisive with regard to the dispersal and subsequent settlement of pelagic RKC larvae (Pedersen et al., 2006). Conditions above the sea surface may thus affect more than one life stage of the RKC, and consequently, behavioral responses affecting the spatial distribution of adults may facilitate larval dispersal. As such, a direct link between meteorological conditions, dispersal and distributions in coastal waters seems plausible.

Habitat Utilization

Our data from Gamvikfjorden suggest that the habitat choice of the RKC is affected by a trade-off between abiotic factors (e.g., water temperature) and food availability. The king crab is a generalist predator feeding on a wide variety of infauna and epifauna (Fuhrmann et al., 2017), and its movement over the seasonal cycle is likely a response to a combination of food encounter rate, seasonal differences in thermal tolerance, reproduction and trade-offs with e.g., predation risk. Indeed, this is likely behind the general model of seasonal migration patterns observed in some areas, whereby crabs migrate between shallow (winter- and springtime) and deep waters (summer and autumn; Sundet and Hjelset, 2010). Fuhrmann et al. (2015) found 75% lower infaunal biomass in areas of a north Norwegian fjord inhabited by king crabs compared to fjord areas where the crab was absent. Clearly, therefore, movement patterns can at least partially represent a response to food availability, and more detailed investigation of prey fields relative to movement patterns is needed. Tagged crabs were generally active, but typically operated at surprisingly local scales of $\sim 225\text{ m}^2$ over the entire study period, suggesting factors other than the potential chance of finding food in other areas of the fjord must be acting here.

The crabs that remained in the study area for a prolonged period showed a spatial distribution with clear seasonal variation, moving deeper as the increasing water temperatures made the shallow parts of the fjord progressively less suitable as habitats. These individuals generally utilized a surprisingly small portion of the fjord. Interestingly, a distinct sexual segregation was observed early and late in the study period. Females were predominantly found deeper than 40 m, experiencing lower water temperatures than the males, the latter being commonly found as shallow as 30 m before the first water exchange event (i.e., the 4th of June) and after the deeper parts of the fjord started to cool (i.e., early October). Sexual segregation in RKC has previously been reported (Stiansen et al., 2009; Falk-Petersen et al., 2011), but research data supporting the existence of such behavior is rare (Stone et al., 1993; Taggart et al., 2008;

Sundet and Hjelset, 2010). Mating is known to occur in shallow waters during springtime (e.g., Stone et al., 1993; Sundet and Hjelset, 2010). We can therefore assume that the tagged females, all of which were sexually mature, had completed the mating before the tagging and therefore carried eggs throughout the study period. To avoid accelerated egg development and early hatching, the females likely seek cold water masses most of the year. Indeed, RKC in the Barents Sea were found in deep waters (>150 m) from April through December (Sundet and Hjelset, 2010), where the water temperatures were likely low. Possibly constrained to the study area due to the thermal barrier outside Gamvikfjorden, the tagged ovigerous females may have been forced to reside in deep and cold parts of the fjord already from the beginning of the study period. The males, on the other hand, apparently tolerated the slightly higher temperatures found in shallower waters early in the study period and were therefore allowed to feed both in deep and in relatively shallow waters. As such, females likely had to base their diet on polychaetes while the males could initially benefit from a more diverse diet consisting of polychaetes, bivalves, echinoderms and crustaceans. After the first water exchange event, the males were forced to move progressively into deeper and colder water masses as the ambient water temperature rose. Nevertheless, although the crabs eventually experienced temperatures in the central, deep trench that were substantially higher than they apparently prefer (e.g., Christiansen et al., 2015), they avoided the cold, presumably food-poor inner deep basin. This study was conducted in one fjord only, and the specific hydrography, bathymetric profile, and benthic community structure may have strongly influenced these results, whereas patterns may be different in other fjords. Yet, our findings highlight a trade-off between physical (e.g., water temperature) and biological factors (e.g., access to suitable food) that likely affect distributions of the RKC in coastal waters. This in turn indicates that the current knowledge base of the species' seasonal migration patterns may need revisions.

CONCLUSION AND IMPLICATIONS

In this paper, we show that the RKC in coastal areas can respond quickly to wind-induced water exchange events, avoiding unfavorable ambient water temperatures. Moreover, our results suggest that the species' habitat selection likely depends on a trade-off between abiotic and biotic conditions. For instance, provided access to appropriate food, the crabs seem to tolerate temperatures that are much higher than previous studies suggest that they prefer (e.g., Christiansen et al., 2015), which clearly has implications for our understanding of its future distribution patterns in coastal waters. Yet, as the water temperatures in the study area rose, the crabs moved into deeper and colder parts of the fjord, and their walking speed decreased. Indeed, unfavorable temperature conditions have previously been shown to cause reduced activity level of other crab species (e.g., in fiddler crabs, *Uca pugilator*; Mat et al., 2017). A reduced activity level implies a reduced intensity in the search for food, and as such, high water temperatures may cause a lower likelihood that the crabs are being captured by traps. To assess the degree to which a reduced activity level may affect the access to food, future

investigations may integrate data on RKC movement patterns and benthic abundance and composition in different environments. This may help estimating the daily amount of potential food covered under differing modes of movement.

About half of the tagged crabs remained in the study area throughout the summer season despite the general expectation that they would move into deeper waters before June (e.g., Sundet and Hjelset, 2010). We propose that the crabs were forced to do so because of a thermal barrier imposed by warm waters in the shallow areas surrounding the study area. Alternatively, other factors (e.g., favorable food conditions or low competition) made the crabs prefer to stay in the area despite sub-optimal water temperatures. In any case, the high proportion of tagged RKC remaining in the study area throughout the summer season, in addition to numerous observations by divers, question the premise that the RKC conduct general seasonal migrations between deep and shallow waters. Indeed, the RKC may occur in shallow, warm waters in summertime, but may remain unaccounted due to a lower catchability during this time of the year. Intuitively, the utilization of a wide depth range (shallow and deep waters) during given periods of the year will affect the density, and consequently the catchability, of the species. To facilitate sound management, future studies should aim to estimate the actual proportion of the RKC stock remaining in shallow fjord areas throughout the year.

Our data also suggest that the crabs may display a means of aggregative behavior, performing migrations as groups of individuals, and that many crabs perform long-distance, high-velocity migrations. The combined effects of aggregative behavior, quick response to environmental changes, and the capability to conduct long and fast migrations, may help explain why many fishermen experience highly variable catches of the RKC despite little variation in the time and geographical location of the fishing. For future studies, we recommend conducting telemetric studies over entire annual cycles, and further investigating whether the RKC follow distinct migration routes along the coast. Furthermore, in recent years, the snow crab (*Chionoecetes opilio*) has recently appeared in the eastern Barents Sea, rapidly expanding into the areas of the southern Barents Sea where the RKC reside. We, therefore, suggest that telemetry be applied to investigate the interplay between these two species of crabs.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are publicly available. This data can be found here: <https://doi.org/10.5281/zenodo.5823339>.

AUTHOR CONTRIBUTIONS

JJ, GC, and KN conceptualized study. JJ, GC, and MA conducted the fieldwork. MA and BM conducted the numerical analyses. MA wrote first draft of the manuscript. All authors contributed significantly to the manuscript and approved the submitted version.

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The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.762087/full#supplementary-material>

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Habitat Selection and Specialisation of Herring Gulls During the Non-breeding Season

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Understanding both the distribution and habitat use of populations through the annual cycle is vital to understanding how vulnerable species are to environmental change. However, distributions and habitat use can vary among individuals and populations, particularly in generalist species, with variation depending on external environmental factors, such as resource availability. Comprehensive information across multiple populations is important to guide spatial planning of protected areas and is increasingly available for breeding individuals, but it is still lacking for many species, particularly seabirds, during the non-breeding season, especially those with declining populations. We investigated within-species variation in migratory strategies, non-breeding habitat selection and habitat and spatial specialisation in a declining, opportunistic, generalist seabird, the European herring gull *Larus argentatus*, from multiple breeding colonies across northwest England and southwest Scotland using global positioning system (GPS) tracking during the non-breeding season of 2014/15. Although several individuals stayed within the area of the breeding colony, the majority of individuals migrated in a southerly direction and spent half of the annual cycle (on average 53%) away from the breeding area and kept moving through the non-breeding period. During non-breeding, herring gulls selected mainly marine intertidal, but also a range of anthropogenic terrestrial habitats. However, habitat selection differed between geographical regions, within a geographical region and among individuals. There was a generalist use of non-breeding habitats at the population level, but some habitat specialisation at the individual level that was repeatable through the non-breeding period despite individuals showing low spatial specialisation. The results highlight the importance of intertidal habitat and a mix of alternative foraging habitats in the wintering areas of herring gulls. The results also highlight that habitat selection in an opportunistic generalist can vary even between nearby regions and that appropriate conservation management plans may need to be tailored to regional differences in specific non-breeding areas.

Keywords: biologging, habitat specialism, spatial specialisation, resource selection function, home range, Laridae, utilisation distribution

INTRODUCTION

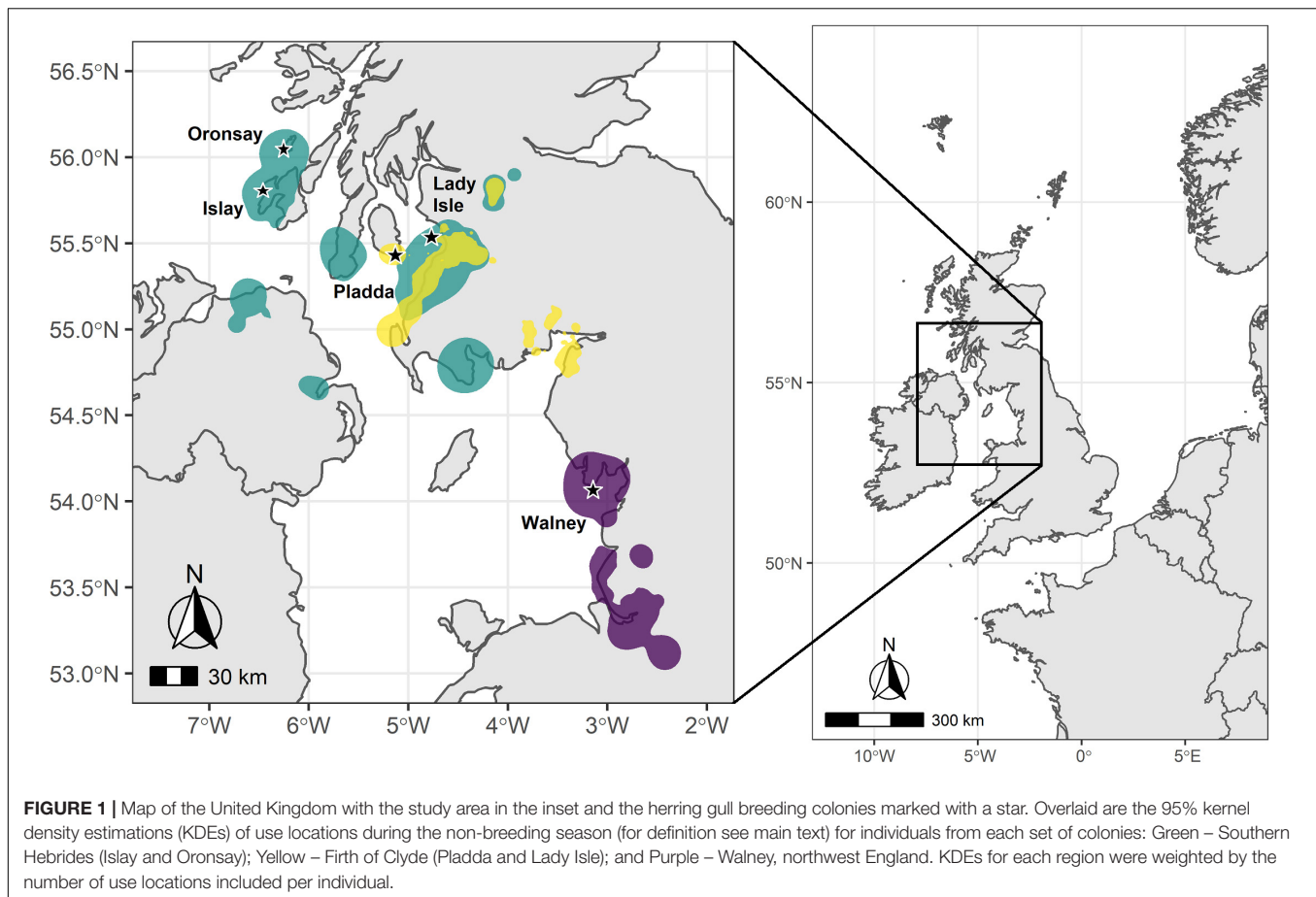
The patterns of space use exhibited by species reflect their movement and habitat selection in response to resource availability, mediated by biotic mechanisms and intrinsic factors acting on individuals (Börger et al., 2008). This process is dynamic, as habitat selection forces and resource availability can vary through time and space (Viana et al., 2018). In temperate climes, the non-breeding period is typically characterised by reduced food productivity, leading to energetically challenging conditions, exacerbated by short days, lower temperatures, and extreme weather (Newton, 2008; Osterblom et al., 2008; Fort et al., 2009). These seasonal changes can lead to nomadic or migratory movements at the end of the breeding season away from the breeding area to avoid the seasonally deteriorating conditions. The costs of such movements in terms of time, energy, and mortality risk need to be balanced against advantages of more favourable conditions at non-breeding sites (Alerstam et al., 2003). Ultimately, the different periods of the annual cycle when individuals experience different ecological circumstances are inextricably linked, and carry-over effects between different periods can have important consequences for the individual and consequently the population (Fretwell, 1972; Marra et al., 1998, 2015). To better understand species' and populations' vulnerability to environmental change and anthropogenic pressures it is therefore necessary to understand habitat use of individuals during the entire annual cycle. Movements and habitat selection in the non-breeding period can be different from the breeding period as individuals are no longer constrained in space and time to a central breeding location (Phillips et al., 2009; Quillfeldt et al., 2010; Dias et al., 2011; McFarlane Tranquilla et al., 2013; Anderson et al., 2019). The rapid development of modern tracking technology (Wilson et al., 2002; Burger and Shaffer, 2008) now provides a promising approach to study individual strategies throughout the annual cycle.

Movement and habitat selection can have important conservation and spatial planning implications (Webster et al., 2002; Esler, 2014). If populations show strong migratory connectivity, that is cohesion of populations among the different phases of the annual cycle (Cohen et al., 2019), then local environmental change might only influence populations that use the affected area but not others. Within an area, reduced resource availability during the non-breeding season can increase inter- and intra-specific competition for limited resources (Schoener, 1968). For many species, intra-specific competition can be reduced through individual resource partitioning and habitat specialisation (Perry, 1996; Wikelski and Wrege, 2000; Pearson et al., 2002; Phillips et al., 2011). This will be the case for generalist species, where individuals can switch to different resources and habitats based on food availability. Although generalist species are expected to consume the most readily available resource within their foraging range (Schoener, 1971), resource selection can vary considerably at the individual level (Bolnick et al., 2003; Araújo et al., 2011). This may result in variation in space use

and habitat selection between individuals of a population, leading to a population being distributed over a larger range of environments, which may buffer the population from localised environmental perturbations.

By contrast, if individuals from different breeding populations use the same non-breeding area (weak connectivity) and habitat, detrimental environmental change occurring at that location may have an effect on a wider spatial scale and can lead to population declines in all breeding populations using that location in the non-breeding period (Webster et al., 2002; Iwamura et al., 2013; Esler, 2014). To ensure suitable conservation actions, a good knowledge of the population distributions in time and space is essential. Although non-breeding distributions may be known to some extent from ring recoveries, this information can be biased (Clark et al., 2009), and tracking studies allow seasonal movements and habitat selection to be studied in more detail. Since movement and habitat selection can vary among individuals and in space (Bonnot et al., 2015; Leclerc et al., 2016; Montgomery et al., 2018), we require multi-site studies to broaden our understanding of a species' non-breeding distribution (Bernard et al., 2021).

Here we studied individual and spatial variation in non-breeding movements and habitat selection in a generalist species, the European herring gull *Larus argentatus*. In the non-breeding season herring gulls make non-extensive movements away from the breeding colony (Harris, 1964; Coulson and Butterfield, 1985; Calladine, 2002; Camphuysen et al., 2011). They are opportunistic generalists that forage year-round on a range of resources including marine (fishery discards, intertidal invertebrates such as worms, molluscs, and crustaceans) and terrestrial (natural and anthropogenic items from farmland, landfill, and built-up areas) habitats (Hunt, 1972; Götmark, 1984; Kubetzki and Garthe, 2003; Enners et al., 2018; Clewley et al., 2021). However, at the individual level herring gulls can show extensive specialism (McCleary and Sibly, 1986; Pierotti and Annett, 1991; van den Bosch et al., 2019). Herring gulls have shown dramatic population declines in Europe (e.g., Hario and Rintala, 2016; Nager and O'Hanlon, 2016), and in the United Kingdom is red-listed as a species of conservation concern (Stanbury et al., 2021). The reasons for the population declines are poorly understood (Nager and O'Hanlon, 2016). For their effective conservation management, we need more information on their habitat and resource requirements throughout the annual cycle. Using global positioning system (GPS) tracking, we recorded individual movements and habitat selection of adult herring gulls throughout the non-breeding period to investigate the distribution of multiple breeding populations and hence their migratory connectivity, and what habitats they selected in their non-breeding area. As herring gulls are opportunistic foragers exhibiting flexible foraging strategies, we expect that there is among-individual and within-season variation in space use and habitat selection. Having a better understanding of the among-population and within-species variation in movements and habitat selection and specialisation during specific periods in the annual cycle will give us important insights for spatial planning and



the conservation and management of generalist species in a rapidly changing world.

MATERIALS AND METHODS

Global Positioning System Tracking

Habitat selection of herring gulls during the non-breeding season was studied using data from individuals tracked from 2014 to 2015 from five colonies in two regions along the west coast of the United Kingdom: in the southwest Scotland region we tracked birds in the Southern Hebrides (Oronsay and Islay) and Firth of Clyde (Lady Isle and Pladda), and in the northwest England region from Walney (**Figure 1**). Between May 16 and June 6, 2014, breeding birds were captured on the nest during incubation with either a wire mesh walk-in trap (Bub, 1991) or a remote-controlled noose trap. A solar-powered GPS device (Nanofix PathTrack Ltd, Otley, United Kingdom) was attached to 50 birds across colonies, using a cross-over Teflon wing harness (see Thaxter et al., 2014). At Walney, we deployed devices with an internal antenna (combined device and harness weight: 16 g; device dimensions = 52 mm × 22 mm × 14 mm) and at all other colonies, devices with an external antenna (14 g, 41 mm × 22 mm × 14 mm). The combined device and harness weight was 1.0–1.6% of an individual's body mass. A further 56

individuals were also caught and ringed but not tagged giving a total of 106 birds (*Lady Isle*: six tagged, eight controls; *Pladda*: six tagged, four controls; *Islay*: four tagged; *Oronsay*: 10 tagged, three controls; *Walney*: 24 tagged, 41 controls). All caught birds were measured [head-bill length, gonys depth, maximum wing chord (all ± 1 mm), and body weight (± 10 g)], marked with a metal ring and an alphanumeric colour ring enabling individual identification in the field. They were also sexed by taking a small blood sample for molecular sexing or, when blood sampling was not possible, from head plus bill length measurements (Coulson et al., 1983). For individuals where sex was determined ($N = 42$), the sex ratio at deployment was female-biased (31 females and 12 males).

Devices with the same harness attachment but a relatively heavier weight (maximum 2.9% of body mass) had no detectable impacts on breeding success and local return rate for up to 3 years in the closely related lesser black-backed gull *Larus fuscus* (Thaxter et al., 2016; Kavelaars et al., 2018). To further check whether devices and harnesses impacted the local return rates of our study birds, we monitored colour ring sightings of tagged and control birds at their breeding colonies up to 3 years after device deployment. Resighting probability did not differ between tagged and control herring gulls [Cox regression in the R-package *survival* (Therneau, 2020), accounting for when individuals were last seen; tagged versus control individuals: $\chi^2_1 < 0.1$, $P = 0.825$,

device type with or without external antenna: $\chi^2_1 = 1.8$, $P = 0.182$, $N = 106$].

GPS-devices were set to record fixes throughout the day and night between March and September (the period covering the breeding season) at least every 5 min, but less frequently when the battery power was low (typical range 5–40 min). From October until February, recording intervals were increased to at least once every 30 min (Walney, Northwest England) or 20 min (all southwest Scotland colonies, where devices were also switched off between 22:00 and 04:00 to conserve battery power). On an individuals' return to their breeding site in 2015, time-stamped GPS fixes that had been stored in the devices were downloaded remotely to a base station. Thirty-five tagged birds were re-sighted in 2015 in the colony where they were tagged the previous season and a further two tagged birds were re-sighted outside a breeding colony in a later year. Of the 35 tagged birds that were re-sighted in their colony, eight devices had failed by the time of return.

The number of daily fixes taken per individual varied through time. There were on average ca. 120 fixes per day per individual in July and August. However, due to low sunlight and short days during the winter at high latitude, which reduced solar charging of the devices, it dropped to ca. 2 fixes per day per individual in December and January. The number of fixes varied between individuals with some birds having periods of no fixes. Where periods of insufficient numbers of daily fixes in late winter coincided with the time individuals started to move back to the breeding colony, we were unable to accurately identify the end of the non-breeding period (see below). We therefore excluded data from seven returning individuals with working GPS-devices. Thus, we obtained information for the complete non-breeding period for 20 individuals with at least one GPS fix obtained on 40–100% of days (mean = 76.8%, SD = 19.4, $N = 20$) during the non-breeding period (see **Supplementary Table 1**).

The raw GPS fixes were processed to remove erroneous fixes and those during nocturnal roosting. First, erroneous locations, identified by travelling speeds exceeding 66 km h^{-1} , the maximum reported flight speed of a herring gull (Schnell and Hellack, 1979), were removed. The accuracy of location depends on the number of satellites contacted, with GPS fixes obtained from four or more satellites having an error <20 m (G. Brodin, PathTrack pers. comm.). We therefore removed a small number of fixes obtained from fewer than four satellites. Second, as we were interested in how herring gulls associate with habitat for resource acquisition, we removed all fixes earlier than an hour after dawn and later than an hour before dusk that were likely from individuals at a nocturnal roost or commuting to or from their roost. In winter, herring gulls can leave their night-time roost during a period of 3–4 h from just before sunrise, and start returning to the roost from 3 h before sunset onward (Cooke and Ross, 1972). This left a total of 30,806 use locations.

Timing of and Movements in the Non-breeding Period

From the processed GPS fixes we identified the start and the end of the non-breeding period from movement patterns.

Movements of breeding individuals are characterised by regular daily return trips to the colony where they attend and guard territories, nests, and offspring (e.g., Bukacinska et al., 1996). Non-breeding periods can thus be defined by the end and subsequent re-initiation of regular colony attendance. We determined colony-specific polygons that defined each colony's boundary. The last day an individual was recorded within the colony boundary before being absent from the colony for at least 10 consecutive days was classified as the start of the non-breeding period (departure date). The non-breeding period ended when the individual returned to the colony, defined as the first date that it was present within the colony boundary for at least part of each of 10 subsequent days (arrival date). The timing of breeding was similar across all colonies and therefore was not thought to affect colony arrival or departure dates among colonies.

For each GPS fix we calculated its distance from the centre of the breeding site using the *distHaversine* function in the R package *geosphere* (Hijmans, 2019a). The non-breeding day-time distributions of the tagged herring gulls were illustrated with the combined 95% (home range) kernel density estimations (KDEs) maps for all individuals from each of the three breeding locations: Southern Hebrides (Oronsay and Islay) and Firth of Clyde (Pladda and Lady Isle) in southwest Scotland, and Walney in northwest England (**Figure 1**). KDEs were combined for the two Southern Hebrides and two Firth of Clyde colonies due to the overlap of birds' movements and because of the small sample sizes per colony. KDEs were calculated using a grid size of 500 m^2 . For each individual, the most appropriate smoothing parameter (h) was calculated using a custom function, reported for each individual in **Supplementary Table 2**. To avoid under- or over-smoothing, this function identified a "minimum" (or adjusted) h -reference bandwidth by searching iteratively for the smallest h over progressively smaller scales starting with the h -reference bandwidth value. The smallest h prior to the eventual break-up of the 95% KDE spatial polygons was selected to create the optimum KDE for each individual. We created combined utilization distribution (UD) kernels for each of the three locations, using the individual KDEs weighted by the number of fixes per individual. To quantify overlap between the KDEs of the three breeding locations, we calculated Bhattacharyya's affinity index values in the R package *adehabitatHR*, which range from 0 (no overlap) to 1 (identical KDEs) (Bhattacharyya, 1943; Fieberg and Kochanny, 2005).

Habitat Availability and Use During the Non-breeding Period

To explore daytime habitat selection in the non-breeding period, all retained GPS fixes were considered use locations, which represented places where the birds foraged or loafed, although which potentially, may have also represented some commuting flights. All use locations were compared with random points that represented the availability of different habitats in the area used by the herring gulls. To first describe the available habitat within each region at the landscape scale, which individuals could migrate to, we created a 184.73 km buffer (representing

the maximum distance that tagged herring gulls moved away from their colonies, see section “Results”) around each colony. To create a similar density (2.95 available locations per 10 km²) as for the local scale (see below) we generated 31,593 random locations within the potential migration range of each colony, constant for all individuals. Herring gulls are coastal surface feeders when foraging in the marine environment, and spend most of their time at sea within 40 km of the coast (Kubetzki and Garthe, 2003; Anderson et al., 2019). Therefore, we removed available locations beyond 40 km from the coastline out to sea (13,165 available locations), giving a total of 144,800 available locations at the landscape scale.

To create available locations within the birds' reach from use locations (local scale), we first calculated the daily distance moved by individuals during the non-breeding period as the distance between an individual's consecutive daily centroid positions (based on all daily use locations) using the *distHaversine* function in the R package *geosphere* (Hijmans, 2019a). We then defined the 75% of the distribution of daily distances moved (7.35 km) around each use location as the area accessible to that individual on that day and generated random available locations within that range using the *gBuffer* function in the R package *rgeos* (Bivand and Rundel, 2019). To determine the optimal number of available locations required per use location, we tested the effects of different ratios of use to available, varying from 1:1 to 1:50 at intervals of 5, on the performance of the mixed effects logistic regression models (see Statistical Analysis below). For each use to available ratio we obtained the χ^2 -value of the habitat parameters and the model performance, measured as area under the receiver operator curve (AUC), using the R package *pROC* (Robin et al., 2011). The χ^2 - and AUC-values levelled off by the ratio of 1 use fix to 50 available locations (**Supplementary Figure 2**). Therefore, we used a ratio of 1:50 to be representative of habitat heterogeneity within the relatively large area an individual gull could have covered every day. At the local scale, within the accessible area of each of the 30,806 use locations, we thus generated 50 available locations.

Each use and available location was assigned to one of seven broad habitat categories (referred to as “habitat” hereafter): six known to be used by foraging herring gulls: arable, grassland, built-up, freshwater, intertidal, and marine offshore habitats (Hunt and Hunt, 1973; Götmark, 1984; Kubetzki and Garthe, 2003). All other habitats were pooled into a single “other” category that included habitats that are not typical herring gull foraging habitats (**Supplementary Table 3**). The habitat type at each use and available location was extracted using the *raster* package in R (Hijmans, 2019b) from the CORINE Land Cover 2018 classification of satellite image data (25 ha minimum mapping unit, European Environment Agency, 2019).

In order to validate that use locations did reflect habitats where herring gulls foraged, we also obtained an independent measure of habitats used for foraging by looking at the stable isotope ratios of feathers that herring gulls grow during the non-breeding period (outer primary and head feathers, Olsen and Larsson, 2004). In our study area, feather isotope ratios can discriminate between marine and terrestrial resources (O'Hanlon et al., 2017). We collected three head feathers and 10 barbs of the outermost

primary (representative of the entire feather, Wiley et al., 2010) from individuals at tagging. Collected feather material was first washed in a liquid detergent (EcoverTM) diluted with deionised water (approximate 1:99 dilution), then in a mixture of two parts chloroform and one part of methanol, and finally air-dried. Dried samples were homogenised and 1–2 mg of material was weighed into tin capsules, sealed and combusted to analyse for carbon, nitrogen, and sulphur isotopes by continuous-flow isotope ratio mass spectrometry [using a Elementar vario PYRO cube elemental analyser (Hanau, Germany) linked to a IsoPrime (now Elementar) VisION Mass Spectrometer (Cheadle Hulme, United Kingdom) at the National Environmental Isotope Facility in East Kilbride, United Kingdom]. The stable isotope ratios are expressed as $\delta^{13}\text{C}$ (¹³C/¹²C), $\delta^{15}\text{N}$ (¹⁵N/¹⁴N), and $\delta^{34}\text{S}$ (³⁴S/³²S) in parts per thousand (‰) relative to the international references Vienna PeeDee belemnite (V-PDB) marine fossil limestone for carbon, atmospheric N₂ for nitrogen, and Vienna Cañon Diablo Troilite (V-CDT) for sulphur, respectively. Measurement accuracy was $\pm 0.1\text{‰}$ for $\delta^{13}\text{C}$, $\pm 0.2\text{‰}$ for $\delta^{15}\text{N}$, and $\pm 0.70\text{‰}$ for $\delta^{34}\text{S}$ based on the standard deviation of the repeated analyses of laboratory standards (MSAG2, methanesulfonamide and gelatine; M1, methionine and gelatin; and SAAG, sulphanilamide and gelatine) and International Standards (USGS40 Glutamic Acid and IAEA S1, S2, and S3 silver sulphides). Head and primary feather materials of each individual were analysed separately and then averaged per individual. These isotope ratios allow for a good discrimination between marine and terrestrial food sources (Hobson and Welch, 1995; Hobson et al., 2015; O'Hanlon et al., 2017). Feather stable isotopes and habitat use data were available for 10 gulls tagged in Scotland, all females. We extracted the first principal component in a principal component analysis of the three stable isotope ratios. To determine whether the proportion of use fixes in marine and intertidal habitat (from the 2014/15 non-breeding season) was related to an individual's feather stable isotope ratio (grown during the 2013/14 non-breeding season) we performed a linear mixed-effect model, in the R package *lme4* (Bates et al., 2014), with colony included as a random effect. Although the feather isotope ratio and GPS tracking data related to different, but consecutive non-breeding periods, we assumed individuals would use similar areas and habitats as herring gulls have high between-year site fidelity to non-breeding areas (Clark et al., 2016).

Habitat Selection

All statistical analyses were performed in R, Version 4.0.3 (R Development Core Team, 2020) and throughout we report means and standard deviations (SD). To test for habitat selection, we used resource selection functions (RSFs), a commonly used approach to characterise the pattern of resources that are preferentially used or avoided by animals over a period of time (Manly et al., 2002) and that enables ecological limitations and needs to be identified (Fieberg et al., 2021). The analysis considered a use/availability design where known presences (use fixes) are compared with a random sample of pseudo-absences across “available” resources (available fixes) (Boyce, 2006). Logistic regression provides a useful method to fit RSFs

to quantify resource, or habitat, selection with use-available data (Johnson et al., 2006). This approach is straightforward to perform and allows the inclusion of random effects, which can help account for differences in samples sizes of use locations among individuals (Gillies et al., 2006). We estimated the relative probability of selection for different habitats using mixed effects logistic regression models for binomial data and a logit-link function (Augar et al., 2017) in *lme4* (Bates et al., 2014). Use or available was the binomial response variable (1 and 0, respectively) and habitat category was considered as the explanatory variable. Month nested within Bird ID was included as a random effect to account for the variable number of locations per bird and month. Because of the separation of the non-breeding distributions of birds from colonies in the southwest Scotland and northwest England regions (see section “Results”), we also considered region as an explanatory factor in the analyses. Of the 20 herring gulls with sufficient data, 18 were females and two were males (Supplementary Table 1). Although non-breeding movements can differ between the sexes (Catry et al., 2005), we were not able to formally compare between the sexes and pooled both sexes for the analyses. In the first instance we ran a model on all data with region (southwest Scotland and northwest England) and habitat and their interaction as fixed effects. Given the non-overlapping distribution in the non-breeding period and the difference in habitat availability between the two regions (see section “Results”), we also carried out separate RSFs for individuals from northwest England and southwest Scotland with habitat as the fixed effect. To estimate the variance explained by each model, we calculated conditional and marginal R^2 values in the R package *MuMIn* (Barton, 2012). The marginal R^2 values are associated with the fixed effects alone, while the conditional R^2 values are associated with the fixed and random effects (Nakagawa and Schielzeth, 2013). Diagnostic plots were checked to ensure all model assumptions were met.

From the model outputs, we obtained relative selection strength (RSS) by exponentiating the parameter coefficients for each habitat type; the RSS value reflects how strongly each habitat type is used relative to its availability, expressed relative to a reference habitat (Augar et al., 2017). If the confidence interval of the RSS value overlapped with 1 then there was no selection for a given habitat. An RSS value <1 indicated a habitat was used less than expected from its availability, while an RSS value >1 indicated a habitat was used more than expected from its availability. As the reference habitat category, we used the habitat “other.” The probability of use of “other” was relatively low (2.4% of use locations across both regions) which could affect the confidence interval of the RSS. However, we found the same qualitative patterns when using alternative habitats as the reference category (results not shown) and therefore we retained “other” habitat as the reference category to compare the relative extent to which the remaining six habitats were selected.

Individual Variation in Habitat Selection

Our RSS values are averages per habitat across all individuals (Manly et al., 2002) and assume that all individuals select

similarly between habitats. To explore variation in habitat selection between individuals we used an Eigenanalyses of Selection Ratios (Calenge and Dufour, 2006), carried out in the R package *adehabitatHS* (Calenge, 2006). Eigenanalyses maximise the differences between habitat use and availability on the first factorial axes. If all individuals select the same habitat, then all variation in selection is explained on the first factorial axis whereas if there is among-individual variation in habitat selection the explained variation is distributed across multiple axes (Calenge and Dufour, 2006). As the sum of all the proportions of habitats equals 1, the strength of habitat selection depicted in Eigenanalyses plots is scaled in comparison to all options included (Aebischer, 1993). As herring gulls in the southwest Scotland and the northwest England regions showed non-overlapping non-breeding distributions and the regions differed in habitat availability (see section “Results”), we carried out separate Eigenanalyses for the two regions.

Habitat and Spatial Specialisation

To investigate habitat specialisation of individual gulls we calculated the proportional similarity index (PSi) per individual where a value of 0 indicates an absolute habitat specialist and 1 an absolute habitat generalist (Schoener, 1968; Bolnick et al., 2002), following the equation in Bolnick et al. (2007), using the R package *RInSp* (Zaccarelli et al., 2013). For each individual this was calculated for the entire non-breeding period and for each month.

Spatial specialisation in where individual gulls spent the non-breeding period can be expressed as home range area and distance moved, with spatially more specialised individuals having smaller home ranges and moving over shorter distances (van den Bosch et al., 2019). As a measure of home range area we calculated 50 and 95% minimum convex polygons (MCP) around use fixes using the *mcp* function in the R package *adehabitatHR* (Calenge, 2006) for each individual and month. MCPs were calculated only when a minimum of five individual use fixes per individual and month were available, therefore we were unable to create monthly MCPs for 5 months for three individuals (bird 12,658 in January; bird 12,696 in November; bird 12,703 in December, January, and April). We found no correlation between the number of fixes and the 50 or 95% MCP area ($P > 0.45$, $N = 20$). As a measure of distance moved, we calculated the mean distance between consecutive monthly MCP centroids, calculated using the *distHaversine* function in the R package *geosphere* (Hijmans, 2019a), for each individual. Home range area and distance moved were significantly positively correlated (50% MCP: $r = 0.67$, $P = 0.001$, $N = 20$; 95% MCP: $r = 0.55$, $P = 0.01$, $N = 20$). We therefore used the mean distance between centroids of consecutive monthly 95% MCPs as our measure of spatial specialisation. Finally, we calculated the distance between the centroid of each monthly 95% MCP for each individual and its breeding colony to explore movements during the non-breeding period.

To determine whether spatial specialisation, based on the distance between centroids of consecutive monthly 95% MCP, was related to habitat specialisation (PSi), we ran a Pearson's correlation test. To explore the consistency of an individuals'

habitat and spatial specialisation over the non-breeding period we calculated repeatabilities of monthly PSi and distance between 95% MCP centroids of consecutive months, respectively, using the *rpt.remLMM* function in the R package *rptR* (Schielzeth and Nakagawa, 2011).

Details on the non-breeding season of the tracked individuals by colony is summarised in **Table 1**. To explore differences among colonies we performed a linear model for each variable (departure date, arrival date, length of absence from colony, habitat specialisation, spatial specialisation, mean distance of monthly 95% MCP centroids to the breeding colony, and non-breeding home range size). As there was only one tracked individual from the Pladda colony we omitted this individual from these analyses (**Table 1**). Subsequent Tukey *post-hoc* pairwise comparisons were performed using the *glht* function in the R package *multcomp* (Hothorn et al., 2008) to explore which colonies differed from each other.

RESULTS

Timing of and Movements in the Non-breeding Period

Tagged individual herring gulls left the breeding site over a 2.5 month period (departure dates ranged from June 30 to September 13, 2014), returned back to their breeding site between mid-January to mid-March (range from January 12 to March 19, 2015) and were absent from the breeding site on average for 193 ± 38 days ($N = 20$). Herring gulls from Oronsay, Southern Hebrides, departed earliest and stayed away from the colony longest, while gulls breeding at Walney, northwest England, departed latest and stayed away from the colony for the least time (**Table 1** and **Supplementary Table 4**). For the other colonies, departure dates and length of period absent from the colony were intermediate between Oronsay and Walney (**Table 1** and **Supplementary Table 4**). Differences in arrival date in spring were qualitatively similar among colonies but more variable between individuals (**Table 1**). Herring gulls moved up to 184.7 km (mean = 115.7 ± 47.3 km, range = 10.5–184.7 km, $N = 20$) away from their breeding site. The non-breeding KDEs of individuals tagged from the two most northerly colonies (Oronsay and Islay, Southern Hebrides) spread over a large area of the coastline of southwest Scotland and Northern Ireland and only partly overlapped with the more restricted non-breeding KDEs of Firth of Clyde (Lady Isle and Pladda) individuals (Bhattacharyya's affinity index = 0.19). The non-breeding KDEs of individuals tagged in Walney, northwest England were further south and did not overlap with any of the individuals tagged in Scotland (Bhattacharyya's affinity index = 0; **Figure 1**). Thus, the non-breeding areas of the tagged herring gulls fell into two distinct regions: one in northwest England and the other in southwest Scotland. The frequency of available habitat categories differed between the two regions (χ^2 -test, $\chi^2_6 = 7359.5$, $P < 0.001$) with a greater availability of intertidal and arable but lower availability of freshwater habitats in northwest England compared to southwest Scotland (**Table 2**).

TABLE 1 | Summary information on the non-breeding season of the tracked individuals by colony, including the results of linear models performed for each variable.

Colony	Departure date	Arrival date	Length of absence from colony (days)	Habitat specialisation (PSi)	Spatial specialisation (distance moved, km)	Mean distance of monthly 95% minimum convex polygons (MCP) centroids to the breeding colony (km)	Non-breeding home range size (95% MCP, km ²)
Pladda, Firth of Clyde ($N = 1$)	29/08	17/03	201	0.77	21.55	29.32	99.82
Oronsay, Southern Hebrides ($N = 4$)	16/7 \pm 13.6	19/3 \pm 20.6	247 \pm 30.1	0.75 \pm 0.07	46.7 \pm 11.4	87.7 \pm 40.53	677.1 \pm 709.7
Islay, Southern Hebrides ($N = 3$)	13/8 \pm 11.5	27/2 \pm 19.1	199 \pm 17.2	0.76 \pm 0.02	59.6 \pm 28.6	52.3 \pm 15.3	715.0 \pm 183.5
Lady Isle, Firth of Clyde ($N = 3$)	09/8 \pm 11.0	08/2 \pm 26.5	183 \pm 28.2	0.68 \pm 0.02	8.9 \pm 2.5	44.2 \pm 47.2	100.1 \pm 46.1
Walney, northwest England ($N = 9$)	04/9 \pm 15.9	19/2 \pm 15.0	169 \pm 26.1	0.55 \pm 0.18	27.0 \pm 14.3	52.2 \pm 21.3	362.0 \pm 261.3

$F_{3,15} = 11.07$, $P < 0.001$ $F_{3,15} = 3.25$, $P = 0.051$ $F_{3,15} = 8.30$, $P = 0.002$ $F_{3,15} = 3.11$, $P = 0.058$ $F_{3,15} = 6.69$, $P = 0.004$ $F_{3,15} = 1.67$, $P = 0.217$ $F_{3,15} = 2.00$, $P = 0.157$

Details on the single individual tracked from Pladda is included in the table but was omitted from the below analyses.

TABLE 2 | Composition of available habitat at the landscape scale within migration range of each herring gull colony in southwest Scotland (combined Southern Hebrides and Firth of Clyde) and in northwest England (Walney).

Non-breeding area	Colony (Location)	Proportion land use category (% contribution to the total χ^2 score in parenthesis)						
		Other	Built-up	Arable	Freshwater	Grassland	Intertidal	Marine
Southwest Scotland	Mean of the four colonies	0.270 (0.12)	0.026 (0.32)	0.046 (0.76)	0.012 (2.91)	0.231 (0.30)	0.008 (3.51)	0.406 (0.44)
Northwest England	Walney	0.166 (1.32)	0.065 (3.46)	0.139 (8.37)	0.003 (31.88)	0.296 (3.31)	0.014 (38.45)	0.317 (4.85)

TABLE 3 | Rank of general linear mixed effect models explaining variation in habitat use of herring gulls by habitat category (habitat) and region using Akaike's information criterion corrected for small sample size (AICc): df is the degrees of freedom, w_i is the Akaike weight, and $\Delta AICc$ is the AICc difference.

Variables included in the model	df	AICc	$\Delta AICc$	w_i	R^2
Habitat * Region	16	276626.1	0	1	0.31
Habitat + Region	10	279596.0	2969.91	0	0.30
Habitat	9	279608.6	2982.53	0	0.31
Null Model	3	303257.6	26631.55	0	0.00
Region	4	303259.6	26633.55	0	0.00

The most parsimonious model ($\Delta AICc < 2$) is shown in bold. Also reported is the marginal R^2 value for each model.

Habitat Selection

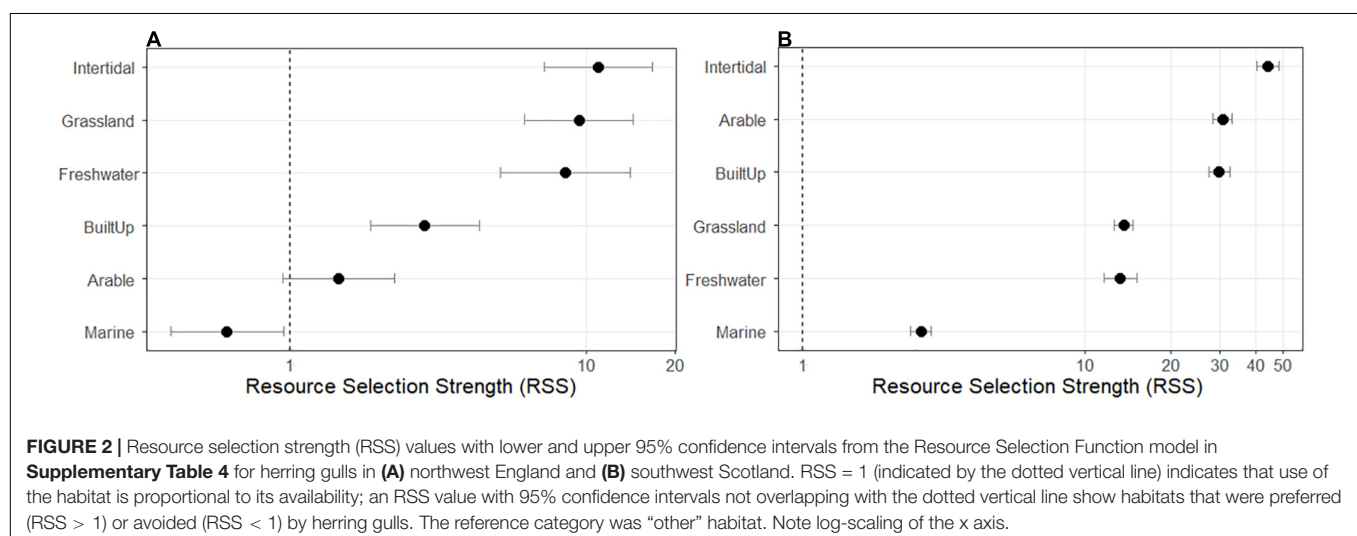
The most parsimonious RSF model, based on Akaike's information criterion (AIC) values (Table 3), included the interaction between region and habitat, indicating that individuals from the two regions were selecting habitats differently. Based on the region-specific RSF models, in both northwest England and southwest Scotland, herring gulls selected ($RSS > 1$) intertidal, grassland, freshwater, and built-up habitats, whilst in Scotland they also selected arable habitat (Figure 2 and Supplementary Table 5). This indicates that these habitats were used more often relative to their availability compared to selection for a control group of "other" habitat. However, the rank of habitats selected by the gulls differed between the two regions. In northwest England gulls showed

the strongest selection for intertidal, grassland, and freshwater habitats (Figure 2A), whilst in southwest Scotland, gulls showed the strongest selection for intertidal habitat, followed by arable and built-up habitats relative to "other" habitat (Figure 2B). Herring gulls in southwest Scotland showed a weak selection for marine habitat whilst birds in northwest England avoided ($RSS < 1$) this habitat. In northwest England, the gulls used arable habitat as would be expected given its availability. The proportion of each individual's use fixes in the different habitats are given in Supplementary Table 6.

The first principal component of the three stable isotope ratios from feathers moulted during the non-breeding season explained 76.6% of the variance and all three stable isotope ratios loaded negatively onto the first principal component (-0.52 to -0.65). The proportion of use points in marine and intertidal habitats significantly correlated with the bird's feather stable isotope ratio (linear mixed-effect model: $\chi^2 = 5.07$, $df = 1$, $P = 0.024$, $r = -0.62$, $N = 10$, Supplementary Figure 3). This supports that the habitat use described by the tracking data indeed reflects the habitats used by gulls for consuming food (as based on the stable isotope ratios of feathers).

Individual Variation in Habitat Selection

Habitat selection varied between individuals within regions as revealed by the Eigenanalyses of Selection Ratios that were run separately for the two regions, northwest England and southwest Scotland (Figure 3). The first factorial axis explained 76.7% of the selection ratio variance for northwest England and



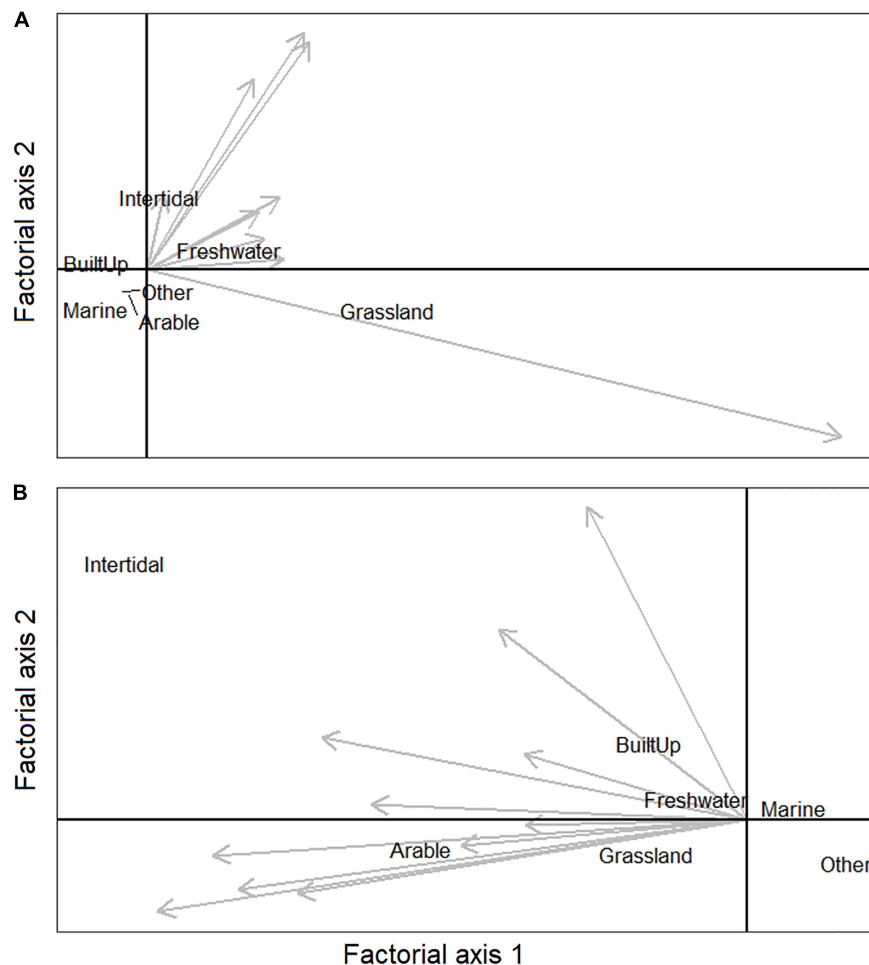


FIGURE 3 | Plot of Eigenanalysis of selection ratios for herring gulls using the non-breeding regions **(A)** northwest England and **(B)** southwest Scotland. The position of habitats reflects the biological significance of the first two factorial axes. The position of the arrows indicates the habitats selected by different individual gulls, with no selection in the centre of the axes. Eigenanalyses maximise the differences between habitat use and availability on the first factorial (horizontal) axes. If all individuals select the same habitat types, then all variation in selection is explained on the first factorial axis whereas the among-individual variation in habitat selection is distributed across the second factorial (vertical) axis. The first factorial axis explained 76.7% of the selection ratio variance for northwest England and 49.2% for southwest Scotland. The second factorial axis explained 23.3% of the selection ratio variance for northwest England and 50.8% for southwest Scotland.

49.2% of the selection ratio variance in southwest Scotland. The remaining variance on the second factorial axis thus revealed variation in habitat selection between individuals. In southwest Scotland (50.8% of the variance on the second factorial axis) some individuals showed a stronger selection for grassland and arable habitats whilst others showed a stronger selection for intertidal habitats (**Figure 3B**). In northwest England, the among-individual variation was less pronounced (23.3% of the variance on the second factorial axis), partly driven by one individual showing a strong selection for grassland habitat with the remaining gulls having a stronger selection for intertidal and freshwater habitats (**Figure 3A**).

Habitat and Spatial Specialisation

Individual variation in habitat use was also reflected by the range of habitat specialisation shown by individuals, with PSi values ranging from 0.32 to 0.82 (median: 0.72, **Supplementary**

Table 5). Most individuals had PSi values >0.5 and tended to be generalists in the habitats they used over the non-breeding period. Three individuals, however, had PSi <0.4 indicating some level of habitat specialisation; they included the two males and all three individuals specialised on the intertidal habitat (**Supplementary Table 5**). We found a low, but statistically significant repeatability in individual habitat specialisation across months ($r = 0.22$, 95% confidence interval = 0.05, 0.39).

Overall individuals did not migrate far from the breeding colony, with a mean distance of monthly 95% MCPs centroids from the breeding site of 57.0 km (range = 0.6–177.9 km, $N = 20$, **Supplementary Table 1** and **Supplementary Figure 4**). Over the non-breeding season, the mean 95% MCP of individuals was $456 \pm 400 \text{ km}^2$. However, once in their wintering area individuals showed limited spatial specialisation (measured as the mean distance between centroids of consecutive monthly 95% MCPs) with a median value of 30.5 km. Spatial specialisation varied

among individuals (range: 0.07–84.7 km) with individuals from Lady Isle, Firth of Clyde showing greater spatial specialisation than those from the other colonies (Table 1, Supplementary Table 3, and Supplementary Figure 4). This indicates that although some individuals spent the entire non-breeding season in a specific area, most individuals moved between different areas over the course of the breeding season (Supplementary Table 1). Spatial specialisation was only weakly repeatable within individuals across months ($r = 0.15$, 95% confidence interval = 0.00, 0.33) and was not related to habitat specialisation ($r = 0.24$, $P = 0.31$, $N = 20$).

DISCUSSION

Herring gulls tracked from five colonies across two geographical regions (southwest Scotland and northwest England) showed migratory connectivity at the regional level. At the local scale within southwest Scotland, however, migratory connectivity was less pronounced with overlap between the non-breeding areas of individuals from the different breeding colonies. Thus, migratory connectivity in herring gulls is scale dependent. During the non-breeding season, gulls used a range of habitats as would be expected for an opportunistic generalist. However, habitats were not used randomly based on their availability. Habitat selection differed between regions and individuals although populations from both regions strongly selected intertidal habitat suggesting this is an important habitat for wintering gulls. Individuals from the colonies considered moved around during the non-breeding season to different extents and did not show spatial specialisation. Within populations, individuals also differed in habitat selection with a moderate degree of habitat specialisation, independent of spatial specialisation. Hence, individuals sought similar resources at different locations, although given the low within-individual repeatability of habitat specialisation an individual's resource use appeared to be flexible across time and space. Our results provide information on the distribution and habitat requirements of this generalist species during the non-breeding season and highlight considerable among- and within-population variation. The gull's distribution over a broad range of habitats and space may help reduce competition for limited resources and buffer populations from localised anthropogenic pressures during the non-breeding season. However, our results also highlight the importance of intertidal habitats, as well as the availability of a mix of alternative habitats, for herring gulls during the non-breeding season, which should be considered in regional-specific spatial planning or conservation management for this species.

After the breeding season, the majority of herring gulls in the study area moved in a southerly direction. However, the timing of migration varied among colonies. Individuals breeding further north dispersed earlier and stayed away from the colony for longer, consistent with earlier migration at higher latitude in other migrating species (Hagan et al., 1991). We were unable to identify whether breeding attempts were successful or not for all individuals, with early departure rates likely involving failed breeders. Therefore, breeding failures may have influenced colony departure dates. Most individuals stayed away from

the breeding site for roughly half of the annual cycle. Three individuals (two birds from Lady Isle, Firth of Clyde and one from Walney, northwest England) did not move further away from their breeding colony than they typically would in the breeding season (45 km, Clewley et al., 2021; O'Hanlon and Nager, unpublished data), although they stopped visiting the colony site regularly. The remaining individuals moved considerably further (up to 185 km). These migration distances were similar, or slightly shorter, to those estimated for herring gulls in the Netherlands based on ringing recoveries (Camphuysen et al., 2011), and considerably shorter than observed for American herring gulls (*Larus smithsonianus*) breeding in northeastern North America (Anderson et al., 2019; Baak et al., 2021), possibly reflecting the mild oceanic climate of coastal Western Europe compared to northeastern North America.

Herring gulls breeding in northwest England and southwest Scotland spent the non-breeding period in distinct regions, suggesting migratory connectivity across geographic regions. Strong migratory connectivity across larger geographic scale has been previously found for American herring gulls (Anderson et al., 2019). However, on a finer geographical scale migratory connectivity was weaker. While the breeding home ranges of herring gulls from southwest Scotland were distinct (O'Hanlon and Nager, unpublished data) there was overlap between their non-breeding home ranges indicating weak migratory connectivity among populations at this scale. Migratory connectivity in seabirds has been shown to vary between species. For example, Merkel et al. (2021) found strong migratory connectivity in common (*Uria aalge*) and Brünnich's guillemots (*Uria lomvia*) in the Northeast Atlantic, whereas Frederiksen et al. (2012) found weak migratory connectivity among black-legged kittiwake (*Rissa tridactyla*) populations wintering in the Northwest Atlantic. Here we found migratory connectivity varying within a species and depending on spatial scale, as has been shown in other species (Trierweiler et al., 2014; Phipps et al., 2019).

In general, individual herring gulls in our study area had relatively small home ranges during the non-breeding period, and which were considerably smaller than reported for American herring gulls in northeastern North America (Anderson et al., 2019), although different methods were used to calculate home ranges and therefore should be compared cautiously (Börger et al., 2008). Individuals moved relatively short distances between months once in their wintering grounds (distance moved between consecutive monthly MCPs), which varied considerably between individuals. Most individuals visited several areas with little spatial specialisation to a specific location. Movements between distinct areas within the non-breeding season has been reported for a range of North Atlantic seabirds (Amélineau et al., 2021). Herring gulls can show high between-year winter site fidelity (Ceia et al., 2014; Clark et al., 2016) and breeding birds can show high spatial site specialisation in foraging locations within years (Davis, 1975). The lack of spatial specialisation in this study could be due to fewer predictable and profitable foraging sites that are worth concentrating on during the non-breeding season, for example, fish docks (Davis, 1975). Alternatively, resources may be predictable from year-to-year, but only for

short periods of time. Therefore, individuals may show short-term fidelity to multiple locations over the course of the non-breeding season. Across both regions, we observed among-colony differences in the distances moved between months with the greatest between-month movements made by individuals that bred further north in the Southern Hebrides (Oronsay and Islay). Although these individuals spent part of the non-breeding period in the same area as the Firth of Clyde (Pladda and Lady Isle) birds they moved through a wider area of the non-breeding range. This may indicate that changes in local resource availability in some areas, for example through reduced food availability or increased competition, resulted in individuals moving to new areas to find food over the course of the non-breeding season (Loretto et al., 2016). Exploring habitat specialisation alongside spatial specialisation provides complementary information on how individuals use the environment (Carneiro et al., 2017). This approach has been used to better explore spatial specialisation in other marine organisms and is relevant to species with a wide range of ecologies. Cory's shearwaters (*Calonectris borealis*) (Dias et al., 2011), northern gannets (*Morus bassanus*) (Fifield et al., 2014), and tiger sharks (*Galeocerdo cuvier*) (Lea et al., 2015) have all been reported to show high spatial specialisation, or site fidelity, in winter destinations between years, although with variation between individuals. Breeding Cory's shearwaters also show high spatial specialisation within a breeding season, possibly due to having access to sites with long-term high food availability (Navarro and González-Solís, 2009). In contrast, breeding herring gulls have been reported to show weaker spatial than habitat specialisation, but both influenced reproductive output (van den Bosch et al., 2019). The observed weak small-scale spatial specialisation within the broader wintering destination of herring gulls would be beneficial for coping with rapidly changing environments (Dias et al., 2011).

Little has previously been published on the use of habitats relative to their availability by non-breeding gulls, with fishery discards, landfill sites, and intertidal habitats all thought to be important resources for some populations during this period (Kihlman and Larsson, 1974; Monaghan, 1980; Horton et al., 1983; Hüppop and Wurm, 2000; Anderson et al., 2019). The non-breeding home range of herring gulls in our study area covered a range of different habitats and, as expected for an opportunistic forager, they used the available variety of habitats. The use of a range of habitats in non-breeding herring gulls is consistent with observations on breeding individuals, which also forage in a diversity of marine and terrestrial habitats (Harris, 1965; Hunt and Hunt, 1973; Kubetzki and Garthe, 2003; Enners et al., 2018). Individuals from many breeding colonies select intertidal habitat as their main foraging habitat (Camphuysen, 1995; Clewley et al., 2021) as did the non-breeding gulls in our study. This suggests that intertidal areas are also important foraging habitats for wintering herring gulls, at least in our study area. Foraging on intertidal resources can improve productivity of breeding herring gulls compared to other food sources, including in our study area (Pierotti and Annett, 1991; O'Hanlon et al., 2017). Intertidal prey can be richer in energy and/or nutrient content than other prey (O'Hanlon et al., 2017; but see van Donk et al., 2017), particularly in calcium content, which is important for egg formation and

chick growth (Reynolds and Perrins, 2010). Similar energetic or nutritional benefits may also arise for non-breeding birds.

GPS data provided an indication of the habitats used by herring gulls during the non-breeding season. However, at the temporal resolution we obtained, the GPS data could not determine whether individuals were specifically foraging at that location and were therefore consuming resources from that habitat. Temporal resolution of data has also limited the interpretation of actual resource use of other non-breeding herring gull populations (Anderson et al., 2019). Within this study, support for the use of habitats for foraging was shown through analysis of stable isotope ratios in feathers that were grown during the non-breeding period. We found that the stable isotope ratios of feathers from a sub-sample of tagged individuals grown during the previous winter correlated with the use of marine habitat in the following winter based on GPS data. Assuming that herring gulls do have high between-year site fidelity in non-breeding areas (Ceia et al., 2014; Clark et al., 2016), and within-season consistency in habitat specialisation (our results), this indicates that the habitat use described by the tracking data did reflect the habitats used by gulls for consuming food (based on the stable isotope ratios of feathers).

At the population level, herring gulls also used grassland, arable, and built-up habitats to a greater extent than expected given their availability in the landscape. Arable and grassland habitats may be profitable to foraging gulls due to spilt grains or supplementary feeding of livestock (Drury and Smith, 1968; Mitchell et al., 2004). In the mild oceanic climate of the British Isles, soil invertebrates, in particular earthworms, are also accessible for most of the non-breeding period in these habitats (Kruuk, 1978). Earthworms can form an important part of the herring gull's diet during the breeding season (McCleary and Sibly, 1986; Pennycott et al., 2020). Although fish and refuse are thought to be the most energy-rich and easily digestible food items for large gulls (Annett and Pierotti, 1989), preferences for arable and grassland habitat, where foraging might be more predictable and less risky (van Donk et al., 2017), might suggest that in the non-breeding period gulls adopt a more risk-averse resource utilisation strategy than when breeding.

The use of built-up areas and landfill sites by large gulls, including herring gulls, is well-documented (Kihlman and Larsson, 1974; Monaghan, 1980; Horton et al., 1983; Cook et al., 2008; Spelt et al., 2019). Although wintering herring gulls do use built-up areas, they appear to show a greater preference for other habitats and use landfill sites predominantly at high-tide when there is no access to intertidal prey (Kihlman and Larsson, 1974). The relatively frequent use of freshwater, as was also observed by Anderson et al. (2019), is likely due to gulls choosing safe areas on inland water bodies near good foraging locations to preen and roost (Clark, 2014). In addition, herring gulls are likely to require a supply of fresh water near feeding areas (Schreiber, 1967), particularly if they have been foraging in intertidal and/or offshore marine habitats. In our study area, herring gulls infrequently used offshore marine habitat within 40 km of the coast and in northwest England, in a lower proportion to its availability. This contrasts with regular observations of herring gulls offshore in the winter in this area over 20 years ago

(Stone et al., 1995). This may suggest that reduced fisheries and discarding activity, at least in the Firth of Clyde (Thurstan and Roberts, 2010), may have reduced the profitability of foraging out at sea. We, however, need to acknowledge that we only observed mainly adult females and that habitat use patterns may be different for male and immature herring gulls.

Although marine intertidal habitat was the preferred habitat in both regions, the ranking of the remaining habitats differed with grassland and freshwater being the next preferred habitats in northwest England compared to arable and built-up habitat in southwest Scotland. Although the relative importance of habitats appeared to differ between the two regions, this could not be formally tested. Regional differences in what habitats were most selected were also observed in American herring gulls (Anderson et al., 2019). The differences observed in habitat selection between the regions may be due to functional responses to variation in habitat availability (Myserud and Ims, 1998), although differences in the relative quality of habitats between regions cannot be ruled out. For instance, the availability of arable habitat was lower in southwest Scotland than northwest England. If that habitat contains important resources for herring gulls the relative selection strength might be expected to be higher where this habitat is rarer.

Within populations, individual herring gulls varied in their habitat use and their extent of habitat and spatial specialism over the non-breeding season. This pattern of intra-individual variation in habitat selection was found in two different landscapes (southwest Scotland and northwest England), although it was more pronounced in southwest Scotland. Habitat specialisation, although repeatable within individuals, was low and independent of spatial specialisation, potentially because birds moved around during the non-breeding period and flexibly used available resources at each location. These results concur with previous studies in that, although being generalists at the population level, individual gulls can be specialists (Navarro et al., 2017; van den Bosch et al., 2019). The extent of specialisation may be less pronounced in the non-breeding period than in the breeding period, potentially due to individuals no longer being constrained to a central breeding location. Non-breeding individuals may change which habitats they use if there are seasonal changes in relative resource availability in different habitats. Increased specialism can benefit individuals through increased foraging efficiency and energy intake (MacArthur and Pianka, 1958; Dukas and Kamil, 2001; van den Bosch et al., 2019), and through reducing intra-specific competition for resources (Bolnick et al., 2003; Ceia and Ramos, 2015). In this study, individuals did not specialise on one habitat over the course of the non-breeding season, except for three individuals that specialised on intertidal habitats, including the only two males in the study, but they may have reduced intra-specific competition through flexible use of a range of habitats.

It is not clear what factors influence variation in habitat selection between individual herring gulls. The characteristics of an individual may explain some of the variation in habitat selection such as age, sex, body size, or personality (e.g., Hebblewhite and Merrill, 2008; Bonnot et al., 2015; Leclerc

et al., 2016; Montgomery et al., 2018). For example, smaller females and less experienced immature herring gulls might be at a competitive disadvantage compared to experienced, larger adult males, which may result in them utilising a variety of potentially less favourable habitats (Monaghan, 1980; van Donk et al., 2018). As most individuals in this study were females, the low specialisation observed may be due to these individuals being outcompeted by males, or larger wintering individuals from Scandinavia (Calladine, 2002). Understanding what factors shape variation in habitat selection can highlight a species' potential for plastic responses to environmental change (Grist et al., 2014; Müller et al., 2014). Increased environmental heterogeneity and diversity of ecological opportunities are predicted to increase ecological segregation between conspecifics within (Robertson et al., 2015) and among populations (Rosenblatt et al., 2015). Therefore, it would be beneficial to track movements and observe behaviours of a broader section of the wintering population to improve our understanding of variation in habitat and spatial specialisation in wintering gulls.

Conditions in the non-breeding period can have an importance influence on annual survival and carry-over effects on the breeding performance of seabirds (reviewed in Strøm et al., 2021) and can be important for the regulation of seabird populations (Lack, 1966; Gaston, 2003; Sæther et al., 2016). Within this study, herring gull populations, and individuals, differed in their use of foraging habitats during the non-breeding period. Such differences can have important implications for population trends (Corbeau et al., 2021). Differences in adult survival between populations of herring gulls are hypothesised to be associated with differences in the availability of natural foraging habitats (Pons and Migot, 1995; Anderson et al., 2019). Although we do not have separate estimates of adult survival rates for northwest England and southwest Scotland, herring gull populations in the northwest England region are declining (Sellers and Shackleton, 2011) whereas populations in southwest Scotland remained relatively stable over the same period (O'Hanlon and Nager, 2018). The migratory connectivity in northwest England and southwest Scotland could be a factor in the differences in trajectories of populations at the larger regional scale. Differences in habitat availability and use during the non-breeding season may also be a factor affecting differences in population trends. Regional variation in population trends in American herring gull populations in northeastern North America had been hypothesised to be due to migratory connectivity and differences in non-breeding habitat use (Anderson et al., 2019). Despite the high degree of mixing among individuals from colonies in southwest Scotland, individuals were spread over a large area and used a variety of habitats. Consequently, localised environmental changes would be unlikely to affect all herring gull colonies in the region similarly. Indeed, although relatively stable overall, breeding populations in southwest Scotland varied in their population trajectories over a relatively small spatial scale (O'Hanlon and Nager, 2018). Part of the among-colony variation in population trajectories was linked to the availability of local foraging habitats (O'Hanlon and Nager, 2018), however carry-over effects from the non-breeding season may also have had an effect.

CONCLUSION

Herring gulls used a broad range of habitats during the non-breeding season with habitat selection differing between geographical regions and between individuals in the same region. This highlights that information on the habitat preferences of generalist species cannot be generalised, as the habitat preferences of individuals in one region may differ from those in relatively nearby regions. Although intertidal habitat was preferred, it is only available for variable periods depending on the timing of the tide and strength and direction of wind. Therefore, while this habitat provides high-quality food (Pierotti and Annett, 1991; O'Hanlon et al., 2017), alternative foraging habitats may be required. An availability of a range of habitats is thus likely to be important for herring gulls during the non-breeding season.

Identifying the intertidal areas most favourable to herring gulls and providing effective protection during the non-breeding period could benefit populations. For example, through reducing human disturbance, sustainable management of harvesting intertidal invertebrates, and managing conflict between wildlife and shellfisheries, which would likely benefit multiple species using intertidal habitats (Burton et al., 2002; Clarke et al., 2017; Clewley et al., 2021). The majority of individuals we studied tended to be habitat generalists over the non-breeding season but varied in the habitats selected indicating some level of habitat segregation, as well as spatial segregation, that might affect intra-specific competition. Availability of alternative foraging opportunities in the vicinity of favourable intertidal areas may make populations less vulnerable to temporary environmental perturbations and human pressures (Webster et al., 2002; Esler, 2014). However, individual variation in the use of habitat and space during the non-breeding season highlights that individuals within a population are not ecologically equivalent, and that intrinsic factors may drive variation in patterns of space use among individuals of a species. There is a need therefore to better understand the intrinsic drivers of habitat and spatial segregation between individuals, and identify what carry-over effects foraging on different resources during the non-breeding season may have on the following breeding season (Robb et al., 2008; Sorensen et al., 2009). A better understanding of habitat selection and its spatial variation can have important implication for implementing conservation management plans for wintering populations of generalist species of conservation concern across their annual cycle and will necessitate local or regional management plans that incorporate both marine and terrestrial environments.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by Animal Welfare and Ethical Review Body (AWERB) of the University of Glasgow. Birds were tagged under licence, with approval by the Independent Special Methods Technical Panel of the UK Ringing Scheme.

AUTHOR CONTRIBUTIONS

NO'H, CT, NB, and RN contributed to conception and design of the study and wrote sections of the manuscript. NO'H, CT, NC, DG, GCL, GCo, and RM collected and processed the data. NO'H performed the statistical analysis and wrote the first draft of the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.816881/full#supplementary-material>

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Variation in Antarctic Petrel Foraging Ecology: Not All Individuals Specialize on Krill

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Individual heterogeneity in foraging behaviour determines how individuals and populations respond to changes in the availability and distribution of resources. Antarctic krill *Euphausia superba* is a pivotal species in Southern Ocean food webs and an important target for Southern Ocean fisheries. Changes in its abundance could dramatically impact marine predators, with effects depending on the extent to which all individuals rely on krill as prey. The Antarctic petrel *Thalassoica antarctica* is a high latitude seabird thought to be dependent on krill in part of its breeding range. Here, by combining fine-scale GPS tracking of petrel foraging trips with diet data, we examined the level and consistency of inter-individual variation in foraging strategies in breeding Antarctic petrels in Dronning Maud Land, Antarctica, and assessed whether all individuals share a similar reliance on Antarctic krill. We found that Antarctic petrels showed high levels of repeatability in their diet and foraging movements at sea, indicating consistent individual differences in foraging strategies. During consecutive foraging trips, petrels tend to make trips of similar lengths and durations to reach similar terminal locations and to feed on similar prey. These individual differences in diet were spatially structured, with individuals travelling towards the west consuming a more fish-based diet. These different foraging tactics did not appear to be associated with different costs and/or benefits as adult body mass, chick survival and chick growth were unrelated to birds' foraging movements and diet. Our results show that, even if a large part of the population may be dependent on krill, some individuals specialize on fish. Such inter-individual variation in foraging suggests that this population could be more resilient to changes in the marine environment, such as a decline in krill abundance or a shift in krill distributions.

Keywords: diet, foraging, seabird, Antarctic, krill (*Euphausia superba*)

1 INTRODUCTION

Individual heterogeneity is ubiquitous in natural populations and can have a strong influence on population dynamics and ecosystem functioning (Benton et al., 2006; Bolnick et al., 2011; Kendall et al., 2011; Vindenes and Langanen, 2015). Variation among individuals in their foraging behaviour and/or resource use may, for example, lead to differences in demography (Morales et al., 2010), which can ultimately affect the population viability (Okuyama, 2008; Gibert and Brassil, 2014). Such heterogeneity in resource use can be driven by many different factors such as sex, age, and morphology, and can be consistent over various periods of time (Bolnick et al., 2003). It may be the consequence of individual resource specialization *per se* (i.e. individuals are specialized on specific resources among all those available) or of individual variation in foraging habitat in an environment where prey vary spatially (i.e. individuals are not specialist *per se* but the available resources vary among individuals). Whatever the mechanism, such inter-individual variation may affect the way populations respond to environmental perturbations and changes in resource availability (Bolnick et al., 2011; Phillips et al., 2017).

Individual heterogeneity in resource use has been described in many organisms such as marine and freshwater fish (Holbrook and Schmitt, 1992; Chavarie et al., 2021), amphibians (Lunghi et al., 2020), terrestrial and marine mammals (Estes et al., 2003; Edwards et al., 2011), and birds (Woo et al., 2008; Pagani-Núñez et al., 2015). In birds, evidence of inter-individual variation in foraging behaviour and diet exists in different taxonomic groups (e.g., waders, Van De Pol et al., 2010; passerines, De León et al., 2012; raptors, Navarro-López et al., 2014), including seabirds, where such variation seems widespread (Ceia and Ramos, 2015; Phillips et al., 2017). Seabirds, by definition, depend on the marine environment to forage. Marine food resources are generally patchily distributed, and both their composition and abundance show strong spatial variation (e.g., Godø et al., 2012; Tarling and Fielding, 2016; Bergstad et al., 2018). Such spatial heterogeneity may drive variation among individuals in their space use (Fauchald, 1999; Trevaill et al., 2021) and then ultimately in their diet as a way to minimize intra-specific competition (Araújo et al., 2011). This may be especially pronounced during the breeding season when seabirds are central-place foragers and intra-specific competition for resources is intensified (Ashmole, 1963).

Understanding the extent to which individuals in a given population vary in how they use their environment is critical to evaluating the resilience of this population to environmental change. Indeed, the deterioration of a specific foraging habitat or the decline in the abundance of a specific prey will have stronger effects on a population if all individuals depend on this area or prey (Durell, 2000). Such problems are especially pertinent for populations living at high latitudes (i.e. Arctic and Antarctic) where environmental changes like climate warming, are, or are predicted to be, extremely pronounced (Intergovernmental Panel on Climate Change, 2013), with impacts on the distribution and abundance of many key prey species. For populations dependent on harvested resources, it is further necessary to address the

degree of individual specialization within the population, in order to evaluate the potential population-level impacts of resource exploitation.

Here, by combining fine-scale GPS tracking with diet data, we assessed the level and consistency of inter-individual variation in foraging strategies of breeding Antarctic petrels *Thalassoica antarctica* in Dronning Maud Land, Antarctica. In this region, Antarctic krill *Euphausia superba* (hereafter krill) is the main prey for Antarctic petrels, at least during the breeding season (Loretsen et al., 1998; Descamps et al., 2016a). Krill is a pivotal species in the Southern Ocean food webs (Trathan and Hill, 2016) and also an important target for Southern Ocean fisheries (Nicol et al., 2012). Though the status and trend of the Antarctic krill is debated (Cox et al., 2018), some studies suggest that it may be declining (Atkinson et al., 2004). It thus appears even more important to better understand the relationships between krill and Antarctic petrels, and to what extent the entire petrel population may be relying on krill during the breeding season. Antarctic petrels from this population exhibit a wide range of foraging behaviours (e.g., Tarroux et al., 2020), but it is unclear whether these differences remain consistent through time and thus represent individual foraging specialization (in terms of space use and diet). Our study aimed at evaluating the inter-individual variation in resource use in Antarctic petrels and the level of consistency (i.e. repeatability) in their foraging movements and diet. We then assessed whether individual differences in foraging were associated with fitness consequences, by looking at offspring mass and survival. The Antarctic petrel, as well as many polar seabirds (e.g., Ainley et al., 2010; Strøm et al., 2020; Trathan et al., 2020; Descamps and Strøm, 2021), has been declining (by more than 50% in the last 30 years, Descamps et al., 2016b and unpublished data) and to better understand the individual variation in their foraging ecology, and more specifically in their dependence on krill, is especially important in a context of increasing krill fisheries (CCAMLR, 2021).

2 METHODS

2.1 Study System

The Antarctic petrel is a medium-sized petrel weighing *ca.* 600 g that lays one egg between late November and early December. The incubation is shared by both parents and each incubation shift lasts for one to three weeks (Loretsen and Røv, 1995). After hatching (mid-January), the chick is guarded for another two weeks (Loretsen and Røv, 1995). In this period, foraging trips gradually shorten until the chick is left unattended for the first time (end of January). From this point, both parents feed their chick until it fledges at 6-7 weeks of age (early March). During the breeding season, the most common prey is Antarctic krill that represents about two third of the diet by mass on average, but fish (e.g. Antarctic lanternfish *Electrona antarctica*, and Antarctic silverfish *Pleuragramma antarcticum*) are also important prey items and represent on average 30% of the diet (Loretsen et al., 1998; Descamps et al., 2016a). Adult petrels were captured at the Svarthamaren colony (71°53'S, 5°10'E) in

Dronning Maud Land, Antarctica (Mehlum et al., 1988). This colony is located *ca.* 200 km inland and hosts between 20,000 and 200,000 pairs of Antarctic petrels depending on years (Descamps et al., 2016b). All captured birds and their chick were weighed at logger deployment and retrieval. Nests were also monitored (i.e. presence/absence of the chick) from logger deployment (17th–22nd January) until 9th–11th February (i.e. last nest visit). Hatching dates of these nests, and thus chick age, were unknown. All captures, sampling and logger deployments were carried out in accordance with the permit provided by the Norwegian Animal Welfare Authority (Mattilsynet, permit no.7935).

2.2 Tracking Data

Breeding adults were captured on their nest during chick-rearing and equipped with GPS loggers (CatTrack 1, Catnip Technologies Ltd., Anderson, USA). Loggers were deployed in period 17th–22nd January 2016 and retrieved in period 21st January–7th February. The GPS units weighed approx. 20 g (*ca.* 3% of bird body mass) and were taped to tail feathers (using Tesa tape). Additional details about the procedure are given in Tarroux et al. (2016; 2020). Birds were recaptured upon return to their nests to retrieve the loggers and download the data. The loggers recorded the locations of the birds along their foraging trip at 30 min intervals. We deployed 91 loggers and retrieved 41 (5 to 20 days after deployment; median: 12 days); the remaining 50 loggers were either lost by the birds or birds could not be recaptured. Three loggers did not work properly and so did not provide data. One individual's breeding attempt failed after logger deployment but before departure and was excluded from the analyses. In total, data from 37 loggers were included in this study.

We considered a potential foraging trip as a round trip starting or ending when the bird left or entered, respectively, a 5 km-buffer area around the colony (defined as a single point at coordinates 71°53'S, 5°10'E), and reached the sea ice edge (approx. 200 km from the colony). We consequently excluded three short inland trips where birds reached a maximum distance of <25 km from the colony, which likely constitute local flights around the colony. We considered five variables describing each foraging trip: the trip duration, the total distance travelled, the maximum distance from the colony and the coordinates (latitude/longitude) of the farthest point. One trip was incomplete, but the bird was returning towards the colony and its last recorded position was <50 km from the colony (after reaching a maximum distance of almost 600 km from the colony). We thus included this trip in our analyses of maximum distance from the colony and the latitude/longitude of the farthest point, but not in our analyses of trip duration and total distance travelled. In total we recorded 80 foraging trips from the 37 tracked individuals (11 individuals with 1 trip, 12 with 2 trips, 11 with 3 trips and 3 with 4 trips). Data are given in the **Supplementary Table 1**.

2.3 Stable Isotopes and Diet Data

We collected *ca.* 0.3 ml of blood from a subsample of 21 individuals when recovering their GPS unit. Samples were

collected from the brachial vein (using heparinized syringes with a 26G needle) and stored in heparinized tubes. Blood samples were centrifuged within 8 hr after collection at 10,000 rpm for 10 minutes. Plasma and blood cell samples were then frozen until stable isotope analyses at the LIENSs laboratory, La Rochelle University (France). Samples were used to determine the stable isotope ratios of nitrogen ($\delta^{15}\text{N}$), a proxy of the trophic position with higher values indicating higher position (Newsome et al., 2007; Hussey et al., 2014). The stable isotope ratios of carbon ($\delta^{13}\text{C}$) were also analysed (data available in the **Supplementary Table 1**) but were not included in the present study. $\delta^{13}\text{C}$ values are generally used to identify bird foraging areas but in our case, as birds were GPS-tracked, examining variation in $\delta^{13}\text{C}$ values would not provide any significant additional information.

Stable isotopes integrate dietary information over different time scales depending on the tissue type (Bearhop et al., 2004). Stable isotopes in plasma reflect diet integrated several days prior to sampling (and thus, the diet during the last foraging trip before sampling) whereas in blood cells, they reflect longer term integrated diet (i.e., several weeks, Hobson and Clark, 1993). As plasma and red blood cells were extracted from the same blood sample for a given individual, their respective isotopic values were not completely independent. However, given that red cell isotopic values reflect the bird diet over the 3–4 weeks preceding sampling, while plasma isotopic values reflect diet over the 3–5 days prior to sampling (Hobson and Clark, 1993), the red cell isotopic values should only be marginally affected by what the bird ate in the few days before sampling, and the red cell and plasma isotopic values should thus be largely independent.

Subsamples (~0.3 mg) of plasma and blood cells were packed into tin cups and their relative abundance of N isotope were determined with a continuous flow mass spectrometer (Thermo Scientific Delta V Advantage) coupled to an elemental analyzer (Thermo Scientific Flash EA 1112). Stable isotope concentrations were expressed in conventional δ notation ($\delta X = [R_{\text{sample}}/R_{\text{standard}} - 1] \times 1000$) where X is ^{15}N and R is $^{15}\text{N}/^{14}\text{N}$ and R_{standard} is the atmospheric N_2 . Replicate measurements of internal laboratory standards (acetanilide) indicated measurement errors <0.15 ‰.

Additionally, we collected in the same period (Jan/Feb 2016) the stomach content of 10 individuals by stomach lavage (Wilson, 1984), five of them being from tracked individuals when recovering their GPS unit. Collection took place immediately after the return of the bird to its nest from a foraging trip and before it started feeding its chick. Stomach contents were immediately frozen and later transferred to the laboratory for taxonomic analysis, following Cherel et al. (2002). Prey was identified using published keys and descriptions and by comparison with material held in our reference collections.

2.4 Statistical Analyses

All statistical analyses were done with R software version 4.0.2 (R Development Core Team, 2020).

2.4.1 Individual Consistency in Foraging Behaviour

We first quantified repeatability in movement metrics (trip duration, total distance travelled, maximum distance travelled,

latitude and longitude of the farthest location), defined as the proportion of variation in a given trait that can be attributed to between-individual variation (Lessells and Boag, 1987; Nakagawa and Schielzeth, 2010). We used a linear mixed model approach using the rpt() function of the rptR package (Stoffel et al., 2017). We included logger deployment date as a fixed effect and thus estimated adjusted repeatabilities (Nakagawa and Schielzeth, 2010). All individuals, including those tracked during only one foraging trip, were included in the repeatability estimations in order to base these estimations on the best possible estimate of the among-individual variance in the traits considered. All metrics followed a Gaussian distribution, except the longitude of the farthest location which was left-skewed [and was thus transformed as $(\text{Longitude}+30)^2$]. The 95% confidence intervals of repeatability coefficients were estimated using parametric bootstrapping with 1000 bootstraps (Stoffel et al., 2017).

In a second step, we estimated the consistency in individual diet (equivalent to the level of individual specialization in diet) by quantifying the correlation (Pearson's r) between plasma and blood cell isotopic values. Indeed, as these tissues have different turn-over rates (several weeks for blood cells and several days for plasma), a strong correlation between stable isotopic ratios in blood cells and plasma would indicate some level of temporal consistency in individuals' diet, or more exactly its trophic position (Bond et al., 2016; Cherel et al., 2018).

2.4.2 Relationships Between Spatial Distribution and Diet

We tested in a third step whether or not the spatial distribution of petrels (i.e. their farthest latitude and longitude) was associated with their diet. We first used a linear model with $\delta^{15}\text{N}_{\text{plasma}}$ as the response variable and $\text{Long}_{\text{farthest location}}$ and $\text{Lat}_{\text{farthest location}}$ as the explanatory variables. Visual inspection of model residuals indicated that they were normally distributed and homoscedastic. For each individual, we included only the foraging trip made immediately prior to blood sampling (i.e. only one trip per individual) and the $\delta^{15}\text{N}_{\text{plasma}}$ value is expected to represent the diet during this single trip (i.e., these foraging trips averaged $4.6 \text{ days} \pm 1.6 \text{ SD}$, which corresponds to the expected plasma turn-over). Then, using the same data, we performed a cluster analysis based on the distance between the farthest locations of each foraging trip to group individuals into categories representing their space use, and compared the mean $\delta^{15}\text{N}_{\text{plasma}}$ value among these groups. We used the distm function (from package geosphere, Hijmans et al., 2017) to generate a geodesic distance matrix between these farthest locations and the hclust and cutree functions to define clusters, using an arbitrary distance threshold (i.e. cut-of value for the height of the cluster dendrogram) of 400 km (which corresponds to scale of the foraging areas used by Antarctic petrels; Fauchald and Tveraa, 2006). This latter analysis was used to confirm the previous results based on a linear regression and to give a more explicit spatial description of the differences among individuals in their diet but did not intend to identify the optimal number of clusters.

Results from stomach samples were further used to aid interpretation of results from stable isotope analyses, but sample size was too low ($n=5$) to test for a link with the spatial distribution of birds.

2.4.3 Consequence of Individual Foraging Strategies on Adult Mass, Chick Mass and Chick Survival

To test for the effect of petrel foraging strategies (movement metrics and diet) on petrel body mass chick mass and survival, we used linear models with either adult mass, chick mass or chick survival as response variables. For both adult and chick mass we considered mass measurements on adults' return to the nest. We used a Gaussian distribution for mass variables and a binomial distribution with a logit-link function for chick survival. The chick survival was defined based on the last nest visit done in period 9th-11th February. For the mass analyses, we included in the models the adult or chick mass at deployment, as well as the logger deployment date as covariates. For the chick survival analysis, we also included the deployment date as a covariate. Chick age was unknown and could thus not be included in models.

We first tested for the effect of the mean distance travelled per foraging trip and the mean coordinates of the farthest locations on these three dependent variables (adult mass, chick mass and chick survival). We did not include the mean trip duration and mean maximum distance from the colony as these two variables were highly correlated with the mean distance travelled (Pearson's $r=0.85$ and 0.73 , respectively). These analyses were based on all 37 tracked individuals. We then tested in separate models for the effect of $\delta^{15}\text{N}_{\text{cells}}$ (i.e. a proxy of the average trophic position of the birds during the previous weeks) on the three previously described dependent variables. We used separate models to test for an effect of $\delta^{15}\text{N}_{\text{cells}}$ because isotope data were only available for a subsample of tracked individuals ($n=21$ individuals).

3 RESULTS

3.1 Individual Consistency in Foraging Behaviour

Antarctic petrel movement metrics were repeatable (**Table 1** and **Supplementary Figure 1**) indicating that Antarctic petrels show substantial levels of individual consistency in their movements at sea when foraging. More specifically, individuals that travelled far from the colony and/or that had a long foraging trip tend to do the same during consecutive trips. The highest repeatability was obtained for the coordinates (latitude and longitude) of the farthest positions (**Table 1**) suggesting that birds were generally consistent in their most distant foraging areas.

Antarctic petrels did not all feed on the same prey (range of $\delta^{15}\text{N}$ values in plasma and blood cells, respectively: $8.44\text{--}12.36$ and $8.81\text{--}10.18$ ‰; Fig.1) and our results suggest some level of individual specialization in diet. Individuals' plasma (mean \pm SD: 9.71 ± 1.27 ‰) and blood cell (mean \pm SD: 9.46 ± 0.35 ‰) $\delta^{15}\text{N}$ values were highly correlated (Pearson's $r=0.75$, 95%CI=

TABLE 1 | Adjusted repeatability in movement metrics in the Antarctic petrel (data from Jan-Feb 2016, Svarthamaren, Dronning Maud Land).

Trait	Mean \pm SD	Repeatability	95% CI
Trip duration (hours)	95.2 \pm 29.3	0.47**	0.19-0.68
Total distance (km)	2034 \pm 622	0.49***	0.22-0.70
Max. distance (km)	593 \pm 149	0.39**	0.10-0.64
Long. farthest location (°)	5.9 \pm 9.4	0.61***	0.39-0.78
Lat. farthest location (°)	-67.6 \pm 1.2	0.72***	0.52-0.84

Results are based on 80 trips from 37 individuals for the maximum distance and farthest lat/long, and on 79 trips from 37 individuals for trip duration and total distance. All models include the GPS deployment date as a covariate.

** $p < 0.01$, *** $p < 0.001$.

[0.47, 0.89], $p < 0.001$]; **Figure 1**) indicating that individuals were consistently foraging on high, or low, trophic level prey. The relationship between $\delta^{15}\text{N}$ in plasma and blood cells shows an increase in the $\delta^{15}\text{N}$ values in the plasma of the individuals that already had higher $\delta^{15}\text{N}$ values in their blood cells (slope higher than one, **Figure 1**). This suggests that those individuals were feeding on higher trophic levels during their last foraging trip as compared to the trips occurring in the previous weeks.

3.2 Relationships Between Spatial Distribution and Diet

The $\delta^{15}\text{N}$ value of Antarctic petrel was significantly associated with their movements at sea and individuals travelling towards more eastern longitudes were characterized by lower $\delta^{15}\text{N}$ values (effect of the longitude of the farthest position: $\beta = -0.09 \pm 0.03$ SE, $t = -3.58$ $p = 0.002$; **Figure 2**). The effect of the latitude was negative (lower $\delta^{15}\text{N}$ values at higher latitudes) but only marginally significant once the longitude effect was taken into account (effect of the latitude of the farthest position: $\beta = -0.41 \pm 0.20$ SE, $t = -2.03$, $p = 0.06$).

A cluster analysis based on the farthest locations from the colony indicated three different clusters (**Figure 3**). Petrels that

travelled towards the “central” and “east” clusters (**Figure 3**) had similar mean $\delta^{15}\text{N}_{\text{plasma}}$ values equal to 9.5 ‰ (95%CI=[8.7, 9.2]) and 9.0 ‰ (95%CI=[8.8, 9.3]), respectively. The mean $\delta^{15}\text{N}_{\text{plasma}}$ value of those that travelled towards the west was higher and equal to 11.9 ‰ (95%CI=[11.6, 12.3]; **Figure 2**).

Stomach samples revealed a high proportion of fish (72% on average of the wet biomass of the samples, mostly the neritic *Pleuragramma antarcticum*, and the oceanic *Notolepis coatsi* and *Electrona antarctica*) and a low proportion of crustaceans (dominated by krill; 26% of the wet biomass) in Jan/Feb 2016 ($n=10$). While fish appeared to be the dominant prey in 2016, results from stomach content of tracked individuals (representative of the diet of their chick) match results from stable isotopes (that are representative of adult diet) and indicate that the proportion of fish in the diet was higher and the proportion of krill lower in birds that travelled towards the west. If we consider the same areas as the ones depicted in **Figure 2**, we found that food samples of birds travelling towards the east were composed of 27% krill and 71% fish ($n=3$; range for the % of krill and fish respectively: [5, 50] and [50, 88]), whereas for birds travelling towards the west, stomach contents were comprised of 1% krill and 97% fish ($n=2$; range for the % of krill and fish respectively: [1, 2] and [95, 99]).

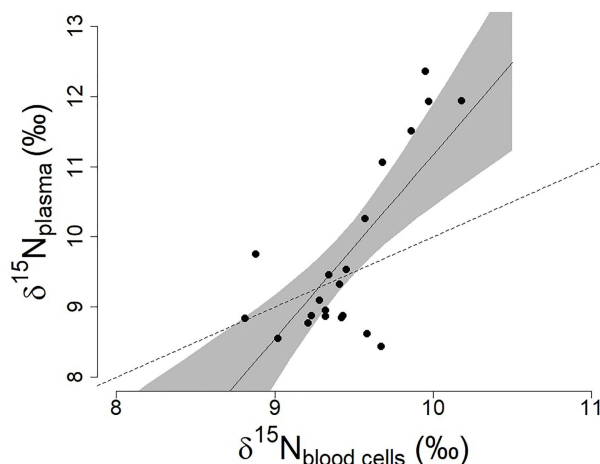


FIGURE 1 | Relationships between $\delta^{15}\text{N}$ values in plasma and blood cells in the Antarctic petrel ($n=21$; data from Jan-Feb 2016, Svarthamaren Dronning Maud Land). The regression line and associated 95% confidence interval (shaded area) are from the single regression model $\delta^{15}\text{N}_{\text{plasma}} \sim \delta^{15}\text{N}_{\text{blood cells}}$ ($\beta \pm \text{SE} = 2.70 \pm 0.55$, $t=4.90$, $p < 0.001$). The dotted line represents the regression with a slope equal to 1.

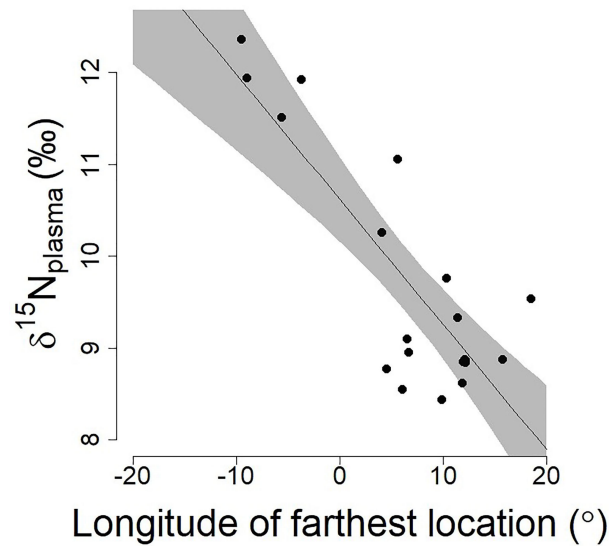


FIGURE 2 | Relationships between the longitude of the farthest position during a foraging trip and the corresponding $\delta^{15}\text{N}_{\text{plasma}}$ values in chick-rearing Antarctic petrels ($n=21$; data from Jan-Feb 2016, Svarthamaren Dronning Maud Land). The regression line and associated 95% confidence interval (shaded areas) are from a single regression model: ($\delta^{15}\text{N}_{\text{plasma}} \sim \text{Long}_{\text{farthest location}}$, $\beta \pm \text{SE} = -0.13 \pm 0.02$, $t=-6.24$, $p<0.001$; $R^2 = 0.67$).

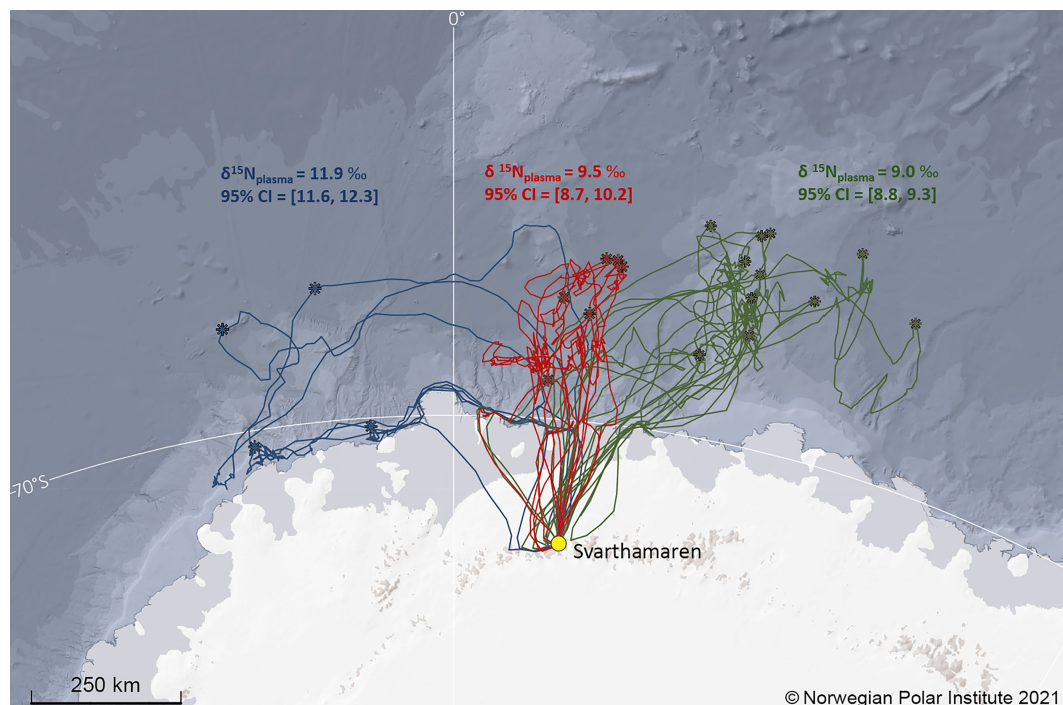


FIGURE 3 | Foraging trips of Antarctic petrels in January-February 2016 ($n=21$ trips from 21 individuals for which blood was sampled at return to the colony for stable isotope analyses). The breeding colony, Svarthamaren, is indicated by a yellow dot. The farthest position from the colony for each foraging trip is indicated by a star. The three colours represent the three clusters of Antarctic petrels based on their farthest positions. The mean (and associated 95% confidence interval) $\delta^{15}\text{N}_{\text{plasma}}$ value is indicated for each group using the same colour code.

3.3 Consequence of Individual Foraging Strategies on Adult Mass, Chick Mass and Chick Survival

After adjusting for the logger deployment date and mass at deployment, we found that petrel movement and diet metrics were not significantly associated with the adult or chick mass at return, nor with the chick survival probability (Table 2).

4 DISCUSSION

Antarctic petrels from Svarthamaren show high levels of repeatability in their diet and movements at sea. During consecutive foraging trips, petrels tend to make trips of similar lengths and durations, reach similar terminal locations and feed on similar prey. These individual differences in foraging are spatially structured, with individuals travelling towards the west feeding more on fish than those travelling to the east.

4.1 Individual Specialization in the Antarctic Petrel?

Our results, based on GPS-tracking, stable isotope and stomach content data, support the hypothesis of individual specialization in foraging behaviour. However, our results are based on relatively short-term tracking of individuals during the chick-rearing period and the longer-term persistence of petrel specialization in foraging behaviour remains unknown. Studies during the other parts of the Antarctic petrel life-cycle (e.g., incubation, migration), and in consecutive years would be needed to get a more complete understanding of the level of individual specialization in this population.

Our results contrast with previous observations made in another Antarctic petrel colony in East Antarctica (Hop Island, Prydz Bay region). Dehnhard et al. (2020) reported that all tracked Antarctic petrels behaved like generalists and did not show any sign of specialization in terms of their foraging sites and habitat use, neither during incubation nor chick-rearing. This was explained by the high variability and low predictability of the petrels' foraging environment surrounding Hop Island. Indeed, individual specialization in foraging is only expected when the environment shows some level of consistency and/or predictability. In a constantly changing foraging environment, being generalist (in terms of foraging habitat and/or diet) is expected to be the most beneficial strategy and there should be limited individual specialization (Futuyma and Moreno, 1988). The apparent individual specialization of Antarctic petrels breeding at Svarthamaren may thus be explained by a more predictable foraging environment than at Prydz Bay/East Antarctica. In support of this, recent observations found that some regions within the Svarthamaren Antarctic petrel foraging range are characterized by recurrent very high productivity (Descamps et al., 2021; Kauko et al., 2021). These studies identified a large late-summer phytoplankton bloom spanning 300 km east of the Weddell Gyre, associated with high krill densities. At-sea observations indicated that this area (that overlaps with the "central" and "East" clusters shown in Figure 3) is used intensively by Antarctic petrels. This bloom happens regularly in this area and such predictability may be linked to the individual specialization observed in petrels from Svarthamaren.

Based on previous satellite and GPS tracking, Fauchald et al. (2006; 2017) suggested that Antarctic petrels from Svarthamaren had no fixed foraging areas and adjust their behaviour and search for food based on real-time cues (i.e. during the ongoing foraging bout). However, our new results indicate that Antarctic petrels

TABLE 2 | Consequence of individual foraging strategies on adult mass, chick mass and chick survival in the Antarctic petrel (Svarthamaren Dronning Maud Land).

Dependent variable	Explanatory variables	Slope \pm SE	Test statistic (p-value)
Adult mass at return	Adult mass at deployment	0.19 \pm 0.17	$t = 1.13$ (0.27)
	Date deployment	-6.39 \pm 9.52	$t = -0.67$ (0.51)
	Mean tot. distance	0.01 \pm 0.02	$t = 0.49$ (0.63)
	Mean Long. Farthest point	2.13 \pm 2.09	$t = 1.02$ (0.32)
	Mean Lat. Farthest point	-15.23 \pm 13.19	$t = -1.16$ (0.26)
Chick mass at return	Chick mass at deployment	0.77 \pm 0.97	$t = 0.79$ (0.44)
	Date deployment	-20.78 \pm 23.41	$t = -0.89$ (0.39)
	Mean tot. distance	-0.07 \pm 0.12	$t = -0.61$ (0.55)
	Mean Long. Farthest point	-3.59 \pm 8.46	$t = -0.43$ (0.68)
	Mean Lat. Farthest point	75.41 \pm 96.18	$t = 0.78$ (0.45)
Chick survival	Date deployment	-0.09 \pm 0.29	$z = -0.31$ (0.76)
	Mean tot. distance	-0.0005 \pm 0.0009	$z = -0.53$ (0.60)
	Mean Long. Farthest point	-0.07 \pm 0.08	$z = -0.88$ (0.38)
	Mean Lat. Farthest point	0.88 \pm 0.81	$z = 1.08$ (0.28)
Dependent variable	Explanatory variables	Slope \pm SE	Test statistic (p-value)
Adult mass at return	$\delta^{15}\text{N}_{\text{cells}}$	-1.95 \pm 10.72	$t = -0.18$ (0.86)
Chick mass at return	$\delta^{15}\text{N}_{\text{cells}}$	20.38 \pm 31.38	$t = 0.65$ (0.53)
Chick survival	$\delta^{15}\text{N}_{\text{cells}}$	0.35 \pm 0.37	$z = 0.93$ (0.35)

(a) The variables "Mean tot. distance", "Mean Long. Farthest point" and "Mean Lat. Farthest point" represent respectively the mean distance travelled per foraging trip for each tracked bird, and the mean longitude and latitude of the farthest point reached during the trips. Sample size for all models is $n=37$ and results are the same when considering each variable separately in single regression models. (b) Models were run separately for testing the effect of the $\delta^{15}\text{N}_{\text{cells}}$ value (a proxy of the birds' trophic position) as data were only available for a subsample of individuals ($n=21$). In (a) and (b), the test statistic column represents either a t -statistic for models based on a gaussian distribution, or a z -statistic for models based on a binomial distribution.

show some level of consistency in their movements and tend to have the same final destination between consecutive foraging trips. This does not necessarily mean that they follow the exact same routes and forage at the same locations along these trips. In fact, when looking at potential foraging areas along each foraging trip (see details in **Supplementary Table 2**), we found that foraging areas were distributed along the tracks and there was very little overlap in these potential foraging areas between consecutive trips. This supports Fauchald et al. (2006; 2017) results and indicates that, even if petrels generally travel to the same destination during consecutive trips, they show a flexible foraging strategy and opportunistically adjust their search areas based on cues they find along the way.

4.2 Antarctic Krill and Petrel Foraging

The differences in Antarctic petrel movements were linked to differences in diet. Birds travelling towards the East were characterized by a diet more based on lower trophic level-prey than birds travelling westward. This indicates spatial differences in prey composition or spatial variation in the isotopic value of the prey. Indeed, the isotope values of fish or krill can vary spatially, which could ultimately affect the isotope values in their predators (e.g., Jaeger et al., 2010; Moreno et al., 2011). More specifically, the $\delta^{15}\text{N}$ values of krill vary with both its size and the chlorophyll-a concentration in their environment (Polito et al., 2019). Such intra-specific differences in krill (or fish) could in theory explain the differences in $\delta^{15}\text{N}$ values observed in the different Antarctic petrel foraging areas. However, both the large $\delta^{15}\text{N}$ difference (2.9 ‰, one full trophic level; **Figure 2**) and the results from food sample analyses do not support this interpretation and rather suggest different diets in these areas, with krill being more important in the eastern areas. These eastern “krill foraging areas” correspond to the phytoplankton bloom area described above and that is characterized in some years by very high primary productivity in late summer and high densities of Antarctic krill (Moreau et al. *in prep.*). On the contrary, Antarctic petrels foraging west of Svarthamaren had a diet dominated by fish, which fits with results from an earlier study (Lorentsen et al., 1998). In this study, ten stomach content samples were obtained from Antarctic petrels shot at sea along the coast, west of Svarthamaren (at 72°25'S, 16°43'W) in February 1994 and these samples were also dominated by fish (87% of the total stomach mass).

Although the sample size is small, our results also indicate that the proportion of krill in the diet in 2016 was much lower than observed in previous years (Lorentsen et al., 1998; Descamps et al., 2016b). Indeed, krill represented only 26% on average of the wet biomass of samples collected in January and February 2016 while it represented $\geq 60\%$ in the 1992, 1994 and 2013 breeding seasons (Lorentsen et al., 1998; Descamps et al., 2016a). Surprisingly, primary production was very high in the “bloom area” in 2016 but not in 2013 (Moreau et al. *in prep.*), while the proportion of krill in the diet was high in 2013 but low in 2016. The relationships between primary production, krill availability and petrel diet in this area may be complex and additional years of data are needed to understand them.

The 2015/2016 breeding season had one of the fewest number of breeders since the work at this colony started in 1984/1985

and was characterized by the lowest number of breeding pairs (ca. 18,000 active nests at the end of January 2016, after the peak of hatching, as compared to 20,000–50,000 in period 2012–2014 and 50,000–200,000 in period 1985–2001, unpublished data). To determine whether this low colony size was linked to the generally low proportion of krill in the diet, which could reflect poor foraging conditions and low krill availability in the marine environment, warrants further investigation.

4.3 Demographic Consequences

Individual variation in habitat use, foraging behaviour and/or diet may lead to differences in demography (Morales et al., 2010). Such relationships have been observed in several seabirds like the wandering albatross *Diomedea exulans* (Weimerskirch, 2018), herring gull *Larus argentatus* (Pierotti and Annett, 1987; van den Bosch et al., 2019) or Adélie penguins *Pygoscelis adeliae* (Chapman et al., 2011; Ainley et al., 2018). In the Adélie penguin, there seems to be clear energetic, and potentially fitness, benefits for the chicks of having fish (more specifically Antarctic silverfish) in their diet as compared to a diet based on krill only (Chapman et al., 2011; Ainley et al., 2018). Our results do not support these findings in petrels, as the different foraging tactics and diet observed in Svarthamaren petrels were not associated with different adult body mass, or in chick survival or growth. Our results suggest that these costs and benefits associated to different foraging strategies were similar for all strategies, at least in the 2016 breeding season. Whether having a fish-based or krill-based diet may bear different costs and/or benefits in different years remain to be elucidated. Moreover, Antarctic petrels share parental care and both parents feed the chick. Consequently, to conclude more firmly that individual variation in foraging strategies does not affect chick growth or survival, information on both parents' foraging behaviour would be needed as one parent could potentially compensate for a low foraging efficiency of its partner (Varpe et al., 2004). Such study would require the tracking of both parents simultaneously.

4.4 Conclusion

Variation among individuals in their foraging strategies and resource use has major implications for our understanding of animal ecology and of how populations can interact with their environment and respond to environmental change. The apparent inter-individual variation in foraging strategies and dependence on krill that we observed in Antarctic petrels from Dronning Maud Land may increase the resilience of this population to future changes in the krill population, and more generally to changes in their foraging environment. In this context, assessing whether the individual specialization we observed at an intra-seasonal scale also exists at an inter-annual scale, and assessing the proportion of the population adopting each different strategy, is a priority.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

ETHICS STATEMENT

The animal study was reviewed and approved by Forsøksdyrutvalget/Mattilsynet (permit 7935).

AUTHOR CONTRIBUTIONS

SD: conception and draft the first version of the manuscript. SD and SP: design of the study. SD, SH and JF: spatial and statistical analyses. PB and M-BF: isotope analyses. YC: stomach content analyses. SD and AT: data collection. All authors revised the manuscript critically and had substantial impact on the final draft of the manuscript.

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SUPPLEMENTARY MATERIAL

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Green Turtles Highlight Connectivity Across a Regional Marine Protected Area Network in West Africa

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Networks of marine protected areas (MPAs) are invaluable for the protection of species with high dispersal capacity, yet connectivity within networks is poorly understood. We demonstrate the connectivity within the regional MPA network in West Africa (RAMPAO), mediated by the largest green turtle population in the eastern Atlantic Ocean. We equipped with satellite tags 45 female green turtles nesting in the Bijagós Archipelago, Guinea-Bissau, and tracked them during internesting, migration, and foraging to quantify the degree of coverage the RAMPAO network provides during each of these critical periods. During the internesting period, turtles were largely concentrated around the nesting islands, with a mean of 94.8% (SD 0.1%, range: 46% - 100%, n = 40 turtles) of tracking positions falling within MPA limits. Among the 35 turtles successfully tracked into the foraging period, we identified variable migratory strategies, with 12 turtles remaining near-resident at distances of 40-90 km from breeding sites, 10 turtles migrating 300-400 km to The Gambia and Senegal, and 13 turtles traveling >1000 km to northern Mauritania. Of the 35 foraging turtles, 26 used MPAs, with a mean of 78.0% (SD 34.8%, range: 3.7% - 100%) of their tracking positions falling within the limits of RAMPAO MPAs, across Guinea-Bissau, Senegal and Mauritania. Migration corridors with high concentrations of passing turtles were mostly located nearshore, and 21% of these high passage areas fell within the MPA network. Overall, we found that this population connects five RAMPAO MPAs, yet some foraging sites (e.g., in the Bijagós) and important migration areas (e.g., Cap-Vert peninsula) described here are currently unprotected. These results are relevant to any considerations of MPA extension or establishment within the regional network, which would contribute towards meeting the Convention on Biological Diversity targets for national marine protected area estate coverage. By documenting biological connectivity across RAMPAO, this study represents an important example of the relevance of international protected area networks for green turtle conservation and for wider conservation action at a regional scale.

Keywords: *Chelonia mydas*, protected area network, connectivity, MPA, satellite tracking, West Africa, GPS, sea turtle

INTRODUCTION

Marine protected areas (MPAs) are a major pillar of global ocean conservation (Laffoley et al., 2019), and the current proposed target under the Convention on Biological Diversity (CBD) for national protected marine area is 30% by 2030 (IUCN, 2016). To meet the large-scale challenges of marine conservation, regional networks of MPAs are becoming preferred management tools over standalone MPAs (Gaines et al., 2010). MPA networks can improve conservation outcomes by increasing the spatial coverage of species distributions, thereby providing safe areas for population persistence or replacement in the face of variable anthropogenic pressures (Gaines et al., 2010; Xu et al., 2020), as well as potentially increasing resilience to climate change (McLeod et al., 2009). Additionally, to be effective, MPA networks should share common conservation targets so that efforts are coordinated and outcomes are achieved across a larger area. Yet the reality is that MPAs within a network often act as isolated management units, partly because connectivity between them is non-existent or has not been empirically demonstrated (Assis et al., 2021). Hence, assessing the degree of biological connectivity across existing and proposed MPA designs is central to ensuring the effectiveness of protected area networks (Santos et al., 2021).

Connectivity within protected area networks is particularly important for the conservation of migratory species that perform cyclical movements between breeding and non-breeding habitats (Hays et al., 2014; Runge et al., 2015; Santos et al., 2021), which are often hundreds or thousands of kilometers apart (Schuster et al., 2019), and bound to different jurisdictions and under different anthropogenic pressures (Lascelles et al., 2014; Thornton et al., 2018; Dunn et al., 2019). However, gathering information on the spatial distribution and movements of marine migrants can be difficult, due to the logistical, technological, and economic challenges involved in monitoring these animals over the vast areas that they move (Hussey et al., 2015). Despite recent advances (e.g. Doherty et al., 2017; Hays and Hawkes, 2018; Irvine et al., 2019; Gredzens and Shaver, 2020), our knowledge of the spatial distributions of marine megafauna is geographically biased, in large part due to the unequal availability of research funding (Amano and Sutherland, 2013) leaving areas of the world understudied. West Africa is generally a data-poor region, particularly when it comes to the marine realm (Failler et al., 2020). Nonetheless, marine regions of West Africa, a major upwelling zone (i.e., the Canary current) with rich coastal ecosystems including seagrass meadows, mangroves and tidal flats, are recognized as hosting globally important populations of coastal birds, marine mammals (e.g., Atlantic humpback dolphins and West African manatee), and marine turtles (e.g. Barnett et al., 2004; Cunha and Araújo, 2009; Campredon and Catry, 2016; Pottier et al., 2021).

To protect these critical ecosystems and conserve their biodiversity, several MPAs were established in the region, most from the year 2000 onwards (Failler et al., 2020), followed by the creation of a regional network of MPAs in 2007 called RAMPAAO (from the French 'Réseau Régional d'Aires Marines Protégées en Afrique de l'Ouest'). The RAMPAAO network extends across seven West African nations: Cabo-Verde, Mauritania, Senegal,

The Gambia, Guinea-Bissau, Guinea, and Sierra Leone (<https://rampao.org/>). Although the existence of migratory species and shared resources were considered in the establishment of RAMPAAO, to date, there is scant empirical evidence that the MPA network contributes to the connectivity of any particular animal population (but see Godley et al., 2010). The green turtle is a marine migratory species of conservation concern (Godley et al., 2020), well represented in the region, which hosts a nesting population among the top six worldwide (SWOT, 2011), with over 25,000 clutches laid annually (Patricio et al., 2019). The core-nesting site is Poilão Island, within the João Vieira - Poilão Marine National Park (JVPMNP), an MPA within the RAMPAAO, located in the Bijagós Archipelago of Guinea-Bissau (Catry et al., 2009; Patricio et al., 2019). A previous study tracked the post-breeding migrations of four green turtles from Poilão Island to the National Park of the Banc d'Arguin in Mauritania (PNBA), also in RAMPAAO, ca. 1000 km north of Poilão (Godley et al., 2010). This was the first indication of biological connectivity within this network, but sample size was limited, and recent research suggested that this population may migrate to different locations after breeding (Patricio et al., 2019), thus requiring further tracking to elucidate the full seasonal distribution.

Here, we investigate the seasonal distributions of reproductive female green turtles to inform international efforts to conserve this globally important breeding population, as well as other biodiversity, which depends on this protected area network in West Africa. Specifically, we tracked turtles to map their spatial distribution throughout the internesting, migration, and foraging periods in relation to the RAMPAAO, and contribute essential baseline information and recommendations for marine spatial planning in the region.

METHODS

Satellite Tag Deployment

We equipped 45 nesting green turtles with satellite tracking devices from 2018 to 2020 at the João-Vieira Poilão Marine National Park (JVPMNP, **Figure 1**), in the Bijagós Archipelago, Guinea-Bissau (hereafter "Bijagós"). The park includes four main islands (João Vieira, Cavalos, Meio and Poilão) and an islet (Cabras) where green turtle nesting occurs, with Poilão hosting the great majority of the nests (Patricio et al., 2019). Satellite tags were deployed in Poilão (n=43) and Meio (n=2), either when turtles were laying or when they were stranded in intertidal rock pools in the morning after nesting or attempting to nest, due to the low tide exposing vast areas of rocks preventing turtles from returning to the sea (Patricio et al., 2018). In the first case, we waited for the turtles to start laying eggs, and then executed the attachment procedure within 20 minutes. All turtles continued with their nesting activity throughout the tag application, therefore we are confident that the procedure did not disturb them. In the second case, we approached stranded turtles, started sanding their second vertebral scute and observed their reaction. Most turtles did not react, as if unaware of our presence, thus, we proceeded with attaching tags. If a turtle was startled, we left her undisturbed. We observed all tagged turtles normally returning

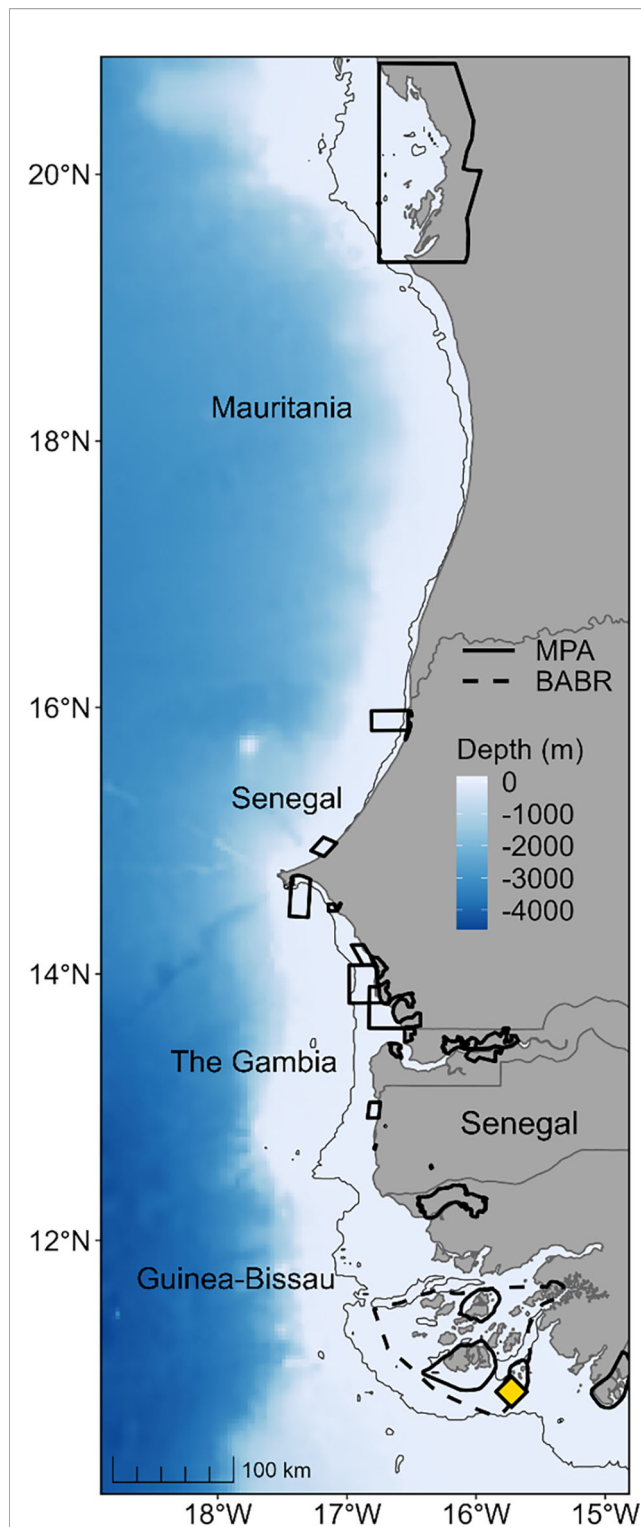


FIGURE 1 | Map of West Africa from the north of Guinea in the south to Mauritania in the north. Solid black polygons show the limits of existing marine protected areas (MPAs). Dashed black line shows the limit of the UNESCO Bolama-Bijagós Archipelago Biosphere Reserve. Yellow diamond indicates the main nesting site of the study population of green turtles (*Chelonia mydas*); Poilão Island. The bathymetry is shown in a scale of blue, and a thin grey line is the 15 m depth contour.

to the sea with the coming of the high tide. For details on attachment protocol, see Supplemental Methods. The green turtle nesting season at these rookeries extends from July to December (Catry et al., 2002), with few nests year-round (Barbosa et al., 2018). About 80% of the clutches are laid from August to end of October (Barbosa et al., 2018), and we deployed tags from August to November, to cover the period when most turtles are nesting (see **Table S1** for details on deployment date). We used two models of Platform Transmitter Terminal (PTT) devices; SPOT-375B from Wildlife Computers, Seattle, Washington ($n = 19$, 2018), which transmit Argos locations, and F6G - 376B from Lotek, Havelock North, New Zealand ($n = 11$, 2019; $n = 15$, 2020), which transmit both Argos and Fast GPS (hereafter 'FGPS') location information *via* the Argos satellite system. Both tag types were set to transmit already collected positions every 15s.

Tracking Data Filtering

We split tracking data into the behaviorally distinct seasonal periods of internesting, migration, and post-nesting foraging (hereafter "foraging") based on close inspection of individual tracks (**Figure S1**). We classified turtles which stayed in the immediate region around the Bijagós archipelago as near-resident and those which performed long-distance movements (i.e., >100 km from the nesting islands) as migratory. For turtles classified as migrating, we defined the start of migration (i.e., the 'migration' portion of a track) as directional and persistent movements at least 10 km from the nesting islands. The 10 km buffer was selected as this is approximately the range in which the turtles spent most time during internesting, so tracking positions outside this area are clearly distinguishable between short forays and long-distance migratory movements. Arrival at the foraging site was identified as localized movements after leaving the internesting area. Foraging turtles did not show stopover behavior (i.e., short stops), and had at least 10 days of localized movements post-nesting. Next, we filtered the raw tracking data to remove positions with high spatial error. For Argos PTT data we retained only positions with a quality index of 1, 2 or 3 (with respective horizontal spatial error radii of <250 m, 250-500 m, and 500-1500 m; Douglas et al., 2012) while for FGPS data we retained positions fixed with 6 or more satellites (Dujon et al., 2014). For data from both sensor types we used a data-driven speed and angle filter (Shimada et al., 2012) to remove biologically unrealistic positions. A total of 28.2% of positions were retained after quality filtering. We used the raw, filtered positions for subsequent analysis, as a sensitivity test showed that interpolation of the data to a regular time interval had little effect on the final outcome (**Table S2**). For each seasonal period, we retained only individuals with at least 10 tracking locations for analysis.

Spatial Analysis

MPA Coverage of Interesting and Foraging Periods

To estimate how the spatial distribution of adult females during the interinteresting and foraging periods falls in relation to marine protected areas, we downloaded MPA spatial polygons from the Protected Planet database (UNEP-WCMC, 2021) and calculated: (1) the number of tracked turtles visiting MPAs, and (2) the

percentage of tracking positions falling within MPA borders. The average percentage of positions within MPAs was calculated first per individual then across individuals to give an estimate at the population level. The breeding site is located within the UNESCO Bolama-Bijagós Archipelago Biosphere Reserve (BABR, **Figure 1**). Despite the current lack of any management regulations specific to this reserve area, we additionally assessed the proportion of locations within the BABR limits to demonstrate the potential benefits if relevant protection measures were introduced.

To be able to infer patterns at the population level based on tracking data, it is important to assess the representativeness of the tracked sample of individuals (Sequeira et al., 2019). Therefore, we estimated the representativeness of our samples during the internesting and foraging periods using an established method for informing conservation (Beal et al., 2021b). Briefly, this method identifies how close the space use of the tracked sample of individuals comes to an information asymptote, a point at which most of the population-level space use has been captured. We estimated that our data were 99% (internesting, $n = 40$) and 76% (foraging, $n = 35$) representative of the home range used by the wider population (**Figures S2, S3**).

To assess whether the spatial error of tracking positions affected our calculations regarding MPA coverage, we performed a sensitivity analysis comparing results using only PTT data (which tend to have higher error) against only FGPS data. For the turtles transmitting both PTT and FGPS positions during internesting ($n = 21$) and foraging ($n = 20$) respectively, we compared the percentage of points within and outside MPAs separately for each geolocation method. We found little difference in the percentage of positions within MPAs between the geolocation methods, suggesting our filters removed positions with large enough error to affect MPA overlap (**Table S3**).

Home Range and Core-Use Areas

To visualize the home ranges and core areas of the tracked turtles during internesting and foraging, we used kernel density estimation (KDE). KDE is a non-parametric technique for smoothing point densities, and can be used to derive probabilistic animal home ranges known as utilization distributions (UD) based on location data (Worton, 1989). The UD of a tracked animal represents space use intensity. An important step when running KDE is determining the smoothing parameter for analysis, which affects the scale of the resulting spatial estimate (Gitzen et al., 2006). We calculated the canonical reference bandwidth for each individual, which reflects the number and spatial variance of tracking positions, and then took the median across individuals as the parameter value for analysis (Beal et al., 2021b). Given that the movement behavior of female green turtles differs between internesting and foraging periods, we made this calculation separately for each period resulting in a smoothing parameter value of 0.9 km for internesting data and 2.1 km for foraging data. To get an estimate of the population-level distribution for each period, we averaged together the individual UD.

Migration Corridors

To estimate migration routes for each turtle and identify population-level high-passage corridors, we used dynamic Brownian bridge

movement models (dBBMM). Brownian bridge movement models estimate the probability of occurrence of animals in space during the tracking period by using a conditional random walk to approximate potential movement paths connecting tracking positions, while taking into account the time gaps between them. Brownian bridge models are able to handle irregular sampling intervals and incorporate positional errors into the occurrence estimation. dBBMMs extend classic Brownian bridge models by detecting behavioral changes within “moving windows” along the movement path and dynamically assigning appropriate Brownian motion variance values (σ^2m) to the random walk procedure. This allows for more accurate estimations of occurrence over lengthy tracking periods, during which the movement behavior of animals may change (Kranstauber et al., 2012).

Following Buechley et al., 2018, we estimated migratory corridors for the adult female green turtle population by calculating the percentage of migration routes (i.e., tracked turtles) overlapping across a gridded surface. A “migration route” was defined as the 95% occurrence probability as estimated by the dBBMM, fitted using filtered locations and their estimated horizontal spatial error for each individual turtle. To estimate the Brownian motion variance, we used a sliding window of seven locations with a margin of three locations. We used a grid cell resolution of 10 x 10 km, which is large enough to identify similar route selection among the turtles, while remaining of relevance for informing spatial protection measures, such as MPA border extension or temporal fisheries restrictions in RAMPAO, where MPAs cover a median of 200 km² (range 0.5 – 12,006 km²). Finally, we identified “high-passage corridors” as grid cells visited by at least 25% of the turtles which migrated north of the Bijagós after nesting. We then calculated the percentage of high passage cells falling within established MPAs, when the center of a high turtle passage grid cell (i.e., cells through which $\geq 25\%$ of turtles likely passed) fell inside an MPA border, the MPA was considered as covering that cell.

RESULTS

We obtained spatial data from 44 of the 45 tagged individuals. Not all 44 turtles contributed data for the three seasonal periods analyzed (**Table S1** and **Figure S1**), due to premature device failure, to a lack of good locations retained after filtering, to nearly resident foraging behavior (i.e., no migratory period) or to leaving the breeding area immediately after tag deployment (i.e., no data on internesting period). After filtering, we retained for analysis the tracks of 40 individuals during internesting (88.9%, $n=45$), 18 individuals during migration (48.9%, $n=45$), and 35 during foraging (77.8%, $n=45$). Of the 40 turtles that contributed with data for the internesting period, 18 were re-sighted at the beach during multiple nesting events/attempts, thus we are confident that they were in their breeding period (see **Table S4**). In total, we analyzed 4,358 tracking days, with each individual tracked between 15 - 332 days (mean 99 days \pm SD 73 days). Mean curved-carapace-length of tagged turtles was 98.5 cm (SD 8.9 cm, range: 78.0 – 121.5), with no significant

differences in curved-carapace-length between years (ANOVA: $F_{1,42} = 0.383$, $p = 0.540$).

The green turtles tracked in this study were distributed between 10.5°N and 20.5°N, an area within which there are 28 MPAs (Figure 1 and Table S5).

MPA Coverage and Home Ranges During Internesting

Tracking during the internesting period extended from August to early December (Figures S1, S4). We found that the 95% home ranges and 50% core-use areas of individual turtles during internesting were highly concentrated around their respective nesting islands (Figure 2). The spatial distribution of breeding females was well covered by MPAs during internesting, with all 40 individuals using MPAs and a mean of 94.8% (SD 0.1%, range: 46% - 100%) of tracking positions falling within MPAs. The mean percent coverage increased to 99.5% (SD 0.01%) of positions when considering the limits of the BABR.

Migration Corridors

The migration period of the tracked turtles extended from September to December (Figure S1). The routes of the 18 individuals which migrated north of the Bijagós followed the shoreline for the most part, with some individuals travelling several hundred kilometers offshore (Figures 3, S5). The areas of highest migration route concentration were used by 61% (11 individuals) of migrating turtles. With 25% of turtles (i.e., 5 individuals) set as a minimum threshold to define high-passage migration corridors, we identified three main coastal stretches as particularly important: from the outer Bijagós to The Gambia, off the city of Dakar in Senegal, and along the south of Mauritania to the south of the Banc d'Arguin (Figure 3). We calculated that RAMPAO MPAs overlapped 18 of the 84 (21%) high-passage corridor cells identified in our analysis. If the BABR area was included, the coverage rose to 30 of 84 (36%) of high-passage cells.

Foraging Areas, MPA Coverage and Home Ranges During Foraging

The nesting population of the Bijagós displayed variable migratory strategies, with 12 turtles remaining resident in the Bolama-Bijagós region (34.2%, $n=35$), foraging at 40-90 km from the breeding sites, including one that relocated ca. 80km southeast of Poilão Island, 10 migrating 300-400 km to The Gambia and Senegal (28.6%, $n=35$), and 13 migrating >1000 km to the north of Mauritania (37.1%, $n=35$, Figure S6). The turtles analyzed here engaged in foraging behavior (i.e., localized movements) for a range of 10 to 288 days (Table S1 and Figure S1) before device failure, and no turtle that migrated north of the Bijagós (i.e. non-resident) stopped to forage within the archipelago.

The 95% home ranges and 50% core-use areas of individual turtles during the foraging period were more dispersed than during internesting (Figure 4). During the foraging period, we found lower MPA coverage than during internesting, with 26 of 35 individuals (74%) using MPAs at some point (i.e., at least 3 locations within an MPA, Table 1). Of the individuals using MPAs, a mean of 78.0% (SD 34.8%, range: 3.7% - 100%) of their tracking positions fell within protected area borders. Disaggregating this result by foraging destination, a mean of 93.3% (SD 16.5%) of positions from turtles which migrated to Mauritania fell within MPAs, 83.9% (SD 28.7%) of positions of those which travelled to The Gambia and Senegal, and 15.1% (SD 20.7%) for turtles which remained in the wider Bijagós region (Table 1 and Figure 4). With the BABR included in the coverage calculation, the percentage of tracking positions occurring within all conservation areas for post-nesting turtles in the Bijagós increased to 99.3% (SD 0.008%).

DISCUSSION

Assessing the seasonal distributions of migratory species is a key step to informing marine spatial planning and to identifying opportunities for cross-regional collaboration for conservation (Beal et al., 2021a). By analyzing the movements of reproductive

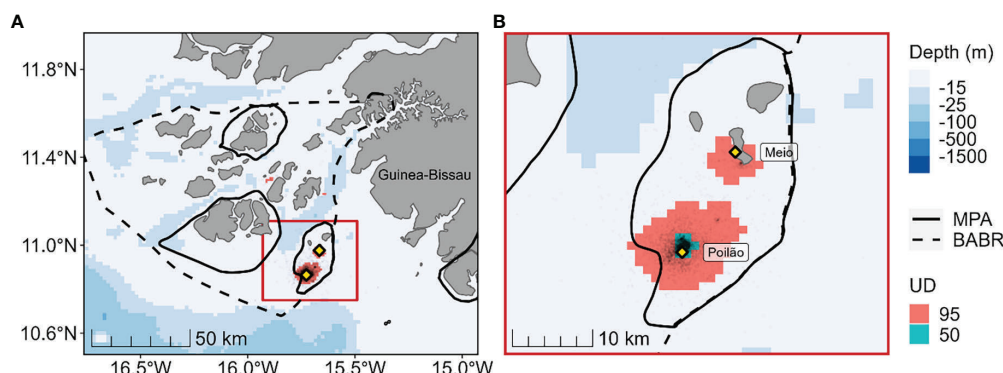


FIGURE 2 | (A) Distribution of 40 female green turtles (*Chelonia mydas*) tracked during internesting. Yellow diamonds indicate the nesting sites where satellite tags were deployed. The 95% (red) and 50% (blue-green) utilization distribution areas are shown, respectively signifying the population-level home range and core-use areas during internesting. The bold solid lines show the limits of existing marine protected areas (MPAs) and the dashed line shows the extent of the Bolama-Bijagós Archipelago Biosphere Reserve (BABR). **(B)** Inset showing close-up of distribution around the nesting sites.

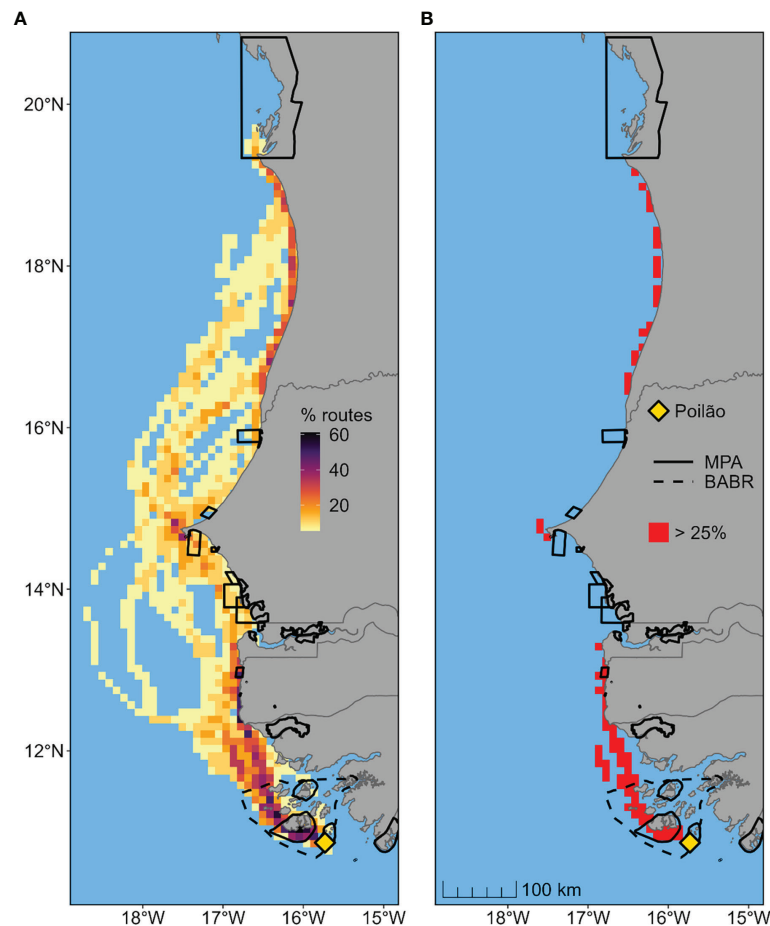


FIGURE 3 | Migration routes of 18 female green turtles (*Chelonia mydas*) travelling from the nesting island in Guinea-Bissau (i.e., Poilão Island) to foraging areas in Senegal, The Gambia or Mauritania. **(A)** Percentage of overlapping migration routes, defined as 95% probability areas estimated using dynamic Brownian bridge movement models. **(B)** Identified high-passage corridors, defined as grid cells used by at least 25% of migrating turtles. Black solid and dotted lines represent existing conservation areas in the region. (Marine Protected Areas [MPA] and UNESCO Bolama-Bijagós Biosphere Reserve [BABR]).

female green turtles across three seasonal periods, we provide novel information on the spatial distribution of this globally significant rookery, which is highly relevant to regional conservation and management efforts. Using tracking data, we identified multiple post-nesting migratory strategies, novel foraging sites, and high-density migration corridors. We then quantified the spatial coverage of seasonally important areas by the West Africa MPA network, RAMPAN. Our findings highlight the biological relevance of the RAMPAN, and its importance for the conservation of this charismatic species and wider biodiversity in the region. We provide recommendations for MPA managers, to improve both the protection coverage and knowledge of this important population.

MPA Coverage During the Internesting Period

During the internesting period, breeding females concentrated near the nesting beaches, remaining within the limits of the João Vieira – Poilão Marine National Park (JVPMP). This supports findings by

Godley et al. (2010), based on the interesting movements of seven turtles tracked in 2001. Indeed, the protection of this globally significant rookery was one of the main motivations for the creation of this MPA (Catry et al., 2002, **Table 2**), but conservation efforts are mostly concentrated on the terrestrial phase (i.e. nesting and egg incubation), particularly at Poilão Island. Illegal fishing is known to occur inside the MPA (186 seized fishing boats from 2011 to 2019, Catry et al., 2018), with fishers mostly from neighboring countries (ca. 62%, Senegal, Guinea, Ghana, Sierra Leone, Catry et al., 2018), where marine turtles have commercial value (notably not the case in Guinea-Bissau, Barbosa et al., 2018). Still, marine surveillance at the JVPMP and enforcement of fines, contribute to deter most illegal activities, and enhance protection during the nesting season.

Small home ranges and high MPA coverage during internesting have been found among other green turtle populations, e.g., at the Chagos Archipelago, Indian Ocean (Hays et al., 2014) and in the Gulf of Mexico, south Florida, USA (Hart et al., 2013). This was also observed among hawksbill turtles from the Solomon Islands, West

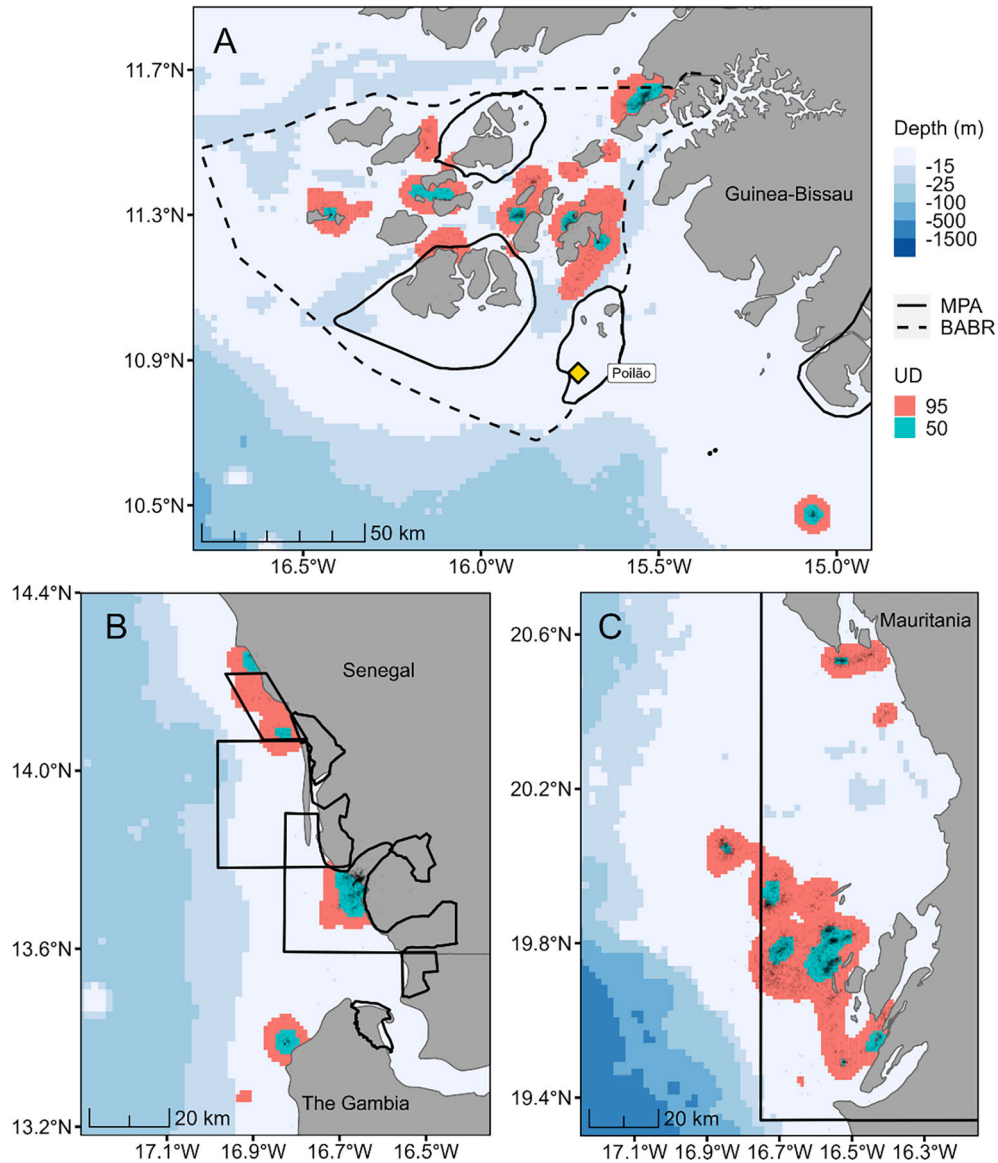


FIGURE 4 | Distribution of 35 female green turtles (*Chelonia mydas*) tracked during the post-nesting foraging period in **(A)** the Bijagós Archipelago of Guinea-Bissau and south of the Bijagós ($n = 12$), **(B)** the Saloum and Gambia river deltas of Senegal and The Gambia ($n = 10$) and **(C)** the Bay of Arguin in Mauritania ($n = 13$). Black dots represent tracking locations, and the underlying colored areas represent the 95% (pink) and 50% (blue-green) utilization distribution areas, respectively signifying the population-level home range and core-use areas during foraging. The bold solid lines indicate the location of existing marine protected areas (MPAs) and the dashed line shows the extent of the BABR biosphere reserve.

TABLE 1 | Coverage of adult female turtles during the post-nesting foraging period in West Africa by marine protected areas (MPA).

Group	All tracked turtles		Turtles using MPAs		
	n turtles	mean % positions inside MPAs	n turtles	% turtles using MPAs	mean % positions inside MPAs
Bijagos	12	5.0 ± 13.1	4	33.3	15.1 ± 20.7
Mauritania	13	93.3 ± 16.5	13	100	93.3 ± 16.5
Senegal/The Gambia	10	75.5 ± 37.9	9	90.0	83.9 ± 28.7
Overall	35	57.9 ± 45.7	26	74.3	78.0 ± 34.8

'Group' refers either to a calculation for all turtles (i.e., Overall) or subsets split by foraging destinations. Mean estimates are shown with ± standard deviation.

TABLE 2 | Summary of relevant management characteristics of five marine protected areas (MPAs) of the West Africa MPA network (RAMPAO), used by the green turtle population breeding in the Bijagós Archipelago, Guinea-Bissau.

MPA name and area	Country	MPA goals	Fishing regulations	Who can fish in the MPA?	Main types of fishing gear used	Active surveillance program?	Initiatives in the MPA and adjacent areas relevant for marine turtle conservation	Sea turtle species present	Important benthic habitats
Parc National Du Banc D'Arguin 11,700 km ²	Mauritania	Maintain productivity of ecosystems Preserve endangered and migratory species Contribute to development of local populations	Only traditional sailing boats allowed, hired or owned by Imraguen fishers Prohibited: fishing at night, blocking channels, traps on mudflats or channels Seasonal fishing restrictions and monthly biological rests in place Some areas closed to all fishing activities	Residents in the park	Mullet net (mesh size 5660mm), meagre net (min. mesh size 20 - 26cm), mellooussa net (min. mesh size: 14 - 18cm), sole net (min. mesh size 50mm) Traps, lines and handlines	yes	Local Imraguen fishers are engaged in in water surveys of sea turtles for research and conservation	<i>Chelonia mydas</i> , <i>Caretta caretta</i>	Seagrass (<i>Cymodocea</i> , <i>Halodule</i> , <i>Zostera</i>), Area of intertidal meadows ~ 1000 km ²
Joal-Fadiouth 174 km ²	Senegal	Biodiversity conservation Enhancement of fishing yields Socioeconomic growth for local populations	Areas with specific regulations with biological rest periods Prohibited: fishing at night, scuba dive, purse seine, beach seine, gillnet and longlines	Residents native to Fadiouth	Up to 5 km from the coast: line and hook or fishing rod Beyond 5 km from the coast: large mesh nets (100 mm)	yes	Awareness campaigns among priests, imams and fishers and law enforcement halted the sale of turtle meat in local markets Fishers take tourists to watch turtles	<i>Chelonia mydas</i>	Seagrass (<i>Cymodocea</i> , <i>Halodule</i>)
Parc National du Delta du Saloum 760 km ²	Senegal	Protection of marine ecosystems and natural resources	Prohibited: gillnets and monofilament nets	Residents on the park perimeter	Line and hook or fishing rod	yes	Communication and awareness campaigns for fishers, law enforcement with offense reports, funding of reconversion activities	<i>Chelonia mydas</i> , <i>Lepidochelys olivacea</i> , <i>Caretta caretta</i>	Seagrass (<i>Cymodocea</i> , <i>Halodule</i> , <i>Zostera</i>)
Orango National Park 1582.35 km ²	Guinea-Bissau	Protection of biodiversity and ecosystems Promote the sustainable use of natural resources for socioeconomic growth of local populations	Four no-take zones, in channels between islands. Prohibited: monofilament nets, fishing camps by non-resident fishers, bottom trawl, catching rays and sharks, fishing techniques blocking channels	Residents and licensed recreational fishers	Gill net (max. 28 mm mesh size) and cast net ('ramanga'), traditional harpoon ('Canhaco'), fishing trap ('Impande'), line fishing (max. 500 hooks/ no. 7, 8)	yes	Community members are engaged in marine turtle monitoring activities and marine monitoring activities for awareness	<i>Chelonia mydas</i> , <i>Eretmochelys imbricata</i> , <i>Dermochelys coriacea</i> , <i>Lepidochelys olivacea</i>	uncharacterized
National Marine Park of João Vieira Pólo 495 km ²	Guinea-Bissau	Protection of biodiversity and ecosystems Conservation of sea turtles and colonial shorebirds Enhancement of Bijagó cultural heritage Regeneration of fish stocks Ecotourism development	No take zone 11,000 ha Prohibited: monofilament nets, big nets to catch sharks or other big fish, fish transshipment Max. engine power: 15 - 40 hp	Residents from Canhabaque and licensed recreational fishers	Hook traps (max. 500 hooks / no.7), gill net (max. 3 bands / max. mesh size 30mm) and cast net, line fishing (hooks no.7, 8)	yes	Community members are engaged in marine turtle monitoring activities and marine monitoring activities for awareness	<i>Chelonia mydas</i> , <i>Eretmochelys imbricata</i>	uncharacterized

Pacific, spending 98.5% of their interesting time within the Arnavon Community Marine Park (Hamilton et al., 2021), and from the Dominican Republic, Caribbean Sea, with 82.7% of their interesting time within the Del Este National Park (Revuelta et al., 2015). Further studies reported restricted home ranges during the interesting period among loggerhead (Schofield et al., 2010) and green turtles (Snape et al., 2018; Shimada et al., 2021). Thus, implementing relevant measures around rookeries of conservation value (e.g. protected areas, fishing restrictions) may be a good strategy to protect vulnerable populations during interesting (Dryden et al., 2008).

Migration Corridors

Turtles passed through several RAMP AO MPAs during the migration period, but overall, MPA coverage during migration was relatively low (21%), with a large portion of coverage provided by the Orango National Park (ONP), located near the nesting islands in the Bijagós. Most turtles followed a similar path after leaving the nesting grounds potentially because they are using the same local environmental cues, such as ocean currents (Hays et al., 2010), wave-direction (Papi et al., 2000) or coastlines (Lohmann et al., 2008), to orient themselves. Yet some individuals diverted this corridor, and other populations display highly dispersed post-nesting migratory paths (e.g. Hays et al., 2014). Similar to our results, high-passage migratory corridors near the nesting beach have been described in several marine turtle populations (Pendoley et al., 2014; Stokes et al., 2015; Hamilton et al., 2021; Santos et al., 2021), as well as near foraging locations (Baudouin et al., 2015; Stokes et al., 2015; Santos et al., 2021), suggesting that these areas can be effective places to implement conservation measures.

The majority of the turtles that migrated to Mauritania converged around the Cap-Vert Peninsula (where the city of Dakar is situated). This prominent promontory acts as a migratory bottleneck (sensu Bayly et al., 2018), funneling huge numbers of migratory seabirds, which are compelled by the promontory to approach the shore (Dubois et al., 2009; Péron and Grémillet, 2013; Paiva et al., 2015). Given our findings, combined with the apparent importance of this site for other taxa, increasing spatial protection here may have a broad impact on biodiversity in the region. The National Park of the Madeleine Islands is a terrestrial only protected area located just offshore of the peninsula in an area of high turtle passage, suggesting that extension of the limits of the park to the marine zone would increase protection coverage for migrating green turtles. As migration is restricted to a well-defined period of the year (e.g. Hart et al., 2019; Santos et al., 2021; September to December in our study), migratory bottlenecks are seasonal and therefore temporal measures in these areas could be effective. We recommend implementing seasonal, spatially explicit bans on fishing practices that cause turtle bycatch.

MPA Coverage of Foraging Grounds and Connectivity Across the RAMP AO

We found that after nesting, females had three distinct migratory strategies, with some turtles remaining resident in the Bolama –

Bijagós region and others performing short or long migrations to foraging grounds in other parts of West Africa. Non-migratory green turtles have also been reported from the Cocos Keeling Islands, in the eastern Indian Ocean (Whiting et al., 2008), and a similar pattern of both near-residents and migratory individuals was observed among green turtles in the Indian Ocean (Hays et al., 2014), and in the Caribbean (Esteban et al., 2015).

We found that this nesting population from the Bijagós connects at least five RAMP AO MPAs, across three countries, which have a marine area with fishing regulations and active marine surveillance programs (Table 2). Overall, the MPA coverage of foraging areas was good (over 70%), but it varied greatly between the foraging regions. At the Bay of Arguin, in Mauritania, most of the foraging occurred within the Banc d'Arguin National Park (PNBA). In Senegal, a very high proportion of the foraging period was spent within the limits of either the Saloum Delta National Park (SDNP) or the Joal Fadiouth MPA (JFMPA). Some turtles foraged around the Bijol Islands of The Gambia, where green turtle nesting is also known to occur (Barnett et al., 2004), and although these islands are part of the Reserve of the Tanji Bijol Island Banks, this MPA does not currently include a marine area. Extending the limits of this reserve to include nearshore waters would enhance protection of both the turtles which nest on the Bijol Islands during interesting, as well as turtles from the Bijagós during foraging. In the Bijagós, the majority of turtles foraged outside MPAs (88%, n=12), but within the limits of the UNESCO Bolama-Bijagós Archipelago Biosphere Reserve (BABR, 98.1%). Notably, the BABR also hosts foraging aggregations of immature green turtles (Monteiro et al., 2021), therefore, creating and implementing relevant regulations within the BABR would greatly enhance the protection of green turtles in West Africa. In this study, our tracking effort was focused during the time of year when the large majority of the Bijagós green turtle population nest, as this is the most relevant period for informing for conservation. However, the tracking data obtained here might not represent the full variability of post-nesting migrations and foraging grounds used by this population. For example, it is possible that the few green turtles that nest outside of the principal nesting season use different foraging areas, a point which may be investigated in the future.

Foraging habitats were not uniformly distributed along the West African coast, which could suggest that food resources are patchy. The PNBA of Mauritania, and the SDNP and JF MPA of Senegal, have vast areas of seagrass (*Cymodocea nodosa*, *Halodule wrightii*, *Zostera noltii*, Vermaat et al., 1993, Cunha and Araújo, 2009), which is one of the food items most consumed by green turtles, globally (Esteban et al., 2020). At the PNBA, green turtles were found to consume seagrasses, along with animal prey, with larger turtles relying more on seagrass than smaller juveniles (Cardona et al., 2009), thus, the distribution of this resource could in part explain the locations of turtle foraging areas. However, although Cunha and Araújo (2009) found the same species of seagrasses along the unprotected stretch of coast from the south of the Bay of Arguin to Nouakchott, Mauritania, none of the turtles we tracked foraged in this area, suggesting that other factors influence their choice of foraging area. An alternative explanation is that the protection afforded by MPAs is defining the spatial distribution of

this population. In the Bijagós seagrass is scarce (Campredon and Catry, 2016), although more benthic surveys are needed for a thorough characterization of the foraging areas in the archipelago. A study using DNA metabarcoding from esophageal swabs of immature green turtles foraging in the westernmost islands of the Bijagós archipelago, also used by adult female green turtles as revealed by our tracking data, identified red algae as their main food source (Rhodomeniophycidae subclass, Díaz-Abad et al., 2022). Seagrass was also detected in the diet, along with invertebrates, but in smaller proportions (Díaz-Abad et al., 2022). Green turtles foraging in São Tomé, Gulf of Guinea, also consumed more macroalgae (mostly red algae *Polysiphonia* sp., Hancock et al., 2018) than seagrass, which was less abundant (Hancock et al., 2018). Future studies will further investigate the diet of green turtles in West Africa, across their main foraging areas.

Final Considerations

Identifying green turtles as a common conservation target for several of the RAMPAO MPAs can motivate and inform collaboration. We recommend that stakeholders from each interested country together define standard monitoring parameters for systematic data collection to increase the knowledge of this globally important population, and reinforce information exchange to support conservation actions and management. Additionally, for a complete picture of the MPA coverage and connectivity of this breeding population, future research should address the spatial distribution of reproductive males. Spatial analyses should also extend to other taxa, to maximize effective MPA design encompassing key ecosystems and a broad range of species of ecological and conservation value.

This study unequivocally demonstrates the importance of an established MPA network, the RAMPAO, for the conservation of a marine migratory species. Ongoing research indicates that connectivity across the RAMPAO is also established by migratory coastal waders (Rocha pers comm). Notably, the green turtle rookery at Poilão Island is growing (Broderick and Patricio, 2019), which can be a possible indication that, despite existing threats (Catry et al., 2002), RAMPAO MPAs are effectively protecting this population. We argue that lessons can be learned from the RAMPAO process, and applied globally. West African countries (and other countries around the world) are well below the previously set 2020 Aichi Target 11 of 10% of marine areas under nature protection (Failler et al., 2020). Therefore, studies of this kind provide highly relevant information to countries of ways they can expand their protected area estate to both meet the targets of the upcoming post-2020 Biodiversity Framework and contribute to international conservation efforts (Hays et al., 2019).

DATA AVAILABILITY STATEMENT

All analysis scripts and data derivatives produced in this study are available for download at <https://doi.org/10.5281/zenodo.6346610>. Tracking data analysed here may be found on

Movebank (<https://www.movebank.org/cms/movebank-main>) using the accession numbers 1988749082 and 1988757157 and 1988638748. Further inquiries can be directed to the corresponding authors.

ETHICS STATEMENT

The animal study was reviewed and approved by Orgão Responsável pelo Bem-estar Animal do ISPA (ORBEA - ISPA). Research permits were granted by the Instituto da Biodiversidade e das Áreas Protegidas, Dr. Alfredo Simão da Silva (IBAP), of Guinea-Bissau. Fieldwork protocols involving sea turtles followed recommended guidelines (NMFS-SFC, 2008), to enhance efficiency and reduce possible disturbance to the turtles, and were conducted by trained personnel, in collaboration with national authorities for biodiversity management.

AUTHOR CONTRIBUTIONS

ARP, FM, CB and PC conducted fieldwork. ARP, PC, MB and BG contributed to conception and design of the study. MB conducted spatial analysis. ARP and MB wrote the first draft of the manuscript. PC, BG wrote sections of the manuscript. CB, AR, CS and ES helped with fieldwork logistics and permits. DD and MT contributed with crucial information on marine protected areas in the region. All authors contributed to manuscript revision, read, and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.812144/full#supplementary-material>

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Sex and Size Influence the Spatiotemporal Distribution of White Sharks, With Implications for Interactions With Fisheries and Spatial Management in the Southwest Indian Ocean

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Human activities in the oceans increase the extinction risk of marine megafauna. Interventions require an understanding of movement patterns and the spatiotemporal overlap with threats. We analysed the movement patterns of 33 white sharks (*Carcharodon carcharias*) satellite-tagged in South Africa between 2012 and 2014 to investigate the influence of size, sex and season on movement patterns and the spatial and temporal overlap with longline and gillnet fisheries and marine protected areas (MPAs). We used a hidden Markov model to identify 'resident' and 'transient' movement states and investigate the effect of covariates on the transition probabilities between states. A model with sex, total length and season had the most support. Tagged sharks were more likely to be in a resident state near the coast and a transient state away from the coast, while the probability of finding a shark in the transient state increased with size. White sharks moved across vast areas of the southwest Indian Ocean, emphasising

the need for a regional management plan. White sharks overlapped with longline and gillnet fisheries within 25% of South Africa's Exclusive Economic Zone and spent 15% of their time exposed to these fisheries during the study period. The demersal shark longline fishery had the highest relative spatial and temporal overlap, followed by the pelagic longline fishery and the KwaZulu-Natal (KZN) shark nets and drumlines. However, the KZN shark nets and drumlines reported the highest white shark catches, emphasising the need to combine shark movement and fishing effort with reliable catch records to assess risks to shark populations accurately. White shark exposure to shark nets and drumlines, by movement state, sex and maturity status, corresponded with the catch composition of the fishery, providing support for a meaningful exposure risk estimate. White sharks spent significantly more time in MPAs than expected by chance, likely due to increased prey abundance or less disturbance, suggesting that MPAs can benefit large, mobile marine megafauna. Conservation of white sharks in Southern Africa can be improved by implementing non-lethal solutions to beach safety, increasing the observer coverage in fisheries, and continued monitoring of movement patterns and existing and emerging threats.

Keywords: conservation, satellite tagging, movement states, marine protected area (MPA), *Carcharodon carcharias*

INTRODUCTION

Human activities in the oceans increase the extinction risk of marine megafauna populations (Lewison et al., 2004; Dulvy et al., 2014; McCauley et al., 2015; Rogers et al., 2020). These iconic species are essential for maintaining the structure and function of marine ecosystems, have high cultural and societal value and contribute significantly to the global economy, primarily through tourism (Heithaus et al., 2008; Cisneros-Montemayor et al., 2010; Estes et al., 2011; Pimiento et al., 2020). However, one-third of these species are at risk of extinction (Pimiento et al., 2020). Megafauna species often have broad distributions and are highly migratory, underpinning the need for collaborative international conservation and management interventions (Barkley et al., 2019; Temple et al., 2019). Unfortunately, protecting mobile threatened species across their range is impractical given the limited resources available for surveillance and enforcement over such vast distances, especially in developing countries (Maxwell et al., 2011; Temple et al., 2019). Therefore, directing conservation and management attention to focus areas is the most promising solution.

White sharks (*Carcharodon carcharias*) are the largest predatory fish and have a circumglobal distribution, but populations are geographically distinct between the northern and southern hemispheres (Bruce and Bradford, 2012; O'Leary et al., 2015; Andreotti et al., 2016). In the global context, the South African population is a local metapopulation with low genetic diversity and needs targeted conservation measures to avoid extinction (Gubili et al., 2012; O'Leary et al., 2015; Andreotti et al., 2016). White sharks are one of the most protected shark species through policy (Rigby et al., 2019), but their populations are inherently vulnerable to human-induced mortality owing to slow growth and low fecundity (Bruce and

Bradford, 2012; Hamady et al., 2014; Braccini et al., 2017; Bowlby and Gibson, 2020). They are protected from all consumptive activities and formally protected in several countries, including South Africa, Namibia (Rigby et al., 2019), and recently, Mozambique. The species may benefit further by protecting areas where they spend significantly more time, potentially indicating important areas for feeding or breeding (Huveneers et al., 2018; Rigby et al., 2019).

Sex and size-specific movement patterns may increase the vulnerability of white sharks at different life-history stages (Mucientes et al., 2009; Kanive et al., 2019). Therefore, it is important to analyse these patterns to protect this species better using spatial and fisheries management measures. In the US, Mexico and Australia, white shark regional movements are influenced by sex or size (Jorgensen et al., 2010; Domeier and Nasby-Lucas, 2013; Hoyos-Padilla et al., 2016; Bradford et al., 2020). However, due to limited satellite tracking data from Southern Africa, size-specific movement patterns have not yet been identified until now, and sex-specific patterns have been identified only at individual aggregation sites (Kock et al., 2013; Jewell et al., 2014; Towner et al., 2016). Tracking data on white sharks of both sexes and various sizes across the southwest Indian Ocean would inform a comprehensive regional management plan.

Although there is scientific debate on the South African white shark population's size, all population estimates are consistently low, ranging from 500 to 2000 individuals (Towner et al., 2013; Andreotti et al., 2016; Andreotti et al., 2017; Irion et al., 2017). In South Africa, white sharks are captured in shark nets and on drumlines along the KwaZulu-Natal (KZN) coast as part of a bather protection program (Dudley and Simpfendorfer, 2006; Rigby et al., 2019). More broadly, in the southwest Indian Ocean, a mean spatial overlap

of 64% of white shark movement and pelagic longline fisheries highlights a potential risk of being caught as bycatch in these fisheries (Queiroz et al., 2019), but capture and mortality rates are unknown. Little is known about the potential threat from other fisheries within South Africa's Exclusive Economic Zone (EEZ), although capture reports in various commercial fisheries are few (Petersen et al., 2009; Attwood et al., 2011; Reed et al., 2020). Identifying potential overlap of threats and the distribution of white sharks across their range, from fisheries capable of catching this species, will help focus and refine management interventions.

Given that fisheries management measures and spatial zonation may be required to reduce the extinction risk of a species, we analysed the movement patterns of white sharks satellite-tagged in South Africa. The overall aim was to identify areas where sharks spend significantly more time (and may thus benefit from spatial zonation) or overlap with fisheries and associated risk (and may thus benefit from additional fisheries management interventions). Consistent with the South African National Biodiversity Assessment for the marine realm (Sink et al., 2019), we refer to these areas as focus areas. These focus areas may, in turn, inform marine protected area (MPA) expansion programmes, Ecologically or Biologically Significant Marine Area (EBSA) delineations, marine spatial planning initiatives (Reed et al., 2020) or fisheries management measures such as effective monitoring and bycatch reduction (Daly et al., 2018; Hays et al., 2019; Heerah et al., 2019). The specific objectives were to: (1) characterise white shark distribution by size and sex; (2) assess the potential relative risk of capture by quantifying the overlap between white shark distribution and longline and gillnet fisheries; and (3) evaluate whether South Africa's MPA network provides benefit to white sharks and to identify focus areas which may benefit from additional spatial protection.

METHODS

Shark Tagging

In March, April and May of 2012, we deployed 34 SPOT5 transmitters (SPOT-257, SPOT-258; Wildlife Computers) on white sharks at South African coastal aggregation sites, namely False Bay (34° 08' S, 18° 35' E), Gansbaai (34° 40' S, 19° 25' E), Struisbaai (34° 30' S, 20° 37' E), Mossel Bay (34° 06' S, 22° 10' E) and Algoa Bay (34° 52' S, 25° 39' E) (**Figure 1**). Sharks were caught from a tender vessel using buoyed hand lines with baited circle hooks and towed to a larger research vessel (M/V OCEARCH). Sharks were then temporarily removed from the water using a hydraulic lift system for transmitter attachment on the research vessel (Domeier and Nasby-Lucas, 2013). A qualified veterinarian on-board supervised all sampling and tagging procedures. Once the shark was out of the water, a wet towel was gently placed over its eyes to reduce stress, and using a hose and pump, seawater saturated with oxygen was directed onto the buccal cavity over the gills to produce a mild narcotic effect. Several team members worked on the shark simultaneously to reduce the overall duration out of the water. All sharks were tagged and sampled within 12 minutes. The veterinarian administered appropriate drugs to reduce shark capture myopathy and antibiotics to reduce the risk of infection at the hooking and tagging sites (see **Supplementary Material** for a list of drugs and dosages). We measured the sharks' total length (TL) and determined whether they were male or female by the presence or absence of claspers. For analyses we categorised sharks as juveniles (male and female: 175–300 cm TL), sub-adults (male: >300–360 cm TL; females: >300–480 cm TL) and adults (male: >360 cm TL; female: >480 cm TL) (Malcolm et al., 2001). Transmitters were attached to the first dorsal fin using methods described by Bonfil et al. (2005). We coated the tags with Prospeed (Oceanmax Manufacturing,

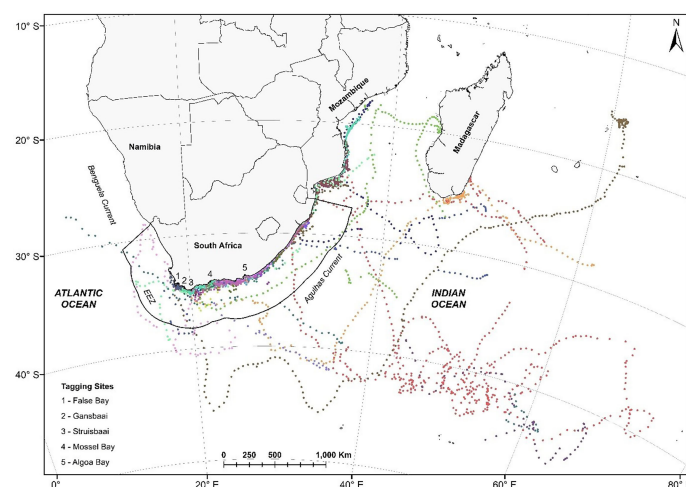


FIGURE 1 | Satellite tracks of 33 white sharks *Carcharodon carcharias* tagged at five locations along the South African coast in 2012. Each colour represents an individual shark's track between 2012 and 2014. These are time-regular predicted locations (one location every 12 hours) from a correlated random walk model fitted to the original data, accounting for the estimated CLS Argos location error, using the foieGras package in R (Jonsen and Patterson, 2020).

www.propspeed.com), an antifouling product, to reduce the effect of biofouling on the transmitter casings (i.e. Jewell et al., 2011).

Track Processing

A total of 20,141 locations were obtained *via* ARGOS CLS (Argos, 2016) from 34 white sharks between March 2012 and April 2014. We removed the Z class locations (invalid locations) and the duplicated time stamps (ARGOS, 2016). Then, we applied a speed filter to remove unrealistic locations (maximum realistic speed 3 m/sec, following Queiroz et al., 2019), leaving 17,317 locations for analysis. The raw tracks of ARGOS locations from individual sharks were made up of time-irregular locations, with time intervals between consecutive locations of up to several days. To avoid reconstructing individual movement trajectories across these large gaps, we split tracks into segments if the time interval between locations exceeded three days. This time interval was arrived at empirically as a practical balance between having time gaps that meant the animal could be anywhere between observed locations and having too many very short track segments, which meant that estimation of locations (described below) failed. As a result, the track of each shark comprised several segments. Segments shorter than 25 locations in length led to non-convergence of the model used to account for location error and reconstruct the movement path (described below), so we excluded these segments from the analysis. This meant that tracks from shark 5 (ID 117468) were excluded from further analysis. The final dataset used to reconstruct the movement paths comprises 13,370 locations from 171 track segments and 33 individual sharks. The mean time difference between observations was 5.86 hours (standard deviation 9.79 hours).

We used a continuous-time state-space model implemented in Template Model Builder (TMB) within the foieGras R package (Jonsen and Patterson, 2020) to obtain improved estimates of the ARGOS satellite locations and to regularise the locations along the individual trajectories (Jonsen and Patterson, 2020). We chose to reconstruct the trajectories at a temporal resolution of one location every 12 hours using a correlated random walk model. Previous studies (e.g., Queiroz et al., 2019) have used a lower temporal resolution of one location every 24 hours. However, owing to the proximity of some locations to land and our interest in behaviour near the coast, we chose a slightly higher temporal resolution of two locations per day. We did not exclude or correct estimated locations that overlapped with land to avoid making changes that could not be applied systematically to the whole dataset. Locations overlapping land are evident in their error. However, the same degree of error is present throughout the dataset in ways not identifiable away from hard barriers, such as the coast. The final dataset used in the next stage of the analysis consisted of 6,680 time-regular shark locations.

Time Series Analysis of Movement Characteristics

We fitted a hidden Markov model (Zucchini et al., 2016) to step lengths and turning angles between consecutive time-regular shark locations. We used the momentuHMM R package (McClintock and Michelot, 2018), which implements

computationally efficient model fitting routines using maximum likelihood. We identified two movement states which we interpreted as “resident” and “non-resident” (hereafter referred to as ‘transient’) and investigated the effect of individual and temporal covariates on the transition probabilities between states. Owing to the lack of information on white shark movement ecology at the scale of ocean basins, the time resolution of the data, and in the interest of biological interpretability (Pohle et al., 2017), we did not explore the possibility of more than two movement states. The candidate covariates included sex (male, female), life stage (juvenile, subadult, adult), TL (cm), day of the year and season. We also explored the effect of the day of the year on the shape of the state variable distributions to check whether the states’ characteristics changed with seasonality, for example, if the mean step length in the transient state increased or decreased at certain times of the year. We compared the candidate models using the AIC weights and used the Viterbi algorithm to calculate the most likely state sequence (global decoding) (Zucchini et al., 2016). We also calculated the probability of the transient movement state at each location (local decoding of state probability), in addition to the most likely state sequence provided by the Viterbi algorithm. State probabilities give an idea of uncertainty in state assignments along each track segment. Details on the candidate models, model fitting and model assessment are included in the **Supplementary Material**.

Spatial Analyses

We carried out two spatial analyses of white shark movement based on the results of the HMM. First, to quantify the exposure of white sharks to the risk of incidental capture in fisheries, we examined the overlap between white shark locations and the spatial distribution of fishing effort in fisheries that could potentially catch them. Second, to quantify the use of MPAs by white sharks, we examined the time spent and distance covered by sharks inside and outside MPAs.

We aggregated the 6,680 time-regular shark location data into 0.1 degree planning units, which we used in spatial analyses. These units corresponded to the approximate error (± 12 km) associated with the poorest location class (B) from the SPOT satellite tags (Patterson et al., 2010). Following Queiroz et al. (2019), data were aggregated within larger planning units (0.25 degrees). However, spatial scales larger than 0.1 degrees were too inaccurate for this study because they often incorporated coastal habitat within pelagic fishing zones, which inflated fisheries overlap, and exceeded the size of the smaller MPAs, making it impossible to test for an effect. Of all white shark locations recorded in this study, most (75%) occurred within the South African EEZ, so we limited our analyses to planning units within the continental EEZ. One of the 33 tagged sharks was excluded from the analyses because no tracks were left inside the EEZ after initial processing (as described under the section “Track Processing” above), leaving data from 32 sharks to be used in this part of the analysis.

The analytical approach used for fisheries and MPAs was different because the fisheries data consisted of counts of hooks or nets within each planning unit. In contrast, the MPA data were binary, either inside or outside an MPA.

White Shark Movement and Fishing Effort Overlap

Due to the high proportion of shark locations within the South African EEZ, we only considered the overlap between tagged white sharks and longline and gillnet fisheries within the EEZ, for which fishing effort data were available for the same period over which sharks were tracked (2012–2014) and used fishing gear capable of potentially catching white sharks. These included the pelagic longline fishery, which targets swordfish, tunas, and large sharks like mako sharks (*Isurus oxyrinchus*) and blue sharks (*Prionace glauca*) and the demersal shark longline fishery that targets soupfin sharks (*Galeorhinus galeus*), smoothhound sharks (*Mustelus mustelus*) and bronze whaler sharks (*Carcharhinus brachyurus*) (Da Silva et al., 2015; Taylor et al., 2016). Additionally, a combination of gillnets and drumlines are deployed along the KwaZulu-Natal coast between Port Edward and Richards Bay to capture large, potentially dangerous sharks for bather safety. Species targeted in this program are white sharks, bull sharks (*Carcharhinus leucas*) and tiger sharks (*Galeocerdo cuvier*) (Dudley and Simpfendorfer, 2006). Beyond the spatial and temporal overlap of white sharks with fisheries, we also obtained white shark catch reports per fishery where possible. We converted precaudal length to total length for reporting purposes, according to Casey and Pratt (1985). In addition to commercial catch data, we obtained catch data from a scientific demersal shark longline survey operated by the Department of Forestry, Fisheries and the Environment under their National Research Surveys.

Total position counts per planning unit were normalised by dividing by the number of individual sharks occupying that planning unit (Walli et al., 2009) to reduce tagging location bias and varying shark track lengths. We refer to this as the normalised shark density. We calculated an exposure index representing sharks' spatial exposure to fisheries by multiplying the total fishing effort (total number of hooks or nets) by the normalised shark density. We restricted the temporal overlap of the analysis to periods when both the respective fishery was actively fishing, and white sharks were present. Following Taylor and Small (2009), we divided each year into quarters: Q1 (Jan-Mar), Q2 (Apr-Jun), Q3 (Jul-Sep), Q4 (Oct-Dec) and calculated the average number of days the sharks overlapped per quarter with the demersal shark longline and pelagic longline fishing sectors. Shark net and drumline effort in KZN are similar all year (except in June and July when some gear is removed due to the annual sardine run). The proportion of spatial overlap with fisheries for sharks in a 'transient or 'resident' state, 'male' or 'female' and 'sub-adult' or 'juvenile' were also calculated. We combined adults and sub-adults into the sub-adult class because of the small sample of tagged adult animals.

White Shark Movement and Marine Protected Area Overlap

MPAs established before and after tagging were deemed to contribute to the MPA estate, referred to as "current MPAs" in the results. However, to compare results, we repeated the analysis

using only those MPAs that existed during the tracking period (we refer to these as "existing MPAs"). Most of South Africa's MPAs were proclaimed in 2019, after the tracking period. Thus "current MPAs" refer to those that existed prior to 2019, combined with those proclaimed in 2019.

Using the 6,680 time-regular white shark locations, we created track lines joining consecutive points of an individual and maintained the transient/resident state information. Track lines were overlaid with the planning units (grid cell used for spatial planning) to calculate the length of the track and the time spent of each individual in each planning unit. For these calculations, we assumed a straight-line distance (d) between shark locations and used the 12-hour time difference (t) between consecutive points to allow calculations of velocity (v) (where $v = d/t$). We used the velocity to determine the proportion of time spent in each planning unit. We coded each planning unit as inside or outside an MPA to calculate the proportion of time that individual sharks spent in MPAs.

Since MPA and planning unit boundaries do not coincide, we allocated planning units to MPAs only if >10% of their area fell within an MPA. A larger cut off was avoided to prevent the exclusion of many smaller MPAs along the coastline from the MPA estate. We then calculated the hours spent by each individual in each MPA (and outside MPAs) when in transient or resident states. We analysed data in ArcGIS (version 10.6) software.

We statistically tested four hypotheses based on a visual assessment of the shark movement data in relation to existing MPAs (i.e. those proclaimed prior to 2019) and current MPAs (i.e. existing and 2019 MPAs combined). The first hypothesis was that white sharks spent more time or covered greater distances in the existing (hypothesis 1a) and current (1b) MPA estate than expected. We defined the planning domain as only those planning units visited by any shark (total area = 235,873 km²). Of this area, 34,896 km² fell in current MPAs (14.8%), and 8,541 km² fell in existing MPAs (3.6%). We used this proportion as a proxy for the proportion of time one would expect the sharks to spend within MPAs if they randomly utilise their planning domain. We used a single sample t-test to compare the mean proportion of time (of all individuals combined) inside MPAs to the expected proportion of time spent. A boxplot confirmed that the data followed a normal distribution. We performed the same analysis for track length instead of time spent which also met the assumption of normality.

The second and third hypotheses were that the mean proportion of time that white sharks spend in MPAs (relative to the planning domain) differs between males and females or between subadult sharks versus juveniles, respectively. We combined adults and sub-adults into the sub-adult class because of the small sample of tagged adult animals and used a Welch two-sample t-test to avoid the assumption of equal variances between the groups. A boxplot confirmed that both variables followed a normal distribution. We performed the same analysis for track length instead of time spent.

The fourth hypothesis was that white sharks spend more time in individual MPAs than would be expected. We defined the

planning domain as only those planning units visited by any sharks that visited that specific MPA for each MPA-specific analysis. We used the proportion of these planning units within the MPA as a proxy for the proportion one would expect the sample of sharks to spend within that MPA if they randomly utilise their planning domain. Sharks visited 29 MPAs, but four of these were visited by only single sharks, and we excluded them from the analyses. Therefore, we ran analyses using 25 MPAs, of which ten were existing MPAs and 15 were proclaimed in 2019. We used a single sample t-test to compare the mean proportion of the track length or time inside an individual MPA to the expected proportion of time spent. The significance level was adjusted for multiple testing using the Bonferroni adjustment. A boxplot confirmed that the data followed a normal distribution. The same analysis was performed for track length instead of time spent.

We then used point density estimation to investigate the areas of utilisation. This analysis aimed to identify focus areas utilised by sharks that do not fall within MPAs, which could then be considered for future protection. We ran all statistical analyses in R Core Team (2020) and the point density estimation in ArcGIS.

RESULTS

Geographic Movements

Argos satellite tracks were obtained for 33 white sharks ranging in size from 251 – 420 cm TL (316 ± 15 ; mean \pm SE, $n = 13$) for males and 228 – 505 cm TL ($369 \text{ cm} \pm 16.4$, mean \pm SE, $n = 20$) for females (Table 1). These represented three adults (2 males; 1 female), 18 sub-adults (5 males; 12 females) and 13 juveniles (6 males; 7 females) (Table 1). The SPOT5 tags' transmission duration ranged from 36 – 1155 days (374.5 ± 277.28 days, median \pm SD). White sharks tagged in South Africa moved across a vast area of the southwest Indian Ocean, encompassing coastal and pelagic zones of South Africa, Mozambique, Madagascar and the high seas (Figure 1). Nine out of 33 sharks (27%) visited Mozambique at least once, and six out of 33 sharks (18%) visited the Madagascar area at least once. Apart from coastal areas of South Africa, southern Mozambique and southern Madagascar were areas frequented by large (>3 m) female white sharks (Figure 1). Only three (8%) of the tagged white sharks swam extensively westwards up the west coast of South Africa.

There was no systematic difference between female and male sharks in the quality or quantity of tracking data (Table 1). This includes the total number of locations (Welch two-sample t-test, $t = -0.62$, $df = 31.00$, $p\text{-value} = 0.54$), the number of days with locations (Welch two-sample t-test, $t = -0.81$, $df = 30.79$, $p\text{-value} = 0.42$) and the number of locations per day (Welch two-sample t-test, $t = -0.16$, $df = 25.04$, $p\text{-value} = 0.88$).

Time Series Analysis of Movement Characteristics

According to the AIC weights, we found that a model with sex, TL and the sine and cosine of the day of the year as covariates

on the transition probabilities had the most support (70%). The only other model with any support was one with life stage (adult, subadult, and juvenile) instead of TL (29%). Since life stage is determined using TL, we consider that both models capture the same patterns in the data. Using the model with the most support, we estimated the state-dependent distributions of step length and turning angle. We found that one state is characterised by slow, undirected movement (mean ~ 11 km per 12 hours, SD 10 km – just under 1 km per hour), and the other fast, directed movement (mean ~ 52 km per 12 hours, SD 28 km – just over 4 km per hour). We refer to the two states as 'resident' and 'transient' movement patterns. The state-dependent distributions are shown in Figure 2 and have been weighted by the proportion of locations assigned to each state by the Viterbi algorithm (Zucchini et al., 2016).

Males and females were more likely to adopt resident movement behaviour near the coast (Figure 3). In contrast, subadult and adult females were the only ones to travel extensively away from the coast over the tagging period (Figure 4).

The effect of time of the year on the probability of finding a shark in a given state differed for males and females and by life stage within sex. Adult and subadult females were consistently more likely to be in a transient state throughout the year, with a high probability (Figure 5), while adult males were only more likely to be transient during the summer months. Subadult male and juvenile female sharks were only more likely to be in a resident state in the winter months (between days 120 and 300), by a narrow margin. Juvenile males were the only group more likely to be in a resident state throughout the year.

We found strong evidence that the probability of finding a female shark in the transient movement state increased with size and was consistently high from about 350 cm (Figure 6). There was weak evidence that the smallest female sharks (200 – 250 cm) were more likely to be in a resident state in winter, and there was uncertainty in the most likely state for this group during summer. Male sharks showed a similar pattern, with an increase in the probability of being transient with size, but there was strong evidence for an increased probability of finding small males (up to about 300 cm) in a resident state in both winter and summer. This suggests a change in behaviour at a larger size than females (approximately 280 cm for females, compared to 350 cm for males). There were fewer small and large males than females in the dataset, seen in the relationship's limits (Figure 6, right column).

White Shark Movement and Fishing Effort Overlap

Over the study period, one white shark died in a gillnet set in Southern Mozambique and another on a KZN Sharks Board drumline (Table 1). White shark tracks and fishing effort varied over the study period (see Supplementary Material), but overall white sharks overlapped with longline and gillnet fisheries within 25% of the total area occupied in the South African EEZ and spent 15% of their time exposed to these fisheries during the

TABLE 1 | SPOT5 transmitter (Wildlife Computers) summary information for white sharks *Carcharodon carcharias* tagged in South Africa in 2012.

Shark no.	Tag ID	TL (cm)	Sex	Maturity status	Deployment date	Start location	End location	Deployment Duration (days)	Number of days with locations	Total number of locations	Number of locations per day
1	117464	350	F	Sub-adult	10-03-2012	-34.07 S, 22.21 E	-34.46 S, 21.20 E	500	117	504	4.3
2	117465*	312	M	Sub-adult	23-03-2012	-34.12 S, 22.13 E	-34.63 S, 19.44 E	714	36	219	6.1
3	117466	309	M	Sub-adult	23-03-2012	-34.12 S, 22.13 E	-34.19 S, 22.30 E	532	44	203	4.6
4	117467	360	F	Sub-adult	12-04-2012	-34.64 S, 19.43 E	-34.15 S, 22.13 E	421	59	201	3.4
5	117468**	310	F	Sub-adult	08-03-2012	-34.07 S, 22.21 E	-34.07 S, 22.20 E	348	87	197	2.3
6	117469	340	F	Sub-adult	23-03-2012	-34.12 S, 22.13 E	-24.38 S, 35.41 E	277	12	37	3.1
7	117470	351	F	Sub-adult	08-03-2012	-34.07 S, 22.21 E	-34.06 S, 22.22 E	717	23	87	3.8
8	117471	318	M	Sub-adult	12-04-2012	-34.68 S, 19.40 E	-29.14 S, 31.91 E	1155	101	342	3.4
9	117472***	371	F	Sub-adult	08-03-2012	-34.07 S, 22.21 E	-24.80 S, 34.83 E	206	135	607	4.5
10	117473	297	F	Juvenile	21-03-2012	-34.12 S, 22.13 E	-34.56 S, 19.27 E	83	37	232	6.3
11	117474	266	M	Juvenile	21-03-2012	-34.12 S, 22.13 E	-25.04 S, 33.68 E	738	174	568	3.3
12	117475	259	F	Juvenile	21-03-2012	-34.12 S, 22.13 E	-34.14 S, 24.79 E	36	26	81	3.1
13	117476	297	M	Juvenile	12-04-2012	-34.64 S, 19.43 E	-28.63 S, 32.32 E	414	67	273	4.1
14	117477	251	F	Juvenile	21-03-2012	-34.12 S, 22.13 E	-34.08 S, 22.27 E	205	96	420	4.4
15	117478	228	F	Juvenile	10-03-2012	-34.07 S, 22.21 E	-34.14 S, 23.19 E	158	86	354	4.1
16	117479	265	F	Juvenile	16-03-2012	-33.73 S, 25.86 E	-34.61 S, 21.70 E	476	86	394	4.6
17	117480	299	F	Juvenile	07-03-2012	-34.07 S, 22.21 E	-34.36 S, 20.49 E	843	43	179	4.2
18	117482****	295	M	Juvenile	08-03-2012	-34.07 S, 22.21 E	-34.40 S, 24.51 E	215	79	310	3.9
19	117483	292	F	Juvenile	21-03-2012	-34.12 S, 22.13 E	-34.47 S, 20.76 E	255	88	372	4.2
20	118845	420	M	Adult	09-05-2012	-34.69 S, 19.42 E	-29.1 S, 32.02 E	508	188	858	4.6
21	118846	418	F	Sub-adult	09-05-2012	-34.69 S, 19.42 E	-34.47 S, 19.34 E	509	30	119	4.0
22	118847	417	F	Sub-adult	15-04-2012	-34.14 S, 18.58 E	-34.49 S, 19.33 E	102	9	37	4.1
23	118848	431	F	Sub-adult	16-04-2012	-34.14 S, 18.58 E	-29.34 S, 32.36 E	52	18	86	4.8
24	118849	505	F	Adult	10-07-2012	-35.28 S, 20.84 E	-34.32 S, 23.10 E	352	35	177	5.1
25	118850	441	F	Sub-adult	22-05-2012	-34.53 S, 20.46 E	-33.47 E, 18.53 E	300	68	336	4.9
26	118852	441	F	Sub-adult	13-04-2012	-34.64 S, 19.43 E	-35.07 S, 20.77 E	1106	263	1367	5.2
27	118853	330	M	Sub-adult	13-04-2012	-34.68 S, 19.40 E	-29.15 S, 32.02 E	240	90	435	4.8
28	118855	382	M	Adult	23-05-2012	-34.53 S, 20.46 E	-27.56 S, 49.57 E	678	139	729	5.2
29	118859	295	M	Juvenile	08-05-2012	-34.68 S, 19.40 E	-34.23 S, 22.84 E	224	145	632	4.4
30	118860	290	M	Juvenile	08-05-2012	-34.68 S, 19.40 E	-31.25 S, 30.07 E	293	83	308	3.7
31	118861	457	F	Sub-adult	16-04-2012	-34.14 S, 18.58 E	-34.43 S, 18.79 E	538	143	518	3.6

(Continued)

TABLE 1 | Continued

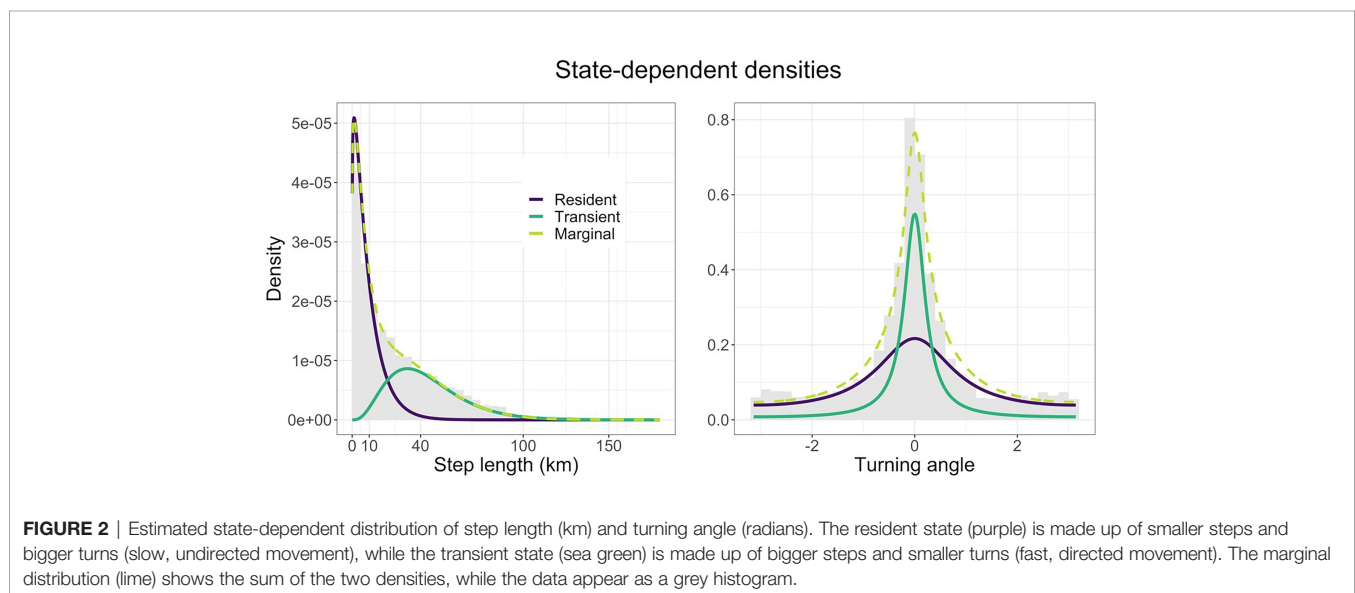
Shark no.	Tag ID	TL (cm)	Sex	Maturity status	Deployment date	Start location	End location	Deployment Duration (days)	Number of days with locations	Total number of locations	Number of locations per day
32	118862	320	M	Sub-adult	08-05-2012	-34.68 S, 19.40 E	-34.62 S, 19.39 E	110	23	88	3.8
33	118863	390	F	Sub-adult	09-05-2012	-34.69 S, 19.42 E	-27.62 S, 56.30 E	694	313	1447	4.6
34	118864	251	M	Juvenile	13-04-2012	-34.64 S, 19.43 E	-25.06 S, 35.00 E	397	180	850	4.7

*Coastal movement data was insufficient to include in the analysis, but offshore data was included.

**Excluded from the analyses because none of the track segments was longer than 25 locations.

***Captured in an artisanal gill net, Quissico, Mozambique.

***Captured on a KZN Sharks Board drumline, KwaZulu-Natal, South Africa.



study period. Spatial and temporal overlap was highest, 14% and 10%, respectively, between white sharks and the demersal shark longline sector, followed by 11% and 4% within the pelagic longline sector, and 1% and 1% within the KZN shark nets and drumlines (**Table 2**).

Sharks most exposed to the demersal longlining were those that were resident (71%), male (59%) and juvenile (82%). The fishery with the second-highest overlap was the pelagic longline sector, with those sharks that were transient (81%), female (67%) and sub-adult/adult (51%) most exposed. The fishery with the third-highest overlap was shark nets and drumlines with those sharks that were transient (62%), female (69%) and juvenile (69%) most exposed (**Table 2**).

Areas of highest fishing exposure included mainly inshore areas within the vicinity of Algoa Bay, Jeffrey's Bay, Sedgfield, Stillbaai and Gansbaai (demersal shark longline), where resident immature sharks were most exposed, as well as central to southern KZN (shark nets and drumlines) where transient immature, female sharks were most exposed (**Figure 7**). The overlap with the pelagic longline sector was relatively widespread and sporadic and overlapped most with transient female sharks (**Figure 7**).

White shark catch records were hard to obtain as there is no central database of white shark incidental catches, and statistics are kept in different databases according to fishery type. We could find no white shark reports in the pelagic shark longline fishery, and only two white sharks (unknown size and sex; one released alive) were reported in the demersal shark longline fishery (DFFE, unpublished data). In the scientific national demersal shark longline survey, 106 demersal shark longlines (11933 hooks) were set between False Bay and Port Alfred between 2008 and 2016. In total, two juvenile white sharks (both female), 200 and 280 cm TL, respectively, were caught in Algoa Bay during one summer survey. One died, and one was released alive. No other white shark interactions were reported. In contrast, 1317 white sharks were captured in the KwaZulu-Natal shark nets and drumlines between 1978 and 2018 (mean 32 sharks/year). A total of 209 (16%) sharks were released alive. More females were caught in the shark nets (527 males, 666 females, 47 unknown) and drumlines (30 males, 43 females, 4 unknown). Most white sharks caught were juveniles of both sexes (**Table 3**). The average size of white sharks caught in the shark nets is 265 cm TL and in the drumlines is 275 cm TL.

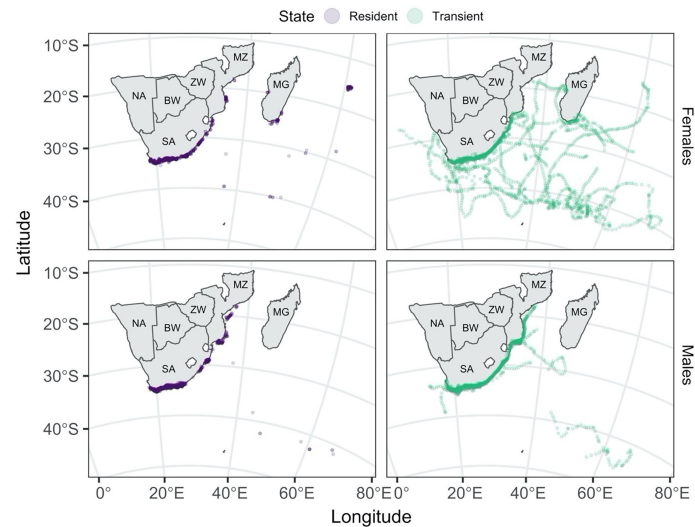


FIGURE 3 | Predicted shark locations coloured by Viterbi-decoded states. The tracks are separated by state (resident in purple: left column, transient in sea green: right column) and sex (females: top row, males: bottom row). Country codes are shown on the map: SA, South Africa; NA, Namibia; BW, Botswana; ZW, Zimbabwe; MZ, Mozambique; MG, Madagascar.

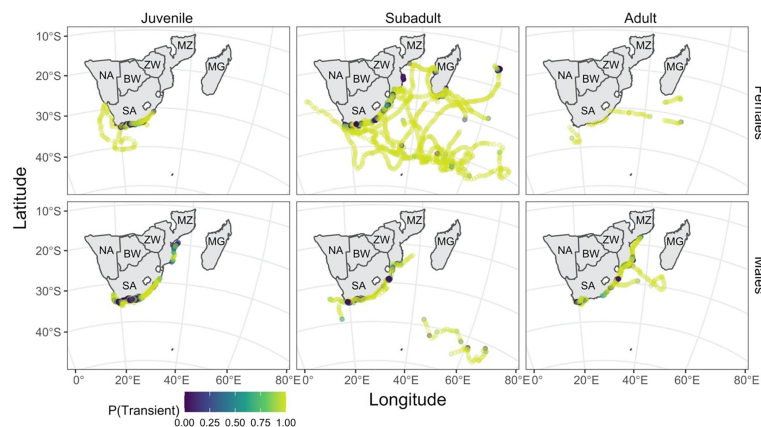


FIGURE 4 | Predicted shark locations are coloured by the probability of a given location belonging to the transient state, where lighter locations indicate a high probability of being transient. This illustrates the level of uncertainty in state assignment; the closer the colour to either end of the colour scale, the greater the certainty in state assignment. The tracks are separated here by life stage based on size (juvenile: left column, subadult: middle column, adult: right column) and by sex (females: top row, males: bottom row). Country codes are shown on the map: SA, South Africa; NA, Namibia; BW, Botswana; ZW, Zimbabwe; MZ, Mozambique; MG, Madagascar.

White Shark Movement and Marine Protected Area Overlap

Inside the South African EEZ, the 32 individual white sharks spent 50,260 hours and covered 68,878 km (73% of the time and 41% of the distance in a resident state). The percent of time spent and distances covered within the current MPA estate were 23% and 21%. **Figure 8** shows the relationship between hours spent and the current MPA estate.

Results for hypotheses 1 to 4 are presented in **Table 4**. White sharks spent significantly more time (and covered significantly longer distances) in MPAs than can be expected based on the size of MPAs relative to the planning domain used by sharks. This was the case for existing and current MPAs. Males and females, and age classes, did not use MPAs differently. At a finer scale in current MPAs, sharks spent significantly more time in De Hoop (existing) ($p = 0.012$), Tsitsikamma (existing) ($p = 0.022$) and

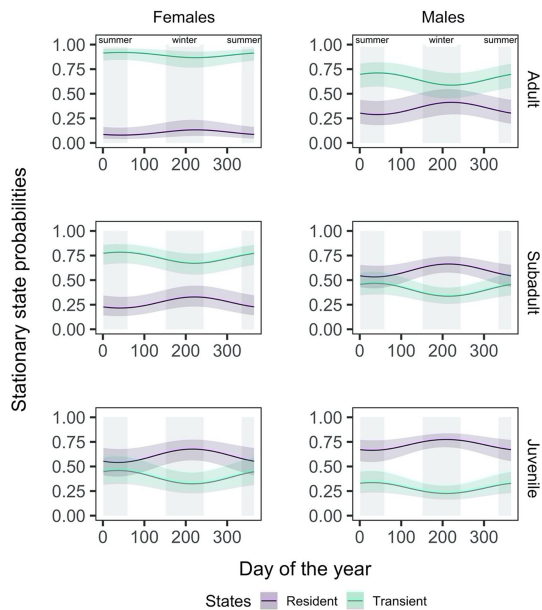


FIGURE 5 | The effect of day of the year on the probability of finding a shark in a given state, shown here by sex (females: left column, males: right column) and life stage (adult: top row, subadult: middle row, juvenile: bottom row). The shading around the state line represents the 95% confidence interval around the mean effect.

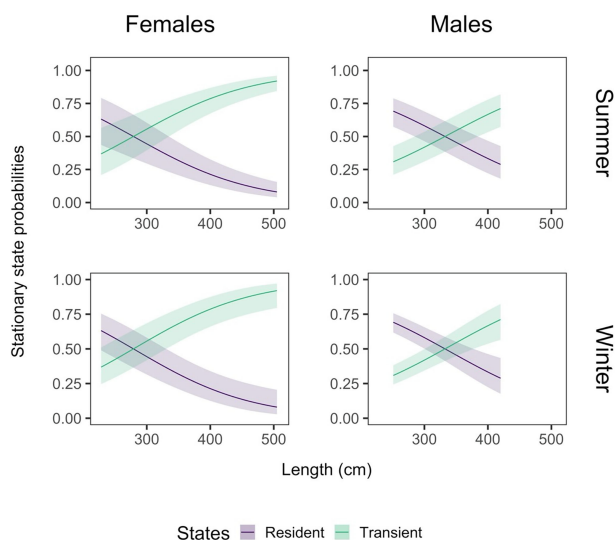


FIGURE 6 | The effect of total length on the probability of finding a shark in a given state. The effect of length is shown here by sex (females: left column, males: right column) and season (summer: top row, winter: bottom row). We define seasonality according to the peak of mature transient movement and the trough of immature resident movement, as seen in **Figure 5**. Therefore, we define summer as day 40 of the year (9 February) and winter as day 220 (8 August). The shading around the state line represents the 95% confidence interval around the mean effect.

Addo Elephant National Park (proclaimed in 2019) ($p = 0.006$) MPAs than can be expected based on the size of these MPAs relative to the planning domain used by the sharks that visit these MPAs. Sharks cover significantly longer distances in De Hoop ($p = 0.011$), Stillbaai (existing) ($p = 0.007$), Tsitsikamma ($p = 0.012$), Addo Elephant National Park ($p = 0.003$), Pondoland (existing) ($p = 0.018$), Protea Banks (proclaimed in 2019) ($p = 0.015$) and Aliwal Shoal (proclaimed in 2019) ($p = 0.014$) MPAs than can be expected. Aliwal Shoal existed before 2019 as a small MPA (125 km²) and was expanded to a much larger MPA in 2019 (678 km²); we thus do not treat it as an existing MPA.

Results of the point density analysis show important areas used by white sharks on the Cape south coast (adjacent to the tagging locations of Gansbaai, Struisbaai and Mossel Bay, as can be expected), with a previously unknown cluster in the northern restricted zone of the uThukela MPA (newly proclaimed), which is >1150 km away from the closest tagging site (**Figure 9**).

Figure 10 shows the percentage of time spent by sharks in individual MPAs when all tracks are combined (all) or if only resident or transient state tracks are used. The cluster noted in **Figure 9** in the uThukela MPA is also supported here.

DISCUSSION

Satellite tracking improves our understanding of species movement across their range. It is also a powerful tool for identifying the overlap of pressures and threats with species' spatial and temporal distribution and opportunities to focus our conservation and management interventions. In this study, we used statistical modelling of satellite tracking data to describe the spatiotemporal movement patterns of white sharks in the southwest Indian Ocean, estimate their exposure to capture risk and their relative use of protected areas. By comparing sex-specific, size-specific and seasonal movement with relevant fishing effort and South Africa's MPA network, we have identified opportunities for improved conservation, spatial planning actions and management interventions.

White sharks tagged in this study moved extensively along the coastal areas of South Africa, crossing borders into Mozambique and even Madagascar. These sharks thus crossed several countries' respective EEZs and spent time in Areas Beyond National Jurisdictions (high seas). The extent of their movements was similar to that reported by Bonfil et al. (2005), which identified temporary residency to coastal bays and long-distance coastal migrations along the Southern African coast. These diverse movement strategies have been identified for white sharks in Australia and the United States (Jorgensen et al., 2010; Bradford et al., 2020) and highlight this species' adaptability and their role in connecting a diverse range of habitats and ecosystems. However, unlike Bonfil et al. (2005), we recorded no transboundary movement between South Africa and Australia. Our results, coupled with previously published movement and genetic results (Pardini et al., 2000; Bonfil et al., 2005; Andreotti et al., 2016), suggest that transboundary movement between South Africa and Australia is rare.

Notably, only three of the 34 tagged sharks (and none of the 32 white sharks tagged in Bonfil et al. (2005)) moved

TABLE 2 | The spatial and temporal overlap between white sharks (*Carcharodon carcharias*) and longline and gillnet fishing effort in the South African Exclusive Economic Zone.

	Spatial shark overlap (%)	Temporal shark overlap (%)	State (%)		Sex (%)		Maturity	
			Resident	Transient	Male	Female	Sub-adult/adult	Juvenile
Pelagic longline	11	4	19	81	33	67	51	49
Demersal shark longline	14	10	71	29	59	41	18	82
Shark nets and drumlines	1	1	38	62	31	69	31	69
Total	25	15						

The proportion of total spatial overlap with each fishery and white sharks by movement state, sex and maturity status is also presented.

extensively westwards of Cape Point. Cape Point is a transition zone between the warmer Agulhas Shelf ecoregion and the colder Southern Benguela Shelf ecoregion (Sink et al., 2019) and acts as an oceanographic barrier for many marine species from invertebrates to teleosts, elasmobranchs and marine mammals (Elwen et al., 2010; Griffiths et al., 2010; Scott et al., 2012). As regional endotherms, white sharks have high metabolic demands (Ezcurra et al., 2012) and high energy requirements (Carey et al., 1982; Watanabe et al., 2019). We propose that the cold, upwelled, and often oxygen-depleted waters along the west coast of South Africa (Jarre et al., 2015) may not provide

suitable conditions for white sharks, especially for extended periods (see also Hammerschlag et al., 2017). Therefore, even though the west coast is highly productive with abundant prey, including several extensive Cape fur seal colonies, it might be too energetically expensive for white sharks to forage or breed in this region.

Movement Influenced by Sex, Size and Season

We found that sex and size influence the spatiotemporal movement of white sharks in Southern Africa, consistent with behaviour described from Australia and the United States (Jorgensen et al., 2010; Domeier and Nasby-Lucas, 2012; Hoyos-Padilla et al., 2016; Franks et al., 2021; Lee et al., 2021). Subadult and adult females ranged across 45 degrees of longitude in the southwest Indian Ocean and regularly occurred offshore. On the other hand, juvenile and subadult males stayed almost exclusively in the coastal region. This is similar to white sharks' behaviour in southwestern Australia (Bradford et al., 2020) and western North Atlantic (Franks et al., 2021), where large females covered broader longitudinal ranges and spent more time in offshore waters, while males mainly stayed on the continental shelf. Our results support Bonfil et al. (2005) conclusion that connectivity between white shark populations is facilitated by females rather than males, as Pardini et al. (2001) proposed. However, we rarely record adult white sharks in South Africa, especially females (Rycklief et al., 2014; Hewitt et al., 2018), with only three tagged in our study and Bonfil et al. (2005). In this study, large white sharks are more likely to be in a transient state near the coast, possibly resulting in fewer opportunities to be recorded or tagged, and this may also partially explain why we see fewer adults at these coastal aggregation sites. However, very large and sometimes pregnant female white sharks have been caught in gillnet fisheries eastwards in Kenya, Tanzania and Madagascar and are suspected to originate from South Africa (Cliff et al., 2000; Zuffa et al., 2002). The current information suggests that South Africa is an important area for juveniles and subadults and that the waters further east and offshore are important when they reach maturity. Focus areas for adult white sharks in Southern Africa remain unknown and present a significant knowledge gap in need of attention.

Feeding is considered an important driver of shark occurrence at coastal aggregation sites as these encompass pinniped colonies and other productive and biodiverse coastal areas (Martin et al., 2005; Dicken and Booth, 2013; Jewell et al.,

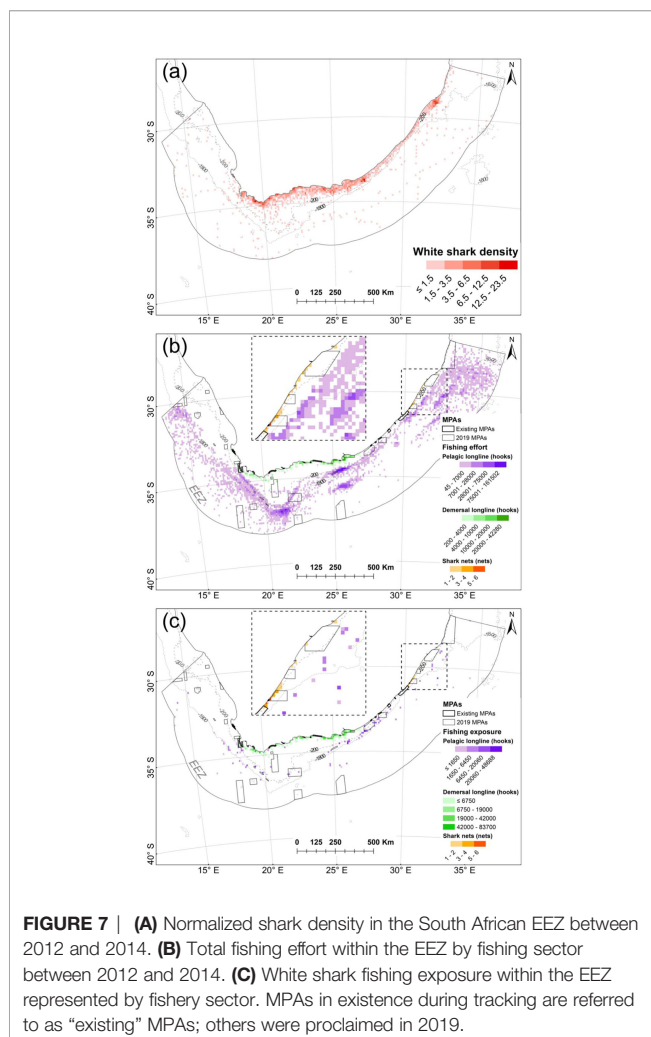


TABLE 3 | Catches of white sharks (*Carcharodon carcharias*) in the KwaZulu-Natal beach safety program from 1978 – 2018 (shark nets) and 2007 – 2018 (drumlines).

	Maturity	Shark nets	Drumlines	Total
Female	Juvenile	495	33	528
	Sub-adult	155	10	165
	Adult	1	0	1
Male	Juvenile	430	18	448
	Sub-adult	63	11	74
	Adult	14	1	15
Total		1158	73	1231*

*86 white sharks had no age class or sex information and were excluded from the table.

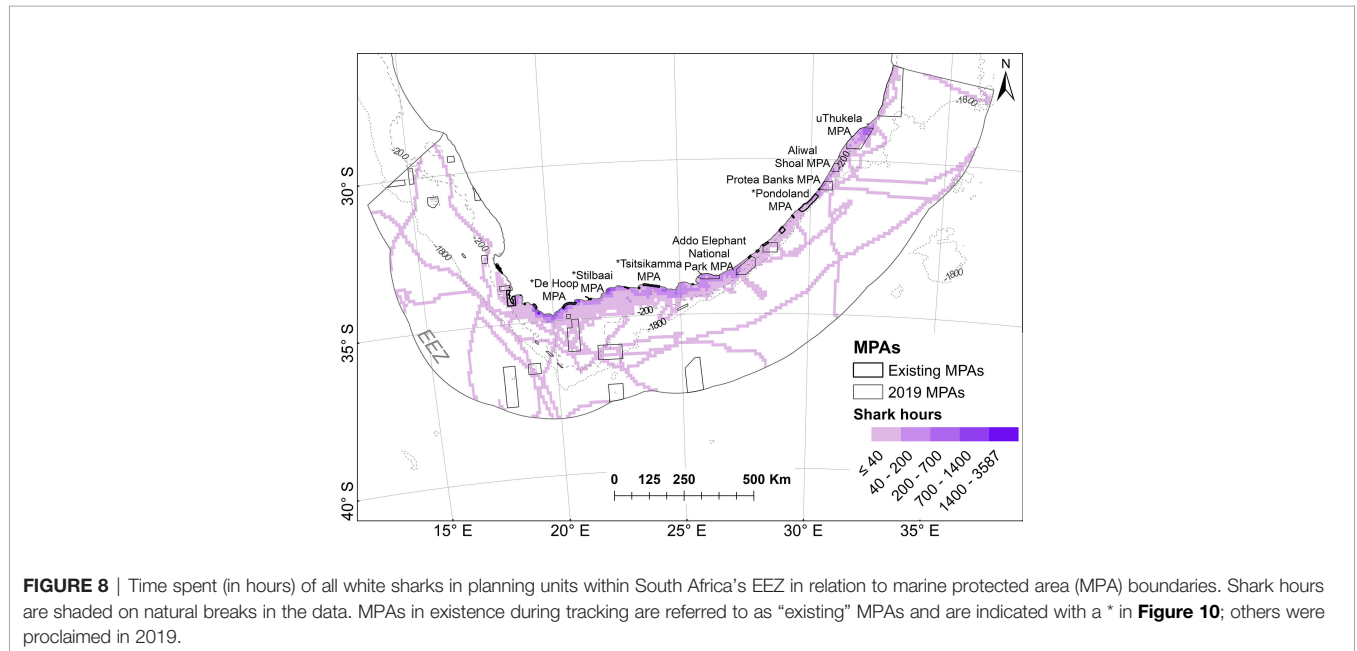


FIGURE 8 | Time spent (in hours) of all white sharks in planning units within South Africa's EEZ in relation to marine protected area (MPA) boundaries. Shark hours are shaded on natural breaks in the data. MPAs in existence during tracking are referred to as "existing" MPAs and are indicated with a * in **Figure 10**; others were proclaimed in 2019.

2013; Kock et al., 2013; Towner et al., 2016; Kock et al., 2018). The dominance of resident movement near the coast by the mostly sexually immature sharks that make up our dataset, and the increase in the probability of transient movement with shark size, suggest a change in needs and constraints with maturity. Therefore, we propose that the resident movement state most likely represents feeding, patrolling or resting at or near important feeding areas, analogous to area-restricted search behaviour (Towner et al., 2016; Bailey et al., 2019), while the transient state likely represents migratory or travelling behaviour, but without precluding feeding. Muscle and blood samples were also collected for stable isotope analysis from the sharks tagged in this study, which, upon later analysis, may provide further insight into the relationship between movement strategies and trophic ecology. The coast may provide more predictable, concentrated foraging opportunities but more competition with conspecifics or other top predators than the open ocean, where sharks may have to travel longer, farther and deeper to find prey. Larger, maturing sharks can expand their foraging range offshore to take advantage of open ocean resources and avoid competition with conspecifics and other

large predators. Mature sharks may also need to travel wider and further to find suitable mates.

The seasonal occurrence of white sharks is pronounced at all major aggregation sites worldwide (Klimley et al., 2001; Martin et al., 2005; Anderson et al., 2011; Dicken and Booth, 2013; Kock et al., 2013; Bruce and Bradford, 2015; Skomal et al., 2017). In our study, the season also influenced the behavioural state of white sharks, with juvenile females and subadult males more likely to be in a resident state during the austral winter months. This coincides with the predictable feeding opportunities and highest predation rates at Cape fur seals colonies (Martin et al., 2005; Dicken and Booth, 2013; Towner et al., 2016). Overall, juvenile female and subadult male white sharks are the most frequently recorded age classes at South African aggregation sites (Rycklief et al., 2014; Hewitt et al., 2018). Juvenile males are more likely to be in a resident state all year round, while the opposite is true for subadult and adult females and adult males. This may explain why they are recorded at South African aggregation sites less frequently than other demographic categories (Rycklief et al., 2014; Hewitt et al., 2018), which can help improve population modelling.

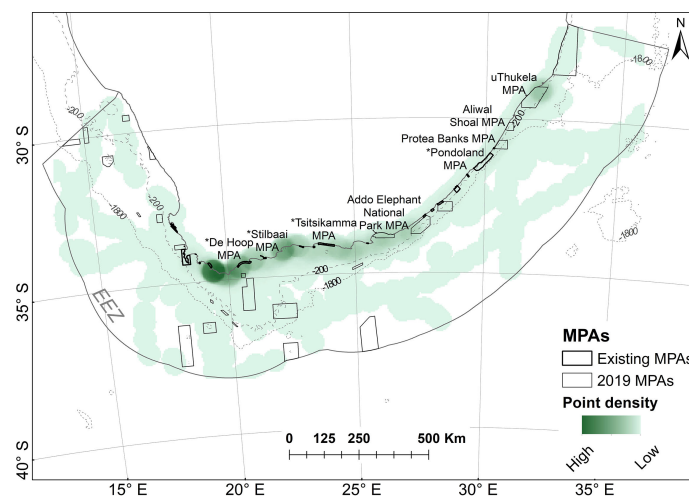
TABLE 4 | Research hypotheses and results of white shark *Carcharodon carcharias* use of marine protected areas (MPAs) using time spent and track length.

Research hypothesis	Statistical hypothesis	Test Statistics	Conclusions
1a. White sharks spent more time and covered greater distances in existing MPAs than would be expected.	$H_0: \mu = 0.036; H_1: \mu > 0.036$ (where H_0 represents the proportion of the planning domain within the existing MPA estate = 3.6%)	Time: $t = 3.5174, df = 31, p = 0.00068$ Track length: $t = 3.5829, df = 31, p = 0.00057$	Reject both null hypotheses and conclude that the mean proportion of time (and track length) within existing MPAs is higher than what would be expected proportionately based on the size of the MPAs relative to the planning domain used by sharks.
1b. White sharks spend more time or cover greater distances in current MPAs than would be expected.	$H_0: \mu = 0.148; H_1: \mu > 0.148$ (where H_0 represents the proportion of the planning domain within the current MPA estate = 14.8%)	Time: $t = 2.4267, df = 31, p = 0.01062$ Track length: $t = 1.9836, df = 31, p = 0.02811$	Reject both null hypotheses and conclude that the mean proportion of time (and track length) within current MPAs is higher than what would be expected proportionately based on the size of the MPAs relative to the planning domain used by sharks.
2. The mean proportion of time spent (or distances covered) by white sharks in current MPAs differs between males and females.	$H_0: \mu_{\text{female}} = \mu_{\text{male}}; H_1: \mu_{\text{female}} \neq \mu_{\text{male}}$	Time: $t = 0.059194, df = 16.997, p = 0.9535$ Track length: $t = 0.14394, df = 17.107, p = 0.8872$	Fail to reject both null hypotheses and conclude that the use of current MPAs does not differ between males and females.
3. The mean proportion of time spent (or distances covered) by white sharks in current MPAs differs between age classes.	$H_0: \mu_{\text{juvenile}} = \mu_{\text{subadult}}; H_1: \mu_{\text{juvenile}} \neq \mu_{\text{subadult}}$	Time: $t = 0.030695, df = 28.756, p = 0.9757$ Track length: $t = -0.071653, df = 28.171, p = 0.9434$	Fail to reject both null hypotheses and conclude that the use of current MPAs does not differ between age classes.
4. White sharks spend more time in individual current MPAs than would be expected.	$H_0: \mu = \mu_0; H_1: \mu > \mu_0$ (where μ_0 represents the hypothesized proportion of time for each individual MPA)	Reported in the text	Reject both null hypotheses and conclude that the mean proportion of time (and track length) within some current MPAs is higher than what would be expected proportionately based on the size of the current MPA relative to the planning domain used by sharks who visited that current MPA. Results were significant for three current MPAs (with respect to time spent) and seven current MPAs (with respect to track length).

White Shark Movement and Fishing Effort Overlap

White sharks overlapped with longline and gillnet fisheries within 25% of South Africa's Exclusive Economic Zone and

spent 15% of their time exposed to these fisheries during the study period. The spatial and temporal overlap was highest for the demersal shark longline fishery, followed by the pelagic longline fishery and the shark nets and drumlines. Sharks most

**FIGURE 9** | Point densities of white sharks in relation to marine protected areas (MPAs). MPAs in existence during tracking are referred to as “existing” MPAs and are indicated with a * in **Figure 10**; others were proclaimed in 2019.

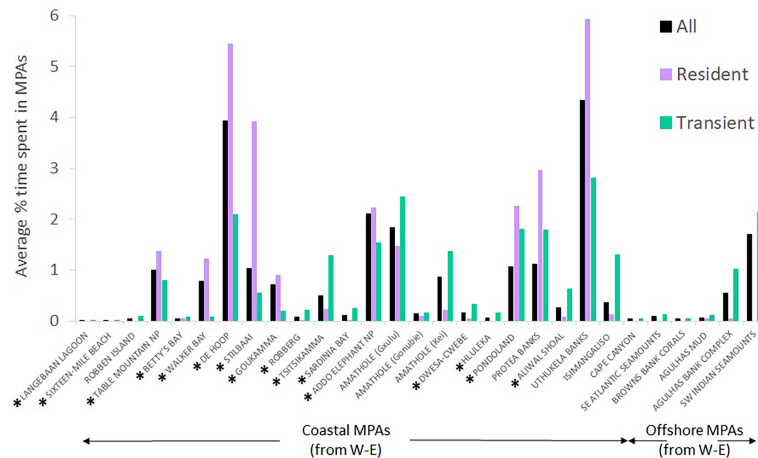


FIGURE 10 | The average percentage of time spent by white sharks *Carcharodon carcharias* in the 29 marine protected areas they visited, depending on whether data were combined (all), or divided into resident versus transient states. MPAs in existence during tracking are indicated with a *; others were proclaimed in 2019.

exposed to the demersal shark longline fishery were disproportionately resident, immature male sharks that spend the most time inshore in areas of the highest fishing effort. However, there have only been two reported white shark captures in this fishery (DFFE, unpublished data). Non-reporting of threatened and protected species is a concern in commercial fisheries (Campana, 2016) and needs to be considered when interpreting catch reports. However, the catches from the demersal shark longline fishery's scientific equivalent (presented in this paper) support the low number of white shark captures, with only two white sharks caught over eight years and >11 000 set hooks. Furthermore, in Australia and the United States, white sharks are rarely caught on the demersal longline fishing gear component of demersal shark fisheries (gill nets capture most white sharks), providing further support for low captures in this fishery (McAuley and Simpfendorfer, 2003; Morgan et al., 2009; Dewar et al., 2013; Curtis et al., 2014; Braccini and Waltrick, 2019). The demersal shark longline fishery targets soupfin and smoothhound sharks and generally uses relatively small baited hooks with nylon traces (no steel) that most white sharks could bite through, although entanglement in longlines is possible.

The exposure risk of white sharks to pelagic longline fisheries within the South African EEZ was lower than for the demersal shark longline fishery and occurred over a larger area and in offshore areas. The exposure risk was disproportionately high for subadult and adult female sharks in a transient movement state. Pelagic longline fisheries use larger hooks than the demersal shark longline fishery. However, no steel traces are permitted, similar to the demersal shark fishery (DFFE permit conditions), although entanglements are also possible. No white shark captures have been reported in this fishery by the industry or independent observers (DFFE, unpublished data; Petersen et al., 2009; Attwood et al., 2011; Reed et al., 2020), but as with other

commercial fisheries, species misidentification (possibly with mako sharks) and non-reporting of threatened and protected species remain concerns. However, like with the demersal shark longline fishery, it is unlikely that substantial white sharks are caught in this fishery and likely present a relatively low risk to white sharks.

The shark nets and drumlines set along the KwaZulu-Natal coast had much lower spatial and temporal overlap (1%) than the demersal shark and pelagic longline fisheries but caught a substantial number of white sharks (on average 32 sharks/year). The exposure risk was highest for juvenile female sharks in a transient state. Indeed, the catch composition from the shark net and drumline programme confirms that juvenile female sharks had the highest catch rates, providing support for this being a meaningful exposure risk estimate. The biggest difference between the shark nets and drumlines and the longline fisheries is that the KZN bather protection program targets large sharks and uses fishing gear capable of catching white sharks such as gillnets and large, baited hooks with steel traces (chain) to prevent sharks' biting through the traces. Our results emphasise the need to combine spatiotemporal shark movement and fisheries overlap with reliable catch reports to assess risks to shark populations accurately. Our results show that the KZN shark nets and drumlines pose the largest relative risk to white sharks out of the fisheries assessed in this study, even though it had the lowest overlap with white shark movement.

One of the fisheries not assessed here, but where we know white sharks are caught, is the recreational sport and trophy angling. Given the high coastal occurrence of juvenile sharks of both sexes in a resident movement state, combined with a fishery that uses equipment to target large sharks, captures are likely sizeable. The Oceanographic Research Cooperative Fish Tagging Project's catch records support this, with 510 records of white

sharks caught over the past 35 years (1984–2020), most before protecting the species in 1991 (Jordaan and Mann, 2020). Furthermore, in one of the identified focus areas, Algoa Bay, a total of 58 white shark catches (1.5–2.5 m total length) were recorded from interviews with shore anglers between July 2009 and December 2011 (Dicken and Booth, 2013). White sharks are caught and released in most cases, but post-survival is unknown, with some records of white sharks washing ashore dead after capture and release (DFFE, unpublished data). The increasing use of technology, i.e. drones and heavy tackle, to target large sharks for sport (Gallagher et al., 2017; Winkler et al., 2022) means that this fishery could be an unknown source of mortality, warranting further investigation.

In addition to the direct risk of capture, fisheries may also have indirect consequences for predator populations in the form of altered trophic interactions or resource competition (Stevens et al., 2000; Piroddi et al., 2011; Grémillet et al., 2018). Negative impacts on marine species from fisheries have mainly been demonstrated for specialist predators or central place foragers that feed on forage fish, e.g. African penguins (Pichegru et al., 2009). However, no published studies so far have demonstrated similar effects on shark populations to the best of our knowledge. Unlike specialist predators, white sharks are generalist predators feeding on a variety of invertebrates, teleosts, chondrichthyans and marine mammals and predate on prey that is most abundant and easy to catch (Cliff et al., 1989; Martin et al., 2005; Kerr et al., 2006; Hussey et al., 2012; Kim et al., 2012; Tamburin et al., 2020). Fishing pressure on prey populations may influence food availability, which could influence shark movement and distribution, but the extent is unknown and needs further investigation. Whether or not fishing impacts white shark survival through resource competition is currently unknown and untested. However, white sharks' generalist diet and diverse movement strategies across several ecosystems, coupled with large, stable Cape fur seal colonies and a range of prey options, increase their resilience to impacts from fisheries. In addition to implementing an ecosystem approach to fisheries management that considers predators' needs (Shannon et al., 2010; Parker et al., 2020), an additional way to mitigate any potential risks from the indirect effect of fisheries is by establishing and effectively managing MPAs.

White Sharks Spend More Time in Marine Protected Areas

Given that white sharks are protected in South Africa, we assume that sharks visiting MPAs benefit from diverse, healthy ecosystems that potentially increase prey availability and have less disturbance. White sharks of both sexes and all age classes spent significantly more time and travelled greater distances inside South African MPAs than can be expected by chance, suggesting a preference for protected areas. This included existing MPAs at the time of tracking and those proclaimed in 2019. In the case of sharks visiting areas that later became MPAs, it is relevant to note that these newer MPAs were designed to expand existing MPAs or represent

highly productive areas that contribute to biodiversity conservation goals with the least impact on competing industries (primarily fishing and mining). Significant use of areas that later became the new MPAs is thus not unexpected, given that their design criteria included known areas of diversity and productivity. There is much scientific debate about the effectiveness of MPAs to conserve large, wide-ranging predators (Breen et al., 2015) like white sharks. However, studies have shown that if positioned in essential breeding or feeding habitats, they can benefit megafauna (Williams et al., 2009; Boerder et al., 2017; Daly et al., 2018). Benefits will depend on the MPA's size, level of protection, the amount of time spent inside MPAs, and the life-history stage protected (Hays et al., 2019; Peñaherrera-Palma et al., 2020). In this study, given that most white sharks were immature, it is likely that these MPAs are important for feeding due to increased prey availability, or for resting, due to less disturbance from anthropogenic activities. Our results contribute to the growing body of evidence that well designed MPAs can benefit large, mobile marine megafauna.

Several coastal MPAs were used by white sharks significantly more than others, namely, the De Hoop, Stillbaai, Tsitsikamma, Addo Elephant, Pondoland, Protea Banks, Aliwal Shoal and uThukela MPAs. We also identified several areas significantly used by white sharks in a resident state that are not yet part of the MPA network. These areas are clear focus areas for marine spatial planning, located in or adjacent to the primary tagging locations of Gansbaai, Struisbaai and Mossel Bay, and not included in MPAs. They may indicate high biodiversity or prey availability, which can be used in MPA expansion, delineating Ecological or Biological Significant Areas (EBSAs) or Critical Biodiversity Areas (CBAs), and in marine area plans as required by South Africa's marine spatial planning legislation. However, some focus areas may not have been identified in this study, e.g. False Bay is a well-known aggregation site year-round (Hewitt et al., 2018; Kock et al., 2013), but only three of the sharks in this study were tagged at this site, and thus it may be under-represented.

Management and Policy Recommendations

South Africa should lead a regional conservation and management plan, given that white sharks move extensively between several Southern African countries. Encouragingly, Mozambique has recently formally protected white sharks from all fisheries alongside other large megafauna (Maritime Fisheries Regulation (REPMAR) — Decree 89/2020). National Plans of Action for Sharks and Shark Biodiversity Plans could be the vehicles for such a plan. Regional marine spatial plans can also facilitate cooperation amongst countries, e.g. the regional marine spatial planning strategy is currently being developed for the Western Indian Ocean by the Nairobi Convention Secretariat of the United Nations Environment Programme. As the fishery reporting the highest catches of white sharks, the KZN bather protection program should continue its ongoing efforts to reduce the number of nets

and drumlines, where possible (Guyomard et al., 2019). In the long-term, lethal methods should be replaced with non-lethal methods (McPhee et al., 2021) and coupled with an education program around shark risk as used in other regions such as Cape Town (Shark Spotters, Kock et al., 2012) or Western Australia (Shark Smart, McAuley et al., 2017). This would have a positive impact on threatened species, including white sharks. Given that the demersal shark longline fishery overlaps with white shark movement, mainly in the resident state, and uses fishing gear that may catch small juveniles, good observer coverage is needed to monitor catches. In the absence of physical observers, a newly established electronic monitoring pilot programme in the demersal shark longline sector should be extended within the sector and to the pelagic longline sector to shed more light on fisheries interactions between these fleets and white sharks. A centralised national database of white shark fishing bycatch risk and mortality across fisheries is also needed to improve population modelling and projections. Lastly, MPAs with a high white shark presence should include white sharks in their biodiversity monitoring programs. Enforcement of current MPAs to safeguard high biodiversity and future MPA expansion efforts may mediate the direct (i.e. capture) and indirect (e.g. resource competition and disturbance) impacts on the Southern African white shark population. Since this study, white sharks have abruptly disappeared from the False Bay and Gansbaai (Hammerschlag et al., 2019, Towner et al. submitted) aggregation sites with sporadic sightings. The reasons for the disappearance are under investigation but emphasise the need for continued monitoring of movement patterns related to environmental and biological drivers and existing and emerging threats. However, the main results from this study and consequently the management recommendations remain relevant.

CONCLUSIONS

By combining animal movement modelling and spatiotemporal analyses of risk exposure from fisheries and protection from MPAs, we have provided policy-relevant results that can be used to inform management interventions. We determined demographic differences in risk exposure, identified the fisheries with the greatest impact relative to spatial or temporal shark exposure and provided a behavioural context for that impact. Our inferences can further refine place-based conservation to protect the most vulnerable demographic groups and ultimately contribute to safeguarding this species from extinction in the southwest Indian Ocean.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: 10.5281/zenodo.5575189.

ETHICS STATEMENT

We collected data according to the South African Department of Environmental Affairs: Oceans and Coasts (now the Department of Forestry, Fisheries and the Environment) protocols and adhered to the legal requirements of South Africa. All research methods were approved and conducted under the South African Department Forestry, Fisheries and the Environment: Oceans and Coasts permitting authority (Permit #RES2012/OCEARCH/umbrella-project).

AUTHOR CONTRIBUTIONS

AAK, TP, ATL, and RD conceptualized the study and the design of the methodology. MM, RJ, CF, AK, PK, EG, AT, OJ, CS, MLD, DI, and MJS collected or contributed data. TP, RD, ATL, VG, and AK analysed and interpreted the data; AK led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.811985/full#supplementary-material>

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The Role of Satellite Telemetry Data in 21st Century Conservation of Polar Bears (*Ursus maritimus*)

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Satellite telemetry (ST) has played a critical role in the management and conservation of polar bears (*Ursus maritimus*) over the last 50 years. ST data provide biological information relevant to subpopulation delineation, movements, habitat use, maternal denning, health, human-bear interactions, and accurate estimates of vital rates and abundance. Given that polar bears are distributed at low densities over vast and remote habitats, much of the information provided by ST data cannot be collected by other means. Obtaining ST data for polar bears requires chemical immobilization and application of a tracking device. Although immobilization has not been found to have negative effects beyond a several-day reduction in activity, over the last few decades opposition to immobilization and deployment of satellite-linked radio collars has resulted in a lack of current ST data in many of the 19 recognized polar bear subpopulations. Here, we review the uses of ST data for polar bears and evaluate its role in addressing 21st century conservation and management challenges, which include estimation of sustainable harvest rates, understanding the impacts of climate warming, delineating critical habitat, and assessing potential anthropogenic impacts from tourism, resource development and extraction. We found that in subpopulations where ST data have been consistently collected, information was available to estimate vital rates and subpopulation density, document the effects of sea-ice loss, and inform management related to subsistence harvest and regulatory requirements. In contrast, a lack of ST data in some subpopulations resulted in increased bias and uncertainty in ecological and demographic parameters, which has a range of negative consequences. As sea-ice loss due to climate warming continues, there is a greater need to monitor polar bear distribution, habitat use, abundance, and subpopulation connectivity. We conclude that continued collection of ST data will be critically important for polar bear management and

conservation in the 21st century and that the benefits of immobilizing small numbers of individual polar bears in order to deploy ST devices significantly outweigh the risks.

Keywords: climate change, conservation, movements, polar bear, radio collar, satellite, telemetry

1 INTRODUCTION

Satellite telemetry (ST) has been widely used to determine the movements, distribution, and habitat selection of mammals, birds and fishes (Hart and Hyrenbach, 2009; Gaidet et al., 2010; Harcourt et al., 2019; Hays et al., 2019; Davidson et al., 2020; Sequeira, 2020). This technology has helped to protect populations, conserve biodiversity, ensure sustainable use, and implement ecosystem-based management by providing data on how animals use the landscape and respond to current or expected environmental changes (e.g., Block et al., 2016). ST data are particularly important for long-lived species that are mobile, difficult to observe directly, or have complex life cycles that complicate other forms of monitoring (e.g., species that feed and reproduce in different locations). In the case of the polar bear (*Ursus maritimus*), a marine carnivore that ranges widely across international boundaries and occurs at low densities across a vast and sparsely populated Arctic (Amstrup, 2003), ST has been a critical research tool for management, conservation, and informing international agreements on environmental protection (PBRs, 2015).

Satellite-linked radio tags (SLRTs), which transmit to polar-orbiting satellites, have been a key tool in the study of polar bears because remote habitats and harsh Arctic conditions preclude the use of other methods (e.g., very high frequency [VHF] signals) that require the transmitter and receiver to be in proximity. As early as 1965, scientists suggested that SLRTs had the potential to provide reliable location data for polar bears, regardless of season or geographic area (PBSG, 1966; Flyger and Townsend, 1968). The first successful use of ST to track polar bears was in 1977 using the NIMBUS 6 satellite system to follow three adult females in Alaska for 8–390 days (Kolz et al., 1980). In 1979, four female polar bears in Lancaster Sound, Canada (Schweinsburg and Lee, 1982) and four bears (one male and three females) in the Greenland Sea (Larsen et al., 1983) were tracked using the NIMBUS 6 system for 40–266 and 18–63 days, respectively. In these studies, the SLRTs were housed in collars that weighed approximately 5 kg and were fastened with a harness consisting of steel cables covered by plastic and rubber tubes. The cables were fastened by a magnesium bolt under the chest to allow for release when the bolt corroded.

Since those initial studies, advances in technology, attachment/release methods, and satellite systems have made SLRTs less cumbersome and improved their ability to remotely monitor polar bears, resulting in widespread and diverse use. Establishment of the Argos Data Collection and Location System in 1978 (CLS, 2016) facilitated ST as a tool for wildlife research (Fancy et al., 1988; Harris et al., 1990; Garner et al., 1994; Belikov et al., 1998; Schwartz and Arthur, 1999; Tomkiewicz et al., 2010), which for polar bears included a new ability to identify

subpopulation boundaries (e.g., Bethke et al., 1996; Taylor et al., 2001; Mauritzen et al., 2002; PBSG, 2018). In the early 2000s, Global Positioning System (GPS) capability revolutionized satellite tracking by providing locations accurate to 30 m (Schwartz and Arthur, 1999; Frair et al., 2010; Tomkiewicz et al., 2010) compared to, at best, 400 m accuracy of Argos locations (Douglas et al., 2012). This allowed for fine-scale analyses of habitat use (Andersen et al., 2008). In 2011, advent of the Iridium satellite system (Iridium Satellite Communications, McLean, Virginia, USA) allowed more data to be transferred at a lower cost than the Argos system (e.g., Thomas et al., 2011; Lone et al., 2018b; Pagano et al., 2020) and enabled two-way communication with SLRTs. This allowed SLRTs to be programmed remotely (e.g., changing the duty cycle) and opened the possibility for release devices that could be triggered by the user. The addition of salt-water sensors, thermometers, accelerometers, and video cameras further extended the types of data provided by SLRTs, allowing detailed behavioral and ecological investigations (Fancy et al., 1988; Lone et al., 2018a; Pagano et al., 2018).

Most SLRTs used in polar bear research have been attached as collars, and almost exclusively to adult female bears as their neck and head morphology maximize retention (**Figure 1**). Subadult bears are generally not collared to avoid potential injury during growth, and adult males are not collared because their necks are larger in circumference than their heads, which causes collars to slip off. Other attachment methods including harnesses, ear-mounted transmitters (Wiig et al., 2017), glue-to-fur transmitters (Rode et al., 2014a), and subcutaneous implants (Mulcahy and Garner, 1999; Amstrup et al., 2001) have been used with limited success.

The International Association for Bear Research and Management (IBA; <https://www.bearbiology.org/>) and the International Union for Conservation of Nature (IUCN) Species Survival Commission (SSC) Bear Specialist Group (BSG) support science-based management and conservation of the world's eight species of bears (IBA, 2009). These groups note that, while alternative or less-invasive methods may be useful in some circumstances, handling and instrumenting bears with SLRTs is essential to address conservation challenges of the 21st century (IBA, 2009). In recent decades, Indigenous communities in parts of the Canadian and United States Arctic have expressed concern about the application of SLRTs on polar bears. Often, opposition to chemical immobilization, handling, and collaring is based on concerns about possible negative physical and behavioral impacts to individual bears, such as collars that become too tight if the bear grows or changes body condition (ITK, 2009; Henri et al., 2010; Wong et al., 2017; AEW, 2019), and on potential health risks to humans who consume the meat of polar bears that have been immobilized

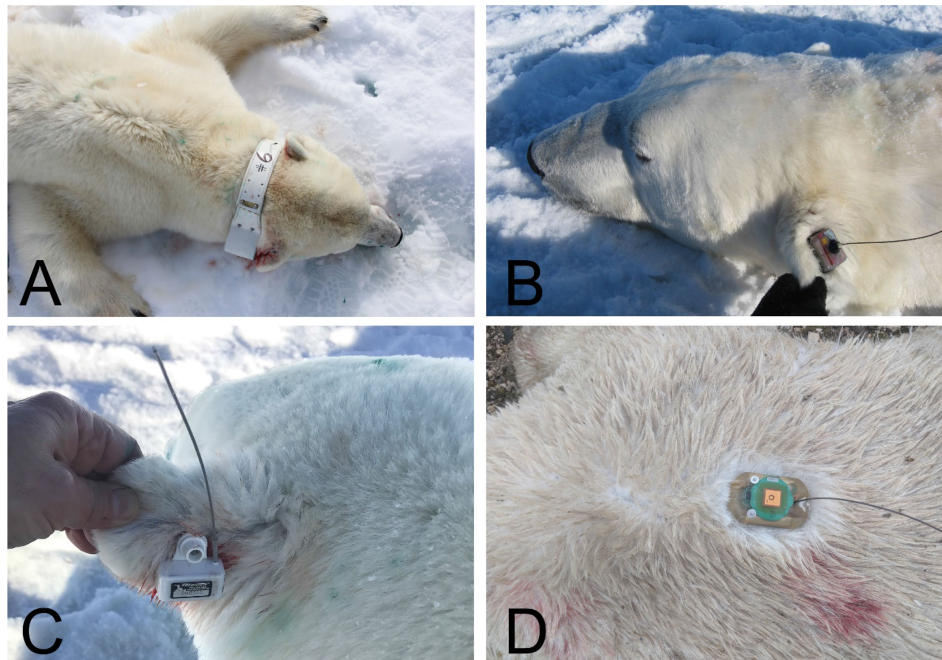


FIGURE 1 | Different types of satellite tags (ST) on polar bears: **(A)**: ARGOS Satellite collar (Telonics), **(B)**: Satellite ear-attached tag (Wildlife Computers, Redmond WA), **(C)**: Satellite ear-attached tag (Telonics), and **(D)**: Glue-on satellite tag (Wildlife Computers, Redmond WA). Collars have been the most robust and reliable way to collect multi-year data from polar bears. Photos by Kristin Laidre **(A)**, George Durner/USGS **(C)** and Karyn Rode/USFWS **(B, D)**.

(Semple et al., 2000). In Svalbard, concerns about the appearance and possible discomfort of collars have been expressed by tourists and the general public. Despite these concerns, no negative effects have been documented in any study focused on addressing them (Messier, 2000; Semple et al., 2000; Thiemann et al., 2013; Rode et al., 2014a; see section 2.1).

For management purposes, the world's population of an estimated ~26,000 polar bears (Regehr et al., 2016) is divided into 19 subpopulations with varying levels of immigration and emigration (PBSG, 2018). Polar bears are distributed widely across remote environments that are already rapidly changing due to sea-ice loss resulting from climate warming, the primary long-term threat to the species (Figure 2, Laidre et al., 2008; Wiig et al., 2008; Amstrup et al., 2010; Kovacs et al., 2011; Castro de la Guardia et al., 2013; Regehr et al., 2016). With an ice-free Arctic predicted to occur in the summer as early as 2034 (Peng et al., 2020), profound changes in the movements and distribution of bears are expected, with attendant challenges to their management and conservation (Atwood et al., 2015). To date, ecological and demographic changes associated with sea-ice loss have been detected for 16 of the 19 subpopulations (noting that changes for some high-latitude subpopulations have not been negative, and that some subpopulations are data deficient; PBSG, 2018). In this paper, we review available information on the effects of chemically immobilizing and attaching SLRTs to polar bears. We examine a suite of scientific areas where ST data have been critical to management and conservation, including the value of auxiliary information collected during ST deployments. We conclude by making the case that ST data from polar bears

will be critical to inform management decisions in the 21st century as climate warming increasingly impacts polar bear subpopulations and as human activities in the Arctic increase. We also discuss potential ways to reduce concerns about possible effects of ST studies on polar bears.

2 BACKGROUND

2.1 Chemical Immobilization and SLRT Deployment

Polar bears must be chemically immobilized to deploy SLRTs (Stirling et al., 1989). Drugs are usually administered *via* helicopter-based darting, although in some areas bears on land are captured in culvert traps or darted from snowmobiles. Ground-darting of polar bears is relatively rare due to safety risks associated with not being able to control the animal's movement from the time a drug is injected to the point at which the animal becomes immobilized. Bears typically remain immobilized and sedated for up to one hour, during which time researchers mark (e.g., using ear tags, tattoos, microchip) or re-identify a previously captured individual, record morphometric data, collect tissue samples, and possibly apply a SLRT.

Since 1985, the most common immobilizing drug for polar bears has been Telazol® (a 1:1 mixture of tiletamine hydrochloride and zolazepam hydrochloride; also sold as Zoletil®; Stirling et al., 1989). Telazol® has proven to be reliable with a high margin of safety (Kreeger and Arnemo, 2012). In the Southern Beaufort Sea

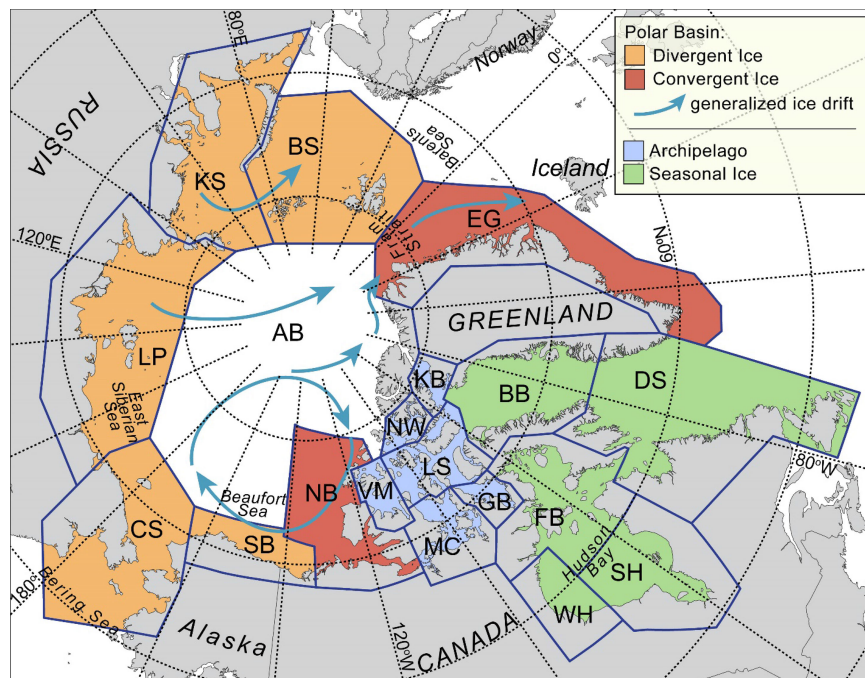


FIGURE 2 | Polar bear ecoregions, 19 subpopulations (AB, Arctic Basin; BB, Baffin Bay; BS, Barents Sea; CS, Chukchi Sea; DS, Davis Strait; EG, East Greenland; FB, Foe Basin; GB, Gulf of Boothia; KB, Kane Basin; KS, Kara Sea; LP, Laptev Sea; LS, Lancaster Sound; MC, M'Clintock Channel; NB, Northern Beaufort Sea; NW, Norwegian Bay; SB, Southern Beaufort Sea; SH, Southern Hudson Bay; VM, Viscount Melville Sound; WH, Western Hudson Bay), and place names mentioned in the text with arrows showing ice drift. Ecoregions as defined by Amstrup et al. (2008).

subpopulation, the mortality rate during chemical immobilization was reduced from 1.4% to 0.1% following a switch from Sernylan to Telazol® (Thiemann et al., 2013; Rode et al., 2014a). Even prior to widespread use of Telazol®, mortality rates during capture and handling were <1% during research in Nunavut and the Northwest Territories, Canada (Messier, 2000). Notably, most deaths of anesthetized bears were due to reasons other than the choice of immobilizing agent (e.g., drowning, dart injury, or being killed by another bear while recovering from anesthesia; Messier, 2000; Rode et al., 2014a).

The persistence of Telazol® in polar bear tissues has been a concern in regions where humans consume polar bear meat. Semple et al. (2000) determined that both Telazol® and its metabolites declined to trace levels in blood serum, kidney, muscle, and adipose tissue of polar bears within 24 hours of dosing, although low levels of metabolites were detectable 11 days after capture. Ryan et al. (2009) in a study of 15 American black bears (*U. americanus*) detected Telazol® in muscle and kidney of one bear, and in the serum of two bears, seven days post-capture; and in the urine of one bear 14 days post-capture. Semple et al. (2000) suggested that a human consuming the meat of a previously immobilized bear would be unlikely to experience the pharmacological effects from Telazol® if it were eaten 24 hours or more post-capture. To avoid any risk of human exposure to metabolites—even though negative human health effects have not been associated with exposure—two studies have suggested avoiding consumption of harvested bear meat within

14 days post-capture (Cattet, 2003; Ryan et al., 2009). Captured polar bears are typically marked with unique numerical identifiers applied as lip tattoos and/or ear tags, and with a more visible but non-permanent mark using fur dye, which can be used to determine if and when a harvested bear was previously immobilized.

Several studies have investigated effects of capture and handling on polar bear behavior and found no long-term negative impacts. Bear movement rates and activity are generally suppressed immediately after capture. Thiemann et al. (2013) and Rode et al. (2014a) showed that polar bear activity and movement rates returned to near-normal levels within 2–3.5 days post-capture, with the majority reaching normal activity and movement within 5 days. Additionally, and importantly, direct observations of polar bears following capture as well as video-camera footage support that bears can successfully kill and eat a seal within 24 hours of capture despite reduced activity and movement (Pagano et al., 2018). Also, Stirling et al., (in press) used approximately 1,800 hours of direct visual observation of polar bears to compare the behavior of animals of the same sex- and age-classes that had, and had not, been previously immobilized. That study found that bears were more likely to sleep, and less likely to hunt, within 48 hours of capture, but no negative behavioral differences were detected beyond that period. Furthermore, Stirling et al., (in press) visually observed three adult bears that successfully killed seals within 50 hours after capture.

Other studies have investigated whether immobilization and handling have longer-term effects on polar bear body condition (i.e., fatness) and reproduction. Rode et al. (2014a) assessed 26 years of capture data in the Southern Beaufort Sea and found no directional change in body condition of 197 polar bears captured 2–10 times (1–2 captures per year). Similarly, the body condition of 309 polar bears captured twice in different years did not differ from the body condition of 734 bears at initial capture (Rode et al., 2014a). Messier (2000) also found no effect of helicopter-based capture on polar bear body condition. Litter size and mass of cubs was unaffected by single or multiple captures of the mother, and capture of the mother was not found to influence cub survival (Amstrup, 1993; Rode et al., 2014a). Further, bears that were captured as dependent young in the spring achieved greater adult body size than bears that were not captured as dependent young (Rode et al., 2014a). These results suggest that effects on activity, movement, and feeding behavior post-capture do not translate to reduced body condition or survival for most sex and age classes. One exception may be pregnant females captured just prior to denning (Lunn et al., 2004). Ramsay and Stirling (1986) and Amstrup (1993) indicated that some pregnant females captured at dens before giving birth relocated to a new den site, while Lunn et al. (2004) found that pregnant polar bears at dens seldom relocated if not disturbed by capture. Capturing females at dens is now largely avoided.

Rode et al. (2014a) also investigated the effects of collaring on polar bear activity and movements, health, and survival of dependent young. Activity and movement rates of collared bears were not different from those wearing glue-to-fur or ear-mounted transmitters, and body condition of females that had worn a collar for one year ($n = 56$) was similar to females that had never worn a collar ($n = 238$; Rode et al., 2014a) (**Figure 3**). Survival of cubs was similar for adult females that had, and had

not, worn a collar the previous year. Currently, all handling of wildlife, including immobilization and deployment of SLRTs on polar bears, must be approved by national agencies and Institutional Animal Care and Use Committees.

2.2 SLRT Types

Various attachment types for satellite transmitters, including collars, glue-to-fur, implants, and ear tags, can be used on polar bears (**Figure 1**). There are trade-offs between retention, operational life, data quality, and the animal's tolerance of the different attachment types. Collars are most frequently used because their size (currently ~1.5 kg; <https://www.telonics.com/>) can accommodate a battery that provides high-quality data for > 1 year (e.g., Amstrup et al., 2004). For an adult female of 200–300 kg, a collar represents 0.5–0.8% of the bear's mass. Additionally, collars allow for the attachment of devices for monitoring behavior, such as video cameras and activity sensors with high spatial and temporal resolution (e.g., Whiteman et al., 2015; Pagano et al., 2018). Although collars are usually only deployed on adult females (**Figure 4**), glue-to-fur and ear-mounted transmitters can be deployed on subadults and adults of both sexes. However, low battery capacity associated with the small size of ear-mounted transmitters (≤ 70 g) and the propensity of bears to remove the transmitters has resulted in a mean functional life of 70 days (Wiig et al., 2017), which is too short to evaluate seasonal patterns in movements and habitat use. Additionally, Wiig et al. (2017) reported injuries to ear pinna resulting from ear-mounted transmitters being forcefully removed (e.g., during intraspecific interaction or while hunting). The use of subcutaneous SLRTs implanted in the dorsal cervical region with a percutaneous antenna was attempted on seven adult male polar bears in 1996 and 1997, with limited success (Mulcahy and Garner, 1999; Amstrup et al., 2001). There have been no attempts to use implanted transmitters on polar bears since 1997.



FIGURE 3 | A satellite-collared female polar bear in East Greenland feeding on a harp seal kill in July 2019. This bear was captured, and the collar deployed two years before the photo was taken. This bear would score high on a body condition index. Several scientific studies have demonstrated that the presence of satellite telemetry devices does not impact body condition over the long term. Photo by Nick Cobbing.

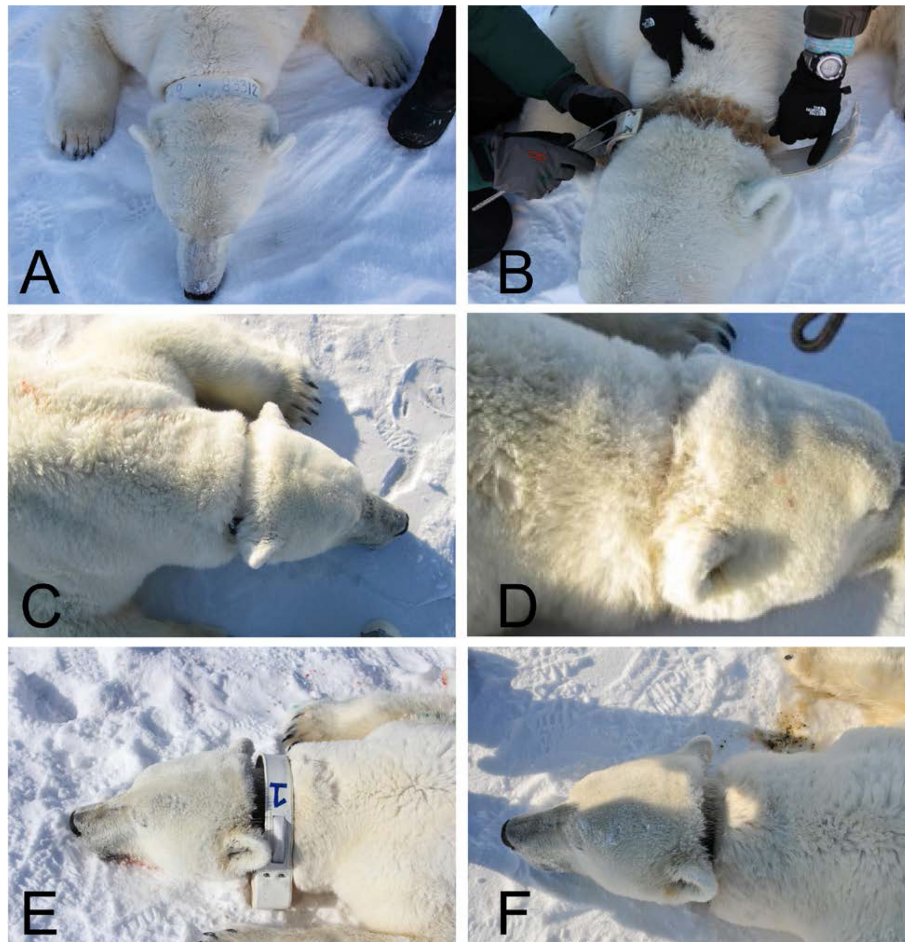


FIGURE 4 | (A-F). Three adult female polar bears shown when satellite telemetry collar was deployed (left) and when it was removed (right). **(A, B)** show bear D24042 from East Greenland after one year. **(C, D)** show bear X35260 from Kane Basin after two years, and **(E, F)** show bear D7388 from Baffin Bay after four years. Satellite telemetry collars can be deployed for different durations and controlled by release mechanisms or removal upon recapture. Discoloration is matted hair under the collar.

3 A REVIEW OF THE ROLE OF ST DATA IN PAST POLAR BEAR MANAGEMENT AND CONSERVATION

3.1 Subpopulation Delineation

Pedersen (1945) suggested that polar bears undertook long migrations around the Polar Basin, and early scientific debate focused on whether there was one or more polar bear populations across the Arctic (e.g., Lentfer, 1972; Vibe, 1976; Larsen and Stirling, 2009). Investigations using locations of captured and marked bears as well as data from VHF radio collars on adult females facilitated the delineation of multiple subpopulations resulting from seasonal fidelity to localized areas and natural obstacles to movement (e.g., land masses; Taylor and Lee, 1995). ST data have been used to quantify exchange among subpopulations (Mauritzen et al., 2001; Laidre et al., 2018a) and identify occasional long-distance movements across subpopulation boundaries of up to 5,000 km in one year

(Durner and Amstrup, 1995; Bethke et al., 1996; Taylor et al., 2001; Mauritzen et al., 2002; Amstrup et al., 2004; Obbard and Middel, 2012; Scharf et al., 2019) (**Figure 5**). ST data also have been used to understand how bear distributions change as sea-ice loss progresses (Durner et al., 2019; Pagano et al., 2021) and ensure that management practices are applied to demographically relevant groupings of animals (e.g., Laidre et al., 2015; Lone et al., 2018a; Lone et al., 2018b). For example, Amstrup et al. (2004) used ST data to develop contours describing the probability that bears belonged to the Southern Beaufort Sea or Chukchi Sea subpopulation. Scharf et al. (2019) expanded methods for subpopulation delineation into a Bayesian framework that accounted for selection by bears of dynamic sea-ice habitats. Both ST and genetic methods (Paetkau et al., 1999; Peacock et al., 2015; Viengkone et al., 2016) have been used to understand the degree to which individual subpopulations are isolated (Bethke et al., 1996; Mauritzen et al., 2001; Taylor et al., 2001), which can affect

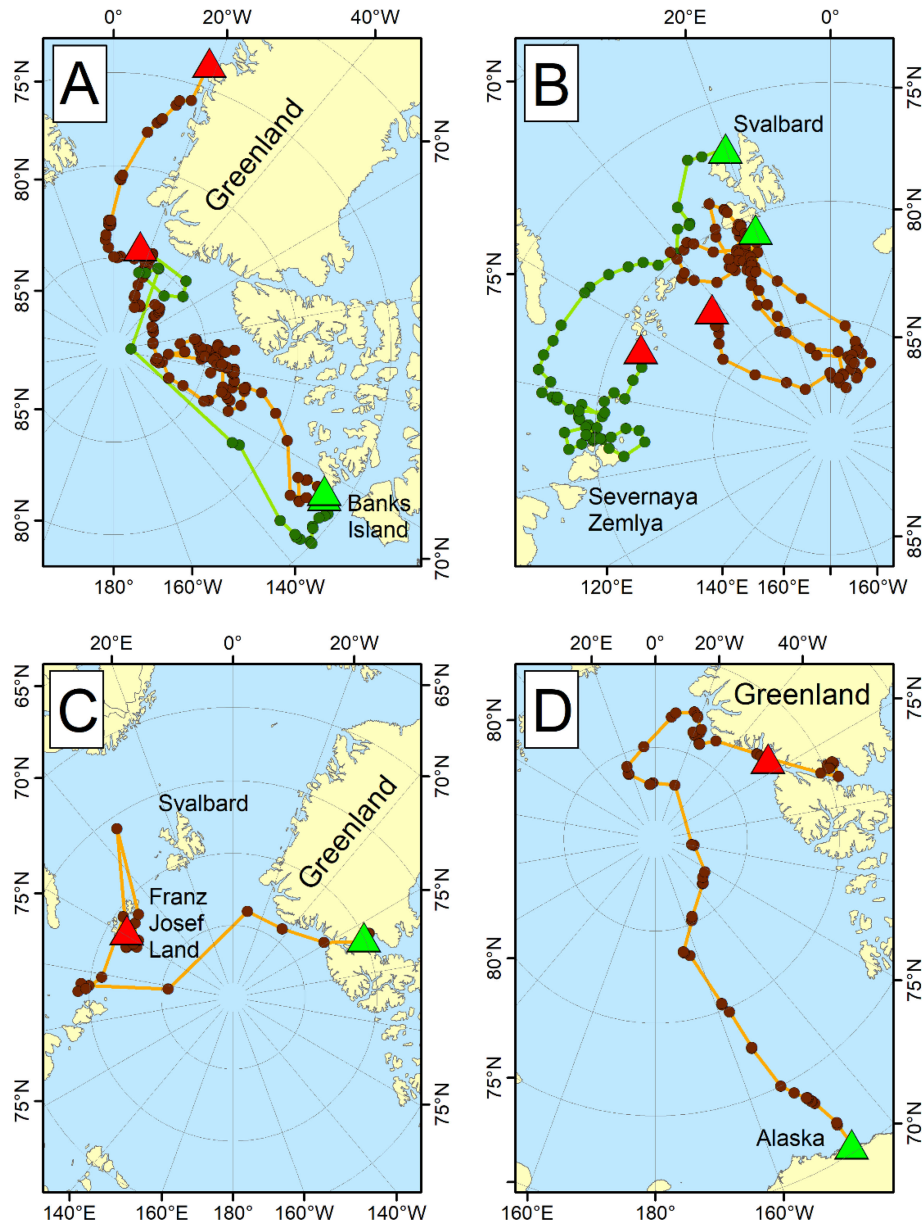


FIGURE 5 | Long-distance movements of satellite-collared adult female polar bears across subpopulation boundaries, with green triangles showing start locations and red triangles showing end locations. Data shown for **(A)** two bears tagged in the Northern Beaufort Sea, one of which traveled to northern Greenland from May to October 1993 (green dots), and the other to eastern Greenland from April 1993 to February 1995 (brown dots; Lunn et al., 1995); **(B)** two bears tagged in the Barents Sea, one of which moved from Svalbard to Severnaya Zemlya in the Kara Sea from April to November 2013 (green dots), and another that moved from Svalbard into the Arctic Basin from April 2014 to September 2015 (brown dots; Aars, unpublished data); **(C)** one bear tagged in Kane Basin between April 2013 and 2015 crossed the Arctic Basin to Franz Josef Land in the Barents Sea (Laidre et al., 2020b); and **(D)** one bear tagged in the Southern Beaufort Sea between May 1992 and December 1993 traveled across the Arctic Basin to Greenland (Durner and Arnstrup, 1995). Distances moved by polar bears in these figures are upwards of 3,500 km across the polar basin.

population viability (e.g., *via* source-sink dynamics or small-population effects).

3.2 Abundance and Demography

Estimates of polar bear abundance are used to monitor subpopulation trend and inform management, including

estimation of sustainable harvest (e.g., Lunn et al., 2016; Stapleton et al., 2016; Obbard et al., 2018; Regehr et al., 2018). Estimates of vital rates (e.g., reproduction, survival) and their relationship with environmental conditions are needed to evaluate subpopulation viability and the demographic effects of sea-ice loss (e.g., Hunter et al., 2010; Regehr et al., 2010). ST data

also have been essential in many demographic analyses to clearly define demographic parameters (e.g., to distinguish between mortality and emigration) and to model nonrandom movements of bears in and out of sampling areas, which lead to substantive bias—usually negative—in parameter estimates (Regehr et al., 2009; Peñaloza et al., 2014).

For example, Regehr et al. (2018) used ST data to model the movement of bears with respect to a geographically limited sampling area in the Chukchi Sea subpopulation, leading to the first biologically plausible estimates of survival and abundance, which were subsequently used to inform harvest management (Regehr et al., 2021b). Similarly, in the Southern Beaufort Sea, ST data were used to model transitions between geographic regions (i.e., “states”) of the study area to help explain heterogeneity in recapture probabilities (Bromaghin et al., 2021). In the Barents Sea subpopulation, ST data were used to design large-scale aerial surveys (Aars et al., 2009; Aars et al., 2017) and extrapolate density estimates to areas not covered by line-transects with a ratio estimator based on the locations of collared females at the time of the survey. In Aars et al. (2017), ST data were used to estimate the number of bears that were swimming and therefore not detectable. Availability of ST data also ensured ecotype-specific movements did not result in biased abundance estimates (Aars et al., 2017).

During an assessment of the Baffin Bay and Kane Basin subpopulations, current and historical ST data showed that both subpopulations had redistributed due to sea-ice loss (Laidre et al., 2018a; Laidre et al., 2018b; Laidre et al., 2020a; Laidre et al., 2020b; Atkinson et al., 2021). Further, for Baffin Bay, ST data identified that the definition of this subpopulation had changed over time because capture-recapture studies in the 1990s did not fully sample the subpopulation’s autumn range. Without this information, comparison of abundance estimates between the 1990s and 2010s would have led to a biased assessment of subpopulation trend.

3.3 Habitat Use

ST data have been instrumental in understanding the relationships between polar bears and their habitats. Wiig (1995) noted large variation in home range size of female polar bears in the Svalbard area of the Barents Sea subpopulation, and Mauritzen et al. (2001) reported females in this subpopulation belonged to one of two ecotypes. “Coastal” bears use land in Svalbard much of the year, as well as nearby sea ice when seasonally available; whereas “pelagic” bears travel longer distances and use the marginal ice zone (MIZ) most of the year. Mauritzen et al. (2003) also found that habitat selection among Barents Sea bears depended on female reproductive status. Further, Brun et al. (2021) identified that coastal females showed high fidelity to local areas within Svalbard, with close relatives using overlapping home ranges. Similar patterns have been shown in East Greenland (Laidre et al., 2015).

Resource selection functions (RSFs, Manly et al., 2002) using ST data have identified three key physical features that define important polar bear habitat: medium to high sea-ice concentrations (Arthur et al., 1996; Ferguson et al., 2000a; Durner et al., 2004; Durner et al., 2006; Durner et al., 2009;

Wilson et al., 2014; Laidre et al., 2015; McCall et al., 2016; Lone et al., 2018b), sea ice cover that exceeds 50% sea-ice concentration (Durner et al., 2004; Durner et al., 2006; Durner et al., 2009; Laidre et al., 2015; Lone et al., 2018b), and sea ice over the biologically productive continental shelves (Durner et al., 2004; Durner et al., 2006; Durner et al., 2009; Wilson et al., 2014; Lone et al., 2018b; Laidre et al., 2018b). RSFs also have identified finer-scale habitat selection based on ice type (e.g., landfast, drift ice), sea-ice stage (i.e., thickness and age; Ferguson et al., 2000a), sea-ice form (i.e., floe size; Ferguson et al., 2000a; Durner et al., 2004), chlorophyll-a concentration (Wilson et al., 2014), and proximity to glacier fronts (Freitas et al., 2012; Hamilton et al., 2017). Activity sensor data from SLRTs have been used to identify differences in activity patterns associated with habitat, such as a decline in activity when polar bears are in suboptimal habitats, likely in response to reduced prey availability (Whiteman et al., 2015; Ware et al., 2017).

For subpopulations with extensive or complete summer sea-ice melt, the distribution of ST locations relative to the timing and duration of breakup or freeze-up, average sea-ice concentration, and spatial extent of ice-free waters, have been used to infer the timing of movement of polar bears to and from land (e.g., Regehr et al., In Review; Stirling et al., 1999; Atwood et al., 2016b; McCall et al., 2016; Laidre et al., 2020a). ST data have been used to identify the environmental thresholds that trigger long-distance swimming (Pagano et al., 2012; Pilfold et al., 2017; Lone et al., 2018a), quantify the energetic costs of occupying an increasingly fractured and mobile sea-ice platform (Auger-Méthé et al., 2016; Durner et al., 2017; Lone et al., 2018a; Pagano et al., 2018; Pagano et al., 2020) (**Figure 6**), and compare the energetic demands on females with different habitat use strategies (Blanchet et al., 2020). For multiple subpopulations, ST data have shown an increasing frequency of short- and long-distance swims (i.e., >50 km) associated with foraging and migrating to land during the annual open-water period (Pagano et al., 2012; SWG, 2016; Pilfold et al., 2017; Lone et al., 2018a).

RSFs using ST data also have been used to make inference about regions used by polar bears but not accessible to humans (e.g., Durner et al., 2009; Wilson et al., 2016; Lone et al., 2018b; Durner et al., 2019) (**Figure 7**), for example by extrapolating habitat-specific polar bear densities to remote areas that could not be directly sampled (Regehr et al., 2018). Also, projections of polar bear habitat to inform the decision to list polar bears as “threatened” under the U.S. Endangered Species Act relied heavily on ST data (USFWS, 2008), as did the definition of critical habitat for polar bears in the Alaskan Beaufort and Chukchi seas (Durner et al., 2009; USFWS, 2010).

3.4 Maternal Denning

General patterns in polar bear denning have been determined by combining information from scientists and Arctic Indigenous residents (e.g., Harington, 1968; Larsen, 1972; Uspenski and Kistchinski, 1972; Lentfer and Hensel, 1980; Larsen, 1985; Stishov, 1991; Stirling and Andriashek, 1992; Van de Velde et al., 2003; Derocher et al., 2011; Aars, 2013), with ST data playing a critical role in reducing bias and uncertainty around denning habitat and locations (Lunn et al., 2004; Yee et al., 2017;

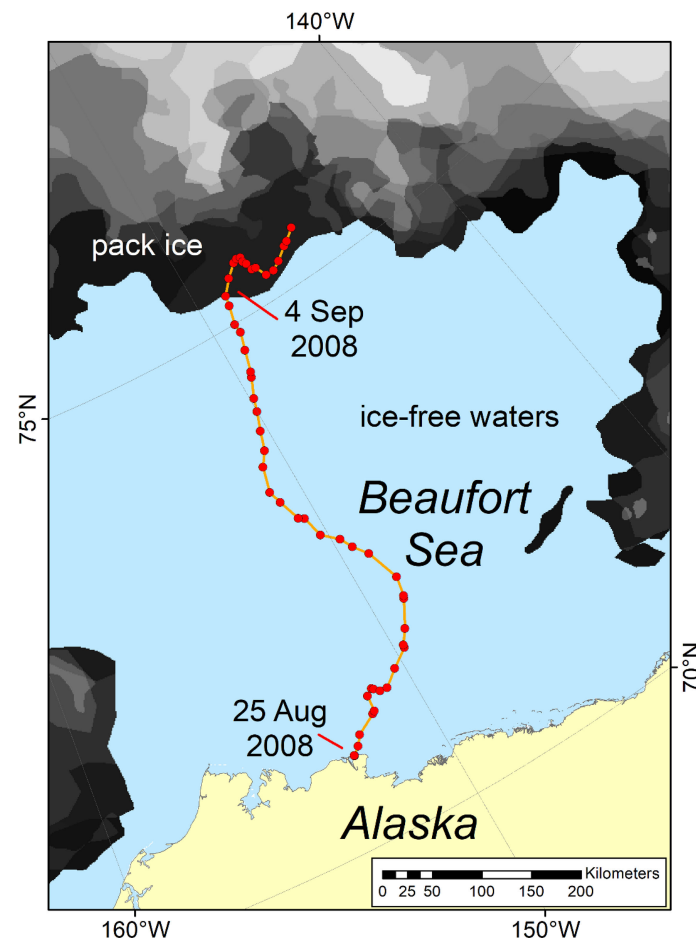


FIGURE 6 | Track of a satellite-collared adult female polar bear that swam north from Alaska (Southern Beaufort Sea subpopulation) through ice-free waters from 25 August to 4 September 2008. For details see Durner et al. (2011).

Escajeda et al., 2018; Durner et al., 2020). ST data have been used to identify “core” denning areas (Harington, 1968), such as Wrangel Island (Rode et al., 2018), Svalbard (Andersen et al., 2012), the Beaufort Sea (Amstrup and Gardner, 1994), the north-central region of the Canadian Arctic Archipelago (Messier et al., 1994), East Greenland (Born et al., 1997; Wiig et al., 2003; Laidre et al., 2015) and Hudson Bay (Lunn et al., 2004; Yee et al., 2017). ST data also have been combined with snow-drift models to predict optimal denning habitat (Merkel et al., 2020).

Temperature and activity sensors on ST collars (Fancy et al., 1988; Ware et al., 2015) have provided data on den entrance and emergence dates based on changes in temperature and activity (e.g., Messier et al., 1994; Wiig, 1995; Lunn et al., 2004; Fischbach et al., 2007; Andersen et al., 2012; Olson et al., 2017). This has allowed comparisons of denning phenology across the polar bear range, including identifying that polar bears in high latitudes enter dens earlier in autumn, sometimes enter temporary dens to shelter from brief periods of intense cold, and exit later in spring (Messier et al., 1994; Ferguson et al., 2000b; Escajeda et al., 2018) compared to bears at lower latitudes (Amstrup and Gardner,

1994; Lunn et al., 2004; Rode et al., 2018a). Wiig (1995) used the denning frequency of individual females in the Svalbard area over multiple years to deduce if they had reproduced successfully, which allowed estimation of reproductive rates.

ST data collected over 30 years from satellite collared bears in the Southern Beaufort Sea have revealed a shift in the distribution of maternal dens from ice to land (Fischbach et al., 2007; Olson et al., 2017) as the stability of sea ice decreased (e.g., Durner et al., 2017). Atwood et al. (2016b) examined ST data collected from 1986 to 2014 and found that the proportion of collared bears coming ashore increased from ~6% prior to 1999 to ~20% from 2000–2014 and the mean length of stay on land increased by 31 days. Further, empirical relationships between sea-ice availability and the duration and proportion of bears summering (Stirling et al., 1999; Rode et al., 2015; Atwood et al., 2016b; Cherry et al., 2016) and denning onshore (Fischbach et al., 2007; Olson et al., 2017) have been used to model the effects of changing energetics on polar bear reproduction and survival (Molnár et al., 2011; Robbins et al., 2012; Molnár et al., 2014; Molnár et al., 2020).

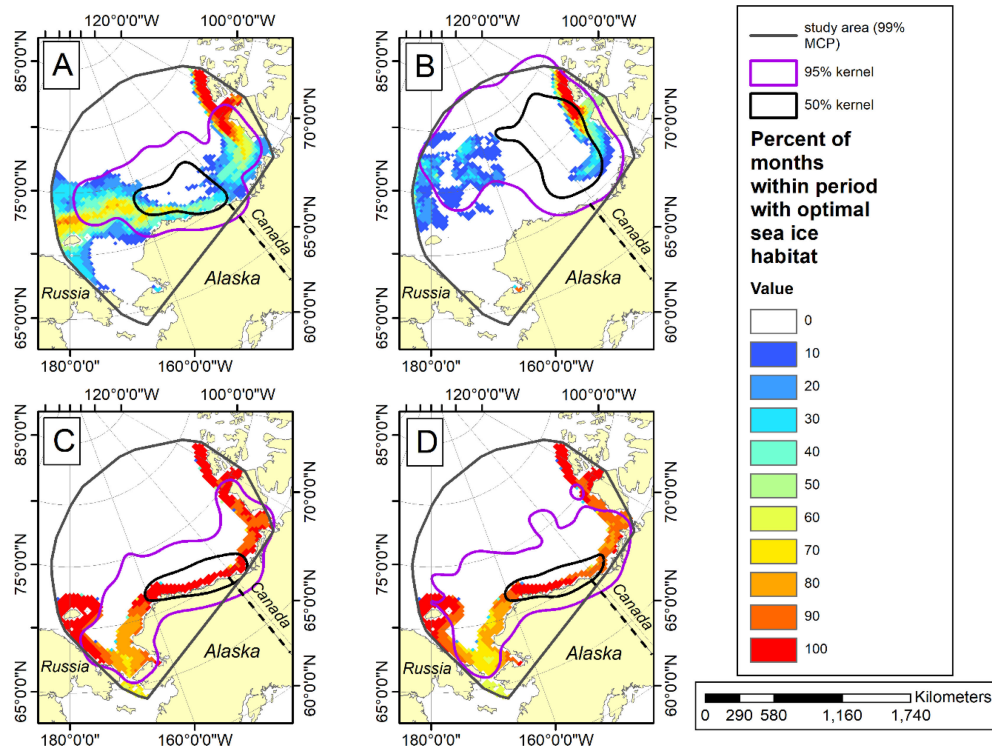


FIGURE 7 | Optimal sea ice habitat (Durner et al., 2019) color-coded by percentage of months with optimal sea ice habitat. The 95% and 50% kernel utilization distributions (contours) show the seasonal distribution of adult female polar bears instrumented with satellite-linked collars in the Southern Beaufort Sea during minimum (summer) and maximum (winter) ice extent for two periods (1985-1995 and 2007-2016). **(A)** summer ice extent season for 1985-1995 and **(B)** for 2007-2016; **(C)** winter ice extent season for 1985-1995 and **(D)** for 2007-2016. For details see Durner et al. (2019).

3.5 Nutritional Ecology and Health

Data collected when immobilizing individual polar bears to deploy SLRTs, including body measurements and samples, provide critical insights into population status and health. Studies using these data have identified mechanisms by which movements and habitat use affect body condition (Stirling et al., 1999; Laidre et al., 2020a; Laidre et al., 2020b; Blanchet et al., 2020), pathogen exposure (Atwood et al., 2017), immune function (Whiteman et al., 2019), diet (Rogers et al., 2015; Tartu et al., 2018; Boucher et al., 2019; Blévin et al., 2020) and energetics (Whiteman et al., 2015; Ware et al., 2017; Pagano et al., 2020; Blanchet et al., 2020). Further, these data have identified the mechanisms by which environmental change has affected individual health and population vital rates (e.g., Stirling et al., 1999; Rode et al., 2014b; Obbard et al., 2016; Pagano et al., 2018).

Divergent space-use strategies identified by ST, together with diet and health data obtained during captures, can be combined for understanding linkages between polar bear energetics, behavior, and pollutant and pathogen exposure (Atwood et al., 2017; Tartu et al., 2018; Blanchet et al., 2020; Blévin et al., 2020). Information on land use combined with diet and energetics studies in the Southern Beaufort Sea indicate that the majority of the subpopulation summers on the sea ice where prey access is

reduced and bears are largely fasting (Whiteman et al., 2015; Atwood et al., 2016b; Ware et al., 2017) whereas a smaller subset of the population summers on shore where they benefit from access to subsistence-harvested bowhead whales (*Balaena mysticetus*) (Rogers et al., 2015). Identifying these divergent behaviors and their potential impacts on vital rates aids in developing and interpreting population models.

Studies have also identified regions and habitat use patterns associated with higher contaminant loads (Olsen et al., 2003; van Beest et al., 2016; Tartu et al., 2018; Blévin et al., 2020) and greater pathogen exposure (Atwood et al., 2017). For example, polychlorinated biphenyls and perfluoroalkyl substances were higher in Barents Sea polar bears that occupied larger offshore home ranges than in bears that used coastal areas in the Svalbard archipelago (Olsen et al., 2003; van Beest et al., 2016), which was further linked to variation in diet, energy needs and proximity to pollutant sources (Tartu et al., 2018; Blévin et al., 2020). In the Southern Beaufort Sea, plasma concentrations of some contaminants (i.e., chlordanes) were lower in land-based bears compared to the offshore ones (Atwood et al., 2017).

3.6 Anthropogenic Disturbance

ST data have been used in observational (Amstrup, 1993) and simulation studies (Wilson and Durner, 2020) on the response of

polar bears to disturbances associated with oil and gas extraction (e.g., Amstrup et al., 2006; Wilson and Durner, 2020). In Alaska, the Arctic coastal plain and nearshore region is home to a large industrial footprint (i.e., Prudhoe Bay and Kuparuk oil fields, the National Petroleum Reserve-Alaska [NPR-A], the Beaufort Sea Oil and Gas Lease Sale Area) (**Figure 8**). Legislation passed in 2017 (public law no. 115-97) included a provision to open the 1002 Area of the Arctic National Wildlife Refuge (ANWR) to oil and gas exploration, which may lead to increased human activity in key denning areas of the Southern Beaufort Sea subpopulation. For several decades, records of maternal den locations in Alaska (including those from ST) have been aggregated into a database that is used by industrial operators to plan winter activities to mitigate disturbance of denning bears (Durner et al., 2020). These data also have been used to monitor the proportion of land-based dens in areas of management interest including the NPR-A, the Prudhoe Bay and Kuparuk oil fields, and in the ANWR (Atwood et al., 2020).

ST data have shown increasing overlap between human activities and polar bear maternal denning as resource exploration in the Arctic expands (Amstrup and Gardner, 1994) and more polar bears use land for summering and maternal denning (Fischbach et al., 2007; Atwood et al., 2016b). Wilson and Durner (2020) used ST data to estimate the incidental take of denning polar bears caused by winter hydrocarbon seismic surveys in ANWR, as required for compliance with the U.S. Marine Mammal Protection Act (16 U.S.C. 1361). Thirty years of ST data on den distribution, denning habitat, and den entrance and emergence dates were critical for designing seismic surveys that reduced the numbers of bears disturbed. More broadly, ST data have been used to understand and mitigate (Regehr et al., In Review; Atwood et al., 2016a) an increasing number of human-bear conflicts

resulting from the loss of Arctic sea ice (Derocher et al., 2004; Schliebe et al., 2008; Towns et al., 2009; Moshøj, 2014; Wilder et al., 2017).

4 HOW WILL SATELLITE TELEMETRY BE CRUCIAL FOR CONSERVATION IN THE 21ST CENTURY?

Depending on the subpopulation, scientific studies to inform polar bear management can cost upwards of 1 million US dollars for one field season (e.g., collection of 100 genetic biopsy samples from a helicopter). Conducting these studies without concurrently collecting ST data is inefficient and leaves managers without information needed to understand the ecological and demographic status of a subpopulation. The importance of ST data will grow as the Arctic changes under climate warming. Here, we discuss crucial applications of ST data in the 21st century, which include designing effective studies, estimating demographic parameters, managing harvest, designating protected areas, improving public safety, forecasting future subpopulation status, and complying with national and international protected species legislation (**Figure 9**).

4.1 Maximizing Data Collection Under Deteriorating Field Conditions

Climate warming—a key threat driving the need for current information on polar bears—is making scientific research more difficult. Over the last decade, the cost and risks to human safety in studying polar bears have increased. In some parts of their range, bears are less accessible during the spring and summer when research has typically occurred, due to sea



FIGURE 8 | A polar bear walking through oilfield infrastructure near Prudhoe Bay on the Arctic coastal plain of Alaska, which is home to a large industrial footprint. Photo credit: BP Exploration (Alaska), Inc., with permission.

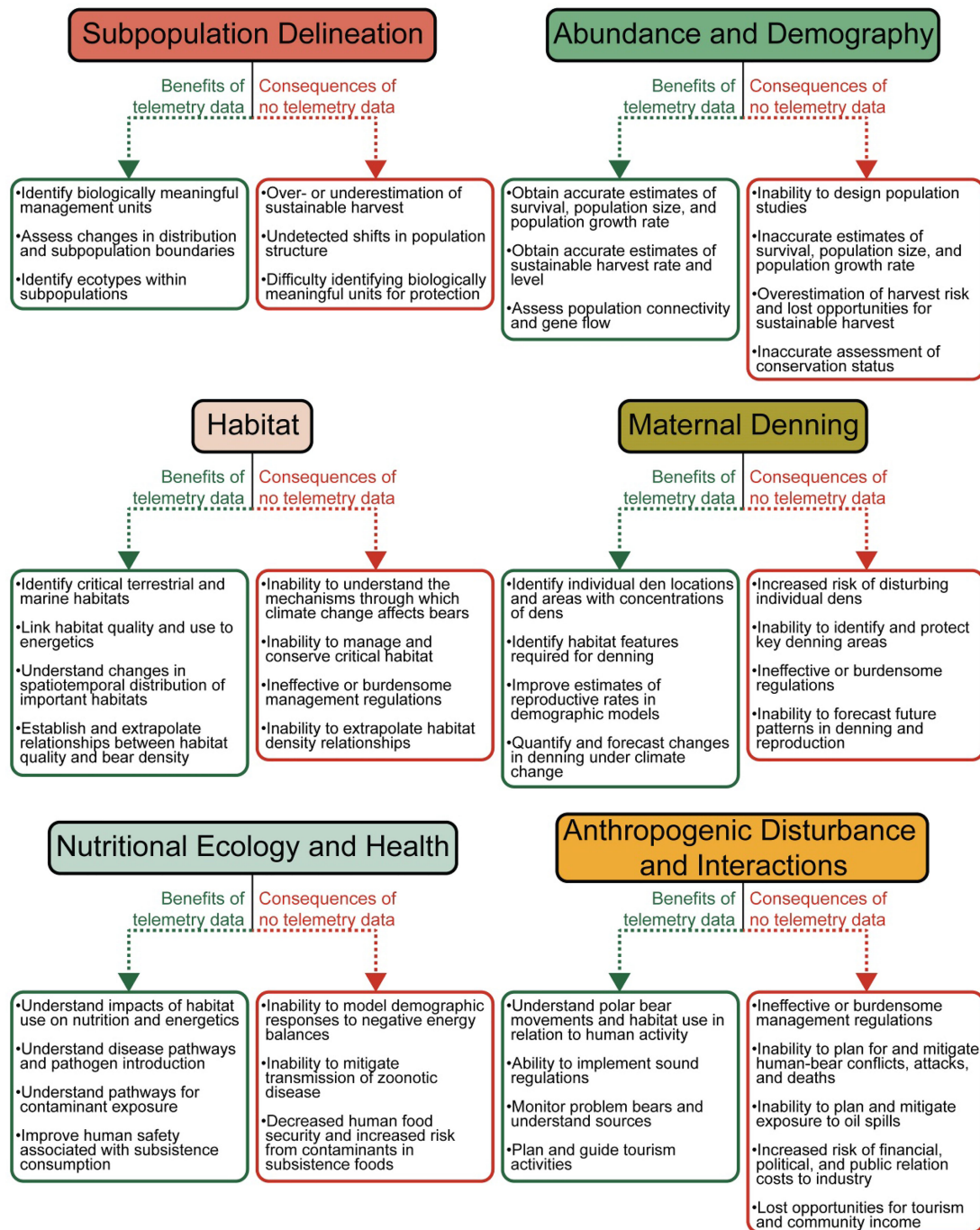


FIGURE 9 | Overview of the uses of satellite telemetry data for conservation and management of polar bears, together with the consequences of not having satellite telemetry data.

ice that is too thin or unstable to work on and fly over. Seasonal windows for sampling bears on their sea-ice habitat have shrunk (Stern and Laidre, 2016) and the number of days with poor weather has increased (Hasemyer, 2021). Thus, opportunities to continue the type of long-term research programs that have been

key to understanding aspects of polar bear ecology and demography to date (e.g., Bromaghin et al., 2021) are disappearing. ST will become increasingly important as future research and monitoring efforts rely on sampling smaller numbers of animals.

Additionally, in the last decade, there has been a shift away from physical-capture studies and toward less-invasive sampling methods (e.g., genetic sampling using biopsy darting, distance-sampling aerial surveys), which also facilitate the collection of fewer basic life-history data useful for demographic modeling. Thus, contemporary ST data have been, and will continue to be, critical to designing less-invasive studies as sea-ice conditions deteriorate and polar bear distribution changes.

4.2 Estimating Subpopulation Abundance When Boundaries Are Changing

The importance of ST data in demographic studies will increase as climate warming alters polar bear habitat use, distribution, and subpopulation connectivity. Due to the high mobility of polar bears and difficulty sampling remote Arctic regions, the number of bears within an area at any given time can differ from the total number of bears that use the area over multiple years (e.g., Regehr et al., 2018). Lack of ST data will likely lead to increased bias in demographic parameter estimates and increased difficulty in defining the study population and distinguishing between changes in space use and changes in the overall number of bears. Without ST data, it will not be possible to model movements in and out of the sampling area and reduce bias associated with non-random temporary emigration (Regehr et al., 2018; e.g., **Figure 10**). It also will not be possible to extrapolate to unsampled areas and interpret changes in estimated abundance over time (i.e., delineating true change in abundance from changes in distribution); see section 3.1.

Without ST data or methods to correct estimates of abundance for polar bear movements, managers can expect bears may be “double-counted” in capture-recapture studies of adjacent subpopulations that experience immigration and emigration. This can artificially inflate abundance estimates,

resulting in overharvest or misapplication of policy decisions that require accurate estimates of abundance, such as negligible impact determinations under the U.S. Marine Mammal Protection Act.

4.3 Improving Harvest Management in a Warming Arctic

ST data will be integral to identifying sustainable strategies for subsistence harvest (as well as guided sport hunting, where allowed) under climate change. The biological effects of human-caused removals (i.e., the combination of subsistence harvest, defense kills, and other sources of direct human-caused mortality) on polar bear subpopulations are evaluated with demographic models that use estimates of reproduction, survival, and abundance (e.g., Taylor et al., 2008; Regehr et al., 2017). Accurate assessment of harvest effects requires the ability to identify demographically meaningful groups of bears and obtain unbiased demographic inputs which, as discussed above, often require ST data. This will become increasingly important as polar bears exhibit variable responses to climate change, which necessitates subpopulation-specific harvest assessments. For example, the previous standard application under stable environmental conditions of a 4.5% harvest rate at a 2:1 male-to-female ratio (Taylor et al., 1987; Regehr et al., 2021a; Regehr et al., 2021b) may not be supportable in the future for some subpopulations. Furthermore, modern methods to evaluate harvest use stochastic frameworks where larger uncertainty (e.g., environmental, statistical, model-based) often translates into increased risk of negative demographic effects, which can lead to lower harvest levels aimed at reducing risk. In the Southern Hudson Bay (SH) subpopulation, lack of ST data made it difficult to confirm whether declining abundance estimates, obtained from sequential aerial surveys (Obbard et al., 2015; Obbard et al., 2018), were caused by declines in

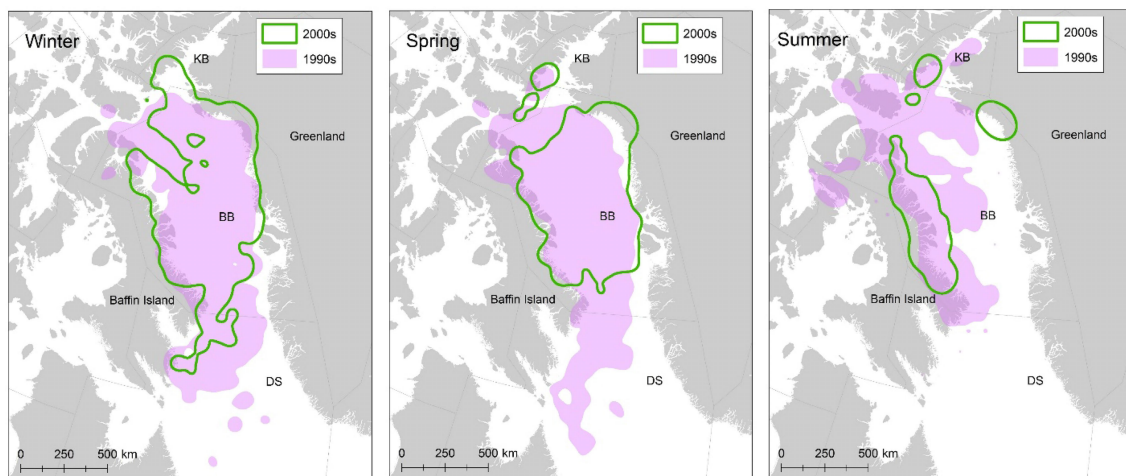


FIGURE 10 | Satellite telemetry data allow for identifying shifts in polar bear space use over time and have proven critical to interpreting data collected during population assessments (e.g., Laidre et al., 2020a). These data from the Baffin Bay subpopulation demonstrated large shifts in seasonal space use over two decades.

polar bear numbers or changes in polar bear distribution. This uncertainty was propagated through a quantitative harvest risk assessment (Regehr et al., 2021a).

4.4 Forecasting the Future of the Species and Complying With Protected Species Legislation

ST data are needed to build RSFs (see section 3.3) that identify essential habitats and project their future availability under different greenhouse gas emission scenarios (Amstrup et al., 2010; Atwood et al., 2016a). Habitat assessments are a fundamental requirement for implementation of protected species legislation in a warming Arctic. Article II of the 1973 Agreement on the Conservation of Polar Bears requires the contracting parties to “take appropriate action to protect the ecosystems of which polar bears are a part, with special attention to habitat components...”. Furthermore, the Polar Bear Range States Circumpolar Action Plan (CAP) considered goals for defining essential habitat and multiple other agreements on polar bears (e.g., Article 2 of the U.S-Russia Polar Bear Agreement; United States T. Doc. 107-10) require the identification and conservation of key polar bear habitats. Projections of future polar bear habitats will also require ST data combined with projections of pollutant transport to and dynamics in Arctic ecosystems to predict future exposure to contaminants.

4.5 Reducing Disturbance and Human-Bear Interactions in a Warming Arctic

Sea-ice decline has led to increases in commercial shipping and made coastal and offshore industrial development more economically viable (Smith and Stephenson, 2013; Eguíluz et al., 2016). For example, the Mary River iron ore mine on Baffin Island (Nunavut, Canada) ships to worldwide markets at a rate of one freighter every 48 h from July through October and is planning for an eventual increase to 3 ships per day, during the period of sea-ice formation (Nunavut Impact Review Board, 2009; Baffinland Iron Mines Corporation, 2018). Increased shipping will lead to direct disturbances of polar bears. ST data from collared adult females will be critical to evaluate this (e.g., Born et al., 2011; Born et al., 2012).

Using ST data to establish empirical relationships between reduced sea ice and increased land use by polar bears will be important for projecting interactions with humans and developing mitigation plans. Declines in sea-ice habitat are resulting in a growing reliance on terrestrial habitat for resting during summer and fall and for maternal denning in winter. This will pose challenges to balancing industrial development and human safety with polar bear conservation (Stirling et al., 1999; Cherry et al., 2013; Rode et al., 2015; Atwood et al., 2016b). As bears spend more time on land (Regehr et al., In Review), they will become increasingly vulnerable to anthropogenic stressors, particularly those associated with industrial activities (Atwood et al., 2016a).

Several new ST applications have potential to monitor and mitigate the risk of human-polar bear conflict. For example, in Churchill, Manitoba, ear-mounted transmitters are being

deployed on polar bears captured in town to determine whether those bears travel north and contribute to the increasing number of human-bear interactions in coastal communities along the Kivalliq, Nunavut coast of Hudson Bay (Government of Manitoba unpublished data). Elsewhere, real-time bear location data are being used to alert communities when bears are approaching. In Longyearbyen, Svalbard, geo-fenced ST collars have been deployed to provide alerts when collared polar bears come within a 25 km radius of the community (J. Aars, Norwegian Polar Institute, unpublished data) (**Figure 11**). Further, applications to deter wildlife-livestock conflict may be adapted for polar bears. For example, radio-activated guard (RAG) devices employ a scanning radio receiver to monitor the proximity of radio-collared animals to a protected area (Breck et al., 2003) and may have applications in Arctic communities and at industrial facilities. If a radio-collared animal approaches a delineated protected area, the RAG unit activates a non-lethal deterrent (e.g., strobe light, sound effects) to discourage the animal from advancing. In sum, ST represents a valuable tool for monitoring the risks that polar bears can pose to human safety and reducing conflicts through both reactive (e.g., monitoring the movement of translocated bears) and proactive (e.g., geo-fencing, RAG devices) management applications.

Additionally, in the foreseeable future, ST data are likely to be important to understanding the impacts of the fast-growing ship-based and terrestrial ecotourism industry focused on viewing polar bears in their natural habitats. Understanding movements and seasonal habitat use of bears can help guide future regulations so that ecotourism activities avoid sensitive habitats.

5 RECOMMENDATIONS TO FACILITATE FUTURE COLLECTION OF ST DATA AND REDUCE CONCERNS

In the future, managers who have access to ST data will have information that is critical to conservation of polar bears (**Figure 9** and **Table 1**). Lack of ST data will make management decisions riskier to polar bears and to humans. **Table 1** and references within illustrate the wealth of information obtained from applying SLRTs to a small number of polar bears in a subpopulation, in contrast to other monitoring methods that would require sampling a much larger number of bears. In some cases, deployment of <10 SLRTs per year, over a 3-5-year period, provided information that was necessary to design an effective study and interpret demographic results of capture-recapture studies (e.g., Baffin Bay subpopulation, Laidre et al., 2020a; Laidre et al., 2020b; Atkinson et al., 2021). In other cases, the availability of ST data was a determining factor in whether a capture-recapture study produced useful results. For example, lack of ST data for the M’Clintock Channel subpopulation led to negatively biased estimates of survival and forced analysts to estimate abundance using only two years of data in a closed-population capture-recapture model (Dyck et al., 2021). Similarly, preliminary capture-recapture analyses for the

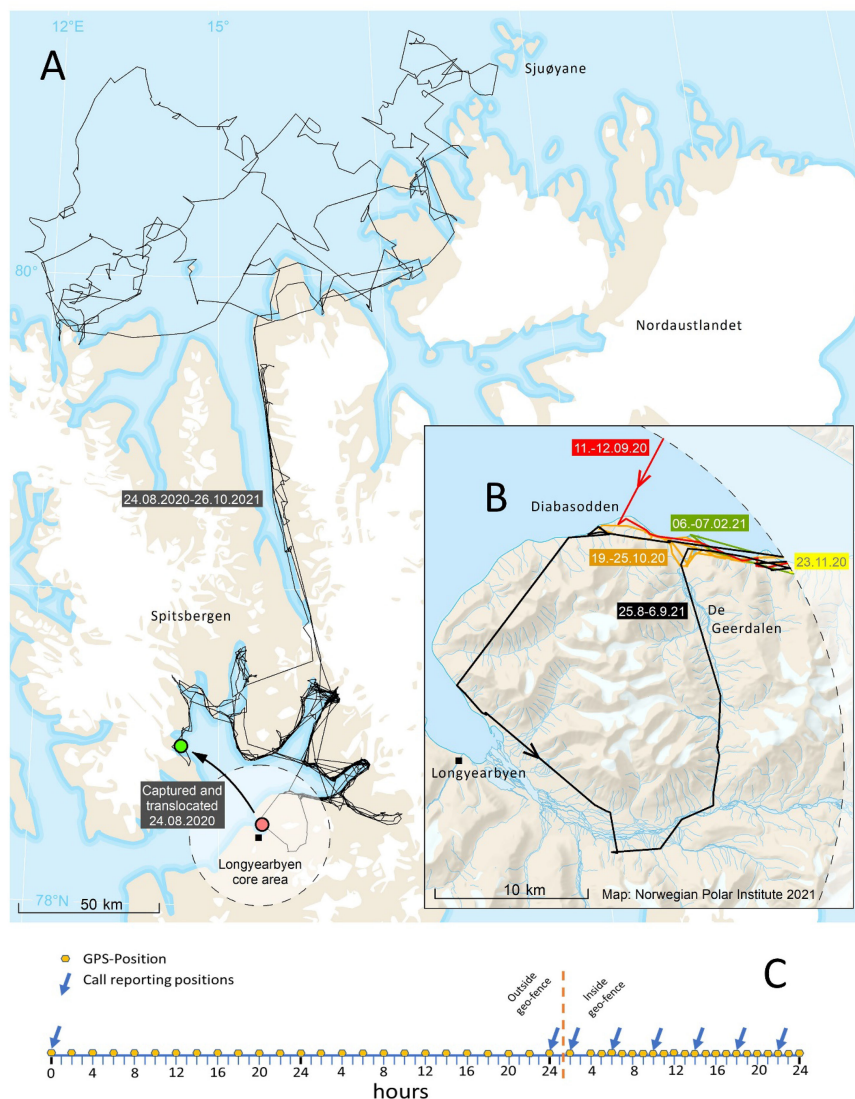


FIGURE 11 | Movements of an adult female polar bear near Longyearbyen, the main settlement in Svalbard, in August 2021 **(A, B)**. The Telonics iridium collar was set to collect GPS positions every other hour and report them every second day. When the collared bear moved inside a circle with radius of 25 km ('geo-fence') from Longyearbyen, the collar sent data more frequently (collecting a GPS location every hour and reporting every 4th hour) so the bear's proximity to town could be monitored **(C)**.

Viscount Melville subpopulation failed to produce biologically plausible results, whereas subsequent analyses that used ST data led to more accurate estimates of survival and abundance. Here we identify three methods that may facilitate collection of ST data and reduce concerns.

5.1 Establish Common Objectives

Scientists, managers, Indigenous partners, and stakeholders should review the status of polar bear subpopulations, identify what information is most important to management and conservation, and determine appropriate methods to collect it. This requires discussing the pros and cons of all research methods and identifying the ramifications if ST data are not collected, such

as increased uncertainty and bias. The discussion should extend to impacts on management decisions (e.g., regarding sustainable harvest level) and potential ramifications for resource users, regulatory entities, and others. In this manner, decisions about whether to collect ST data and the number of bears to be fitted with SLRTs can be based on a transparent assessment of the most effective research methods available to meet objectives, while recognizing approaches vary between subpopulations. We suggest that this type of front-end, collaborative discussion could lead to a better understanding of concerns around ST and help identify mutually acceptable solutions.

Open discussions should occur around the level of disturbance caused by any field study on polar bears. Even genetic capture-

TABLE 1 | Number of bears instrumented with satellite tags (ST) (any type) by subpopulation over the last 40 years.

Ecoregion ¹	Sub-population ²	Sub-population Abundance ³	Number of ST Instruments Deployed (Female/Males)				Institutes responsible for data acquisition (in no particular order)
			1980-89	1990-99	2000-09	2010-19	
Divergent Ice	BS	2650	14/0	161/4	102/0	193/0	Norwegian Polar Institute/USGS/All-Russian Research Institute for Nature Protection/Severtsov Institute of Ecology and Evolution at Russia's Academy of Sciences
	KS	Unknown	–	14/0	–	9/2	US Geological Survey/All-Russian Research Institute for Nature Protection
	LP	Unknown	–	9/0	–	4/3	US Geological Survey/All-Russian Research Institute for Nature Protection/Arctic Research Center LLC (ARC) of Rosneft
	CS	2937	47/0	107/0	21/0	114/61	UW Fish and Wildlife Service/US Geological Survey/Arctic Research Center LLC (ARC) of Rosneft
	SB	907	146/0	72/7	250/9	147/56	US Geological Survey/Environment and Climate Change Canada/Government of Northwestern Territories
Convergent Ice	NB	980	30/0	21/0	9/0	17/0	Environment and Climate Change Canada/Government of Northwestern Territories
Archipelago	EG	Unknown	–	9/0	13/16	71/12	Greenland Institute of Natural Resources/Norwegian Polar Institute
	KB	357	–	14/0	–	20/14	Government of Nunavut/Greenland Institute of Natural Resources
	NW	203	–	4/0	–	–	Government of Nunavut
	LS	2541	–	51/0	–	–	Government of Nunavut
	VM	161	7/0	11/0	–	22/0	Government of Nunavut/Government of Northwestern Territories/Environment and Climate Change Canada
Seasonal Ice	MC	284	–	1/0	–	–	Government of Nunavut
	GB	1592	–	8/0	–	–	Government of Nunavut
	BB	2826	–	44/0	5/6	37/30	Government of Nunavut/Greenland Institute of Natural Resources
	DS	2158	–	24/9	4/0	–	Government of Nunavut/University of Saskatchewan/Environment and Climate Change Canada
	FB	2585	–	–	60/5	–	Government of Nunavut/University of Alberta
	SH	780	–	24/0	37/0	22/0	Government of Ontario
	WH	842	38/0	199/0	112/0	151/45	Environment and Climate Change Canada/University of Alberta/Government of Manitoba
Arctic Basin	AB	Unknown	–	4/0	4/0	2/0	Greenland Institute of Natural Resources/US Geological Survey/University of Saskatchewan
SUM			282/0	753/20	617/36	809/223	

Females and males include both adults and subadults. AB, Arctic Basin; BB, Baffin Bay; BS, Barents Sea; CS, Chukchi Sea; DS, Davis Strait; EG, East Greenland; FB, Foxe Basin; GB, Gulf of Boothia; KB, Kane Basin; KS, Kara Sea; LP, Laptev Sea; LS, Lancaster Sound; MC, M'Clintock Channel; NB, Northern Beaufort Sea; NW, Norwegian Bay; SB, Southern Beaufort Sea; SH, Southern Hudson Bay; VM, Viscount Melville Sound; WH, Western Hudson Bay.

recapture studies, increasingly used as a less-invasive research method (e.g., Atkinson et al., 2021), involve briefly pursuing and temporarily altering the behavior of large numbers of bears from a helicopter (upwards of >1,000 bears biopsy darted in some cases, Atkinson et al., 2021). In this context, the relatively small number of bears that must be physically captured to obtain ST data (Table 1) represents a small amount of disturbance with a potentially large increase in the amount of information. In many situations, improvements to study design and parameter estimation that result from ST data mean that sample sizes of other types of data (e.g., from biopsies) can be substantively reduced while still meeting research objectives.

5.2 Use the Minimum Necessary Sample Sizes

Collar deployment should be guided by research objectives that are explicitly linked to management and conservation needs.

Statistical power analyses can estimate how many representative individuals are needed to answer specific questions, while accounting for potential problems with data acquisition or tag failure. This will ensure that no more ST devices are deployed than are needed to address specific goals. One approach may be to agree upon a minimum sample size and number of sampling years needed for a robust assessment and commit to reengaging all parties prior to increasing sample sizes (e.g., Sequeira et al., 2019). Furthermore, temporal limits could be placed on the duration over which individual bears wear ST collars (e.g., Laidre et al., 2020b). A release mechanism can be programmed for collars to drop off on a specific date or bears can be recaptured and collars manually removed. These approaches require balancing multiple tradeoffs, given that sample sizes and how long individuals wear SLRTs is positively correlated with the probability that ST data will reveal individual variability in the behavior and the adaptive potential of polar bears.

5.3 Advance ST Technology

Improvements in SLRTs have the potential to alleviate concerns about effects on polar bears. Size reduction of collars, reliable

¹ As defined by Amstrup et al. (2008)

² Based on deployment location

³ Current estimate (PBSG 2019)

release mechanisms, and tags that serve as alternatives to collars for short-term data collection, are all useful areas of development (e.g., Wiig et al., 2017). Several such efforts have occurred in recent years but continued technological advances warrant ongoing investment in methods for tracking polar bears. Although much of the current understanding of movements of polar bears comes from the deployment of ST collars on adult females, development of SLRTs that enable the tracking of adult males and juvenile bears for a year or more, would greatly improve knowledge.

Finally, we recommend continued use of field data and modern analytical methods to investigate the potential effects of chemical immobilization and collaring on polar bears. While most studies of capture effects have found no long-term impacts on fitness, the potential for such impacts should be revisited over time. Meta-analyses of data from multiple subpopulations could increase statistical power. For subpopulations with a long history of capture-recapture studies, it is possible to fit models that include “trap effects” (e.g., Regehr et al., 2007; Kéry and Schaub, 2012), which are specifically designed to identify temporary effects on reproduction, survival, or other demographic parameters following capture.

6 CONCLUSION

In this paper, we review how ST data have contributed to polar bear management and conservation and discuss their increasing importance to address current and future challenges. Climate warming is shifting the geographic ranges of bears, inside and outside of historical subpopulation boundaries, resulting in altered metapopulation dynamics and the appearance of bears in new areas. With an ice-free Arctic expected within decades (Wang and Overland, 2009; IPCC, 2019), it will be critical to understand how bears redistribute. Some subpopulations may become genetically or demographically isolated (Maduna et al., 2021), with ramifications for population viability (i.e., as a function of health, energetics, human-caused removals, and contaminant exposure) and sustainable use. Further, increasing development in the Arctic (e.g., new shipping routes, resource extraction) will

require access to contemporary ST data to meet legal requirements for environmental assessments and monitoring. There are vast areas where few or no ST data are available from polar bears due to lack of research efforts, including most of the Russian Arctic, the Arctic Basin, and the Last Ice Area, the latter of which is predicted to be a long-term refuge for the species (Moore et al., 2019). ST data from these regions and their respective subpopulations will be critical to conservation and management of the species. In summary, ST provides critical data that allow managers to make informed management and regulatory decisions and ST will be vital to the conservation of polar bears in the 21st century.

AUTHOR CONTRIBUTIONS

KL lead the writing with contributions from GD, NL, EVR, TA, KR, JA, HR, and ØW. All authors contributed to the article and approved the submitted version.

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A Novel Approach to Using Seabed Geomorphology as a Predictor of Habitat Use in Highly Mobile Marine Predators: Implications for Ecology and Conservation

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Understanding how marine predators find patchily distributed prey resources in a dynamic environment is key to identifying important ecological areas for ecosystem-level conservation management. However, the mechanisms underpinning important foraging areas often result from complex interactions between static and dynamic covariates (e.g. topography and currents). Modelling habitat associations with hydrodynamic processes is rarely useful when attempting to identify and characterise foraging areas across an individual's foraging range. Investigating the influence of static habitat features on predator behaviour can provide a more tractable baseline understanding of habitat associations, upon which additional complexity can be added. Seabed gradient covariates (e.g. slope and aspect) are often used, yet such metrics are computed at singular user-defined resolutions, and provide limited ecological insight when used in isolation. Instead, categorising the seabed into geomorphological features may provide better characterisation of seabed structure. Here we explore the utility of a pattern recognition algorithm to delineate whole geomorphological features ("geomorphons") on the seabed (e.g. valleys, ridges, footslopes) from bathymetry data, and examine the influence of geomorphology on marine predator habitat use. We demonstrate the potential application of this approach in a case study, examining the influence of geomorphons on the at-sea behaviour of a highly mobile predator inhabiting shelf seas: the grey seal (*Halichoerus grypus*). We analyse GPS tracking data from three seals tagged in the southern North Sea, an area with heterogeneous geomorphology. We use hidden Markov models (HMMs) to infer foraging and travelling behaviour and model the effect of different feature types on the probability of switching between states. All three seals showed an increased probability of transitioning from travelling to foraging when encountering slopes, footslopes and hollows, and foraging activity was concentrated at slopes on the fringes of the Dogger Bank. We hypothesise that such features may host prey aggregations, and/or lead to increased prey capture success. The results suggest the importance of such areas for grey seals in the southern North Sea, a region

undergoing rapid and widespread anthropogenic habitat change. This method could be incorporated into future species distribution models to improve estimates of predator distribution, informing conservation management and marine spatial planning.

Keywords: hidden Markov models (HMMs), movement ecology, North Sea, geomorphons, grey seal (*Halichoerus grypus*), satellite telemetry and tracking

INTRODUCTION

Understanding how animals utilise their environment to optimise food intake and maximise fitness is a fundamental question for ecologists (Stephens and Krebs, 1986). Studying the intrinsic and extrinsic mechanisms which underpin the foraging behaviour of animals can provide insights into the functioning of ecosystems and ecologically important areas (Schmitz et al., 1997). It is particularly important to understand the processes which shape the foraging behaviour of high trophic level predators, as they play a vital role in the structure of marine and terrestrial communities through the top-down regulation of prey (Williams et al., 2004; Heithaus et al., 2008). Marine ecosystems are inherently dynamic and prey resources are often patchily distributed (Haury et al., 1978). Therefore, highly mobile predators (e.g. marine mammals, turtles, pelagic fish and seabirds) may adjust their foraging behaviour to maximise time in the most productive areas (Kie, 1999; Weimerskirch, 2007; Kirchner et al., 2018). Understanding how predators use environmental features to optimise foraging is necessary to allow ecologically important areas to be identified, and thus to inform marine spatial planning (Boyd and Murray, 2001; Hindell et al., 2020). Such areas are not easy to identify at sea because we cannot easily observe them, but spatial aggregations of predators can be used as indicators (Block et al., 2011; Montevecchi et al., 2012; Grecian et al., 2016; Hindell et al., 2020).

Observing the behaviour of highly mobile marine predators is challenging as they spend most or all of their time at sea, often far from land or underwater, and can cover large distances (Fedak et al., 2002; Luschi et al., 2003; Skomal et al., 2017). Animal-borne sensors allow for the collection of fine-scale data from which the movements of marine predators can be reconstructed (Wilmers et al., 2015). Such data can be analysed to infer behaviours (Patterson et al., 2008; Carter et al., 2016), to identify important foraging areas (Camphuysen et al., 2012), and to understand the environmental characteristics of these areas using ancillary oceanographic data from animal-borne tags (Lydersen et al., 2002; Boehme et al., 2008a; Boehme et al., 2008b). Locational data collected from animal-borne tags are frequently used to infer discrete behaviours, such as travelling (e.g. commuting to, from and between foraging sites) and Area-Restricted Search (ARS), which in many vagile species has been associated with foraging activity, i.e. searching for, capturing and handling prey (Kareiva and Odell, 1987; Pinaud and Weimerskirch, 2007). Identifying discrete behaviours from animal tracking data is commonly done by analysing aspects of track geometry, such as changes in step lengths (the distance

between two consecutive locations) and turning angles through time (Boyd, 1996; Fauchald and Tverra, 2003; Barraquand and Benhamou, 2008). During ARS, an animal will typically exhibit large turning angles compared to while travelling, combined with a reduction in speed, as a result of searching for, encountering and responding to a food source or in response to environmental cues, for example in areas where prey was previously encountered (Kareiva and Odell, 1987). In recent years, hidden Markov models (HMMs) have emerged as a popular and flexible analytical tool which can be used to identify discrete movement modes (from which behaviours can be inferred) from animal movement data (Patterson et al., 2008; Langrock et al., 2012). The movements of many highly mobile marine predators, including pelagic fish (e.g. Patterson et al., 2009; Towner et al., 2016), seabirds (e.g. Pirodda et al., 2018; Clay et al., 2020) and marine mammals (e.g. Isojunno et al., 2017; Carter et al., 2020) have been investigated using tracking data and HMMs. A major advantage of HMMs over other movement models is that they can be used to investigate the mechanisms that shape animal behaviour through the inclusion of covariate effects, such as environmental variables, on state transition probabilities (Morales et al., 2004; Patterson et al., 2009; Photopoulou et al., 2020). In this way, the effects of encountering a specific feature or habitat type on the probability that an animal will switch from one state to another can be quantified (Morales et al., 2004).

Examining animal behaviour in relation to the variety of environmental conditions that an individual encounters whilst searching for prey can help us to understand what ultimately drives foraging decisions. A wide range of environmental factors are often considered in studies of marine predator habitat associations, including static covariates such as bathymetric depth, which can influence prey accessibility for benthic foragers (e.g., Burns et al., 2004), as well as dynamic covariates that may influence prey distribution, such as sea ice presence for polar species (e.g., Pagano and Williams, 2021) and sea surface temperature in seasonal seas (e.g., Georges et al., 2000; Speakman et al., 2020). Seabed topography (i.e. spatial variation in seabed terrain) can influence predator behaviour and distribution through a variety of complex mechanisms (Cox et al., 2018). These mechanisms may be indirect, for example static features in the open ocean such as seamounts are associated with increased primary productivity (Genin and Boehlert, 1985), creating predictable foraging conditions for marine predators (Morato et al., 2010; Maxwell et al., 2012; Letessier et al., 2019). Similarly, in shelf seas tidal currents moving over offshore banks and uneven terrain can lead to subsurface aggregations of small fish, either through increased plankton concentration (Embling et al., 2012), or the mechanical influence of internal waves

(Embling et al., 2013). Such phenomena create spatially and temporally predictable foraging opportunities (Embling et al., 2012; Scott et al., 2013). Topography may have a more direct relationship to predator foraging behaviour; known foraging areas of bottlenose dolphins (*Tursiops truncatus*) in the Moray Firth (Northeast Scotland) are characterised by steep seabed gradients, which may act as a physical barrier against which to herd prey (Hastie et al., 2003; Bailey and Thompson, 2010). While the individual oceanographic components that characterise foraging sites (e.g. currents, water column stratification, tidal fronts) can be modelled at high resolution, processing and interpretation of such data can be challenging, often requiring specific expertise. Moreover, the hydrodynamic conditions that characterise foraging sites may vary spatially and temporally (e.g. across seasons). Capturing such complexities in models of predator-habitat association is challenging, particularly when studying a species across entire movement tracks rather than at isolated known foraging sites. Furthermore, although hydrodynamic covariates have been shown to be important for a range of species including some aerial and pelagic predators (Cox et al., 2018), the habitat associations of benthic predators may be better described by covariates relating to seabed characteristics. Such static metrics may prove more accessible and tractable indicators of important ecological areas, upon which dynamic covariates can later be added to investigate the specific mechanisms underpinning the importance of discrete areas. Singular metrics of topographic gradients, such as slope and aspect, are frequently used in such studies of marine predator habitat associations. An advantage of such metrics is that they can be computed across wide spatial extents, such as ocean basins. However, given the complexity of processes linking topography to prey described above, such metrics only provide limited ecological insight into predator-habitat associations, especially when used in isolation (Bouchet et al., 2015). Moreover, gradients are computed at a singular user-defined spatial scale, and do not provide insight into geological context or function. For example, it is impossible to determine the relative importance of areas near the top or bottom of a slope using gradient alone. Instead, classification of the seabed into features which have distinct geomorphological shapes provides more information about the underlying structure of the seabed (Bouchet et al., 2015).

In the terrestrial environment, geomorphology has been used to investigate the drivers of movements of wide-ranging species, such as elk (*Cervus* sp.), where the direction of movement was found to be dependent on the topography of the landscape (Kie et al., 2005). For snow leopards (*Uncia uncia*), geomorphology has also been found to influence behaviour, with features such as ridgelines and cliffs being used for both daytime resting and travelling (Jackson, 1996). In the marine environment, seabed geomorphology has been mapped for the global ocean for geological applications, categorising seabed features into a set of landforms (Harris et al., 2014), and a study has combined bathymetric data with seabed backscatter data from acoustic surveys to generate high resolution seabed classifications (“bathymorphons”) for a specific study area (Masetti et al.,

2018). However, only a handful of studies have considered such data in the context of predator-habitat associations (Torres et al., 2013; Bouchet et al., 2020; Claro et al., 2020). These studies have generally investigated the influence of broadscale features, such as canyons, seamounts and plateaus on pelagic species, and the influence of topographic features on shelf sea predators remains largely unstudied using geomorphology. Moreover, the geomorphological dataset presented in Harris et al. (2014) is not resolved to identify discrete features in shelf seas. However, the “geomorphon” pattern recognition algorithm developed by Jasiewicz and Stepinski (2013) presents an opportunity to generate new geomorphological datasets from digital elevation model (DEM) or digital terrain model (DTM) data. Importantly, the algorithm is customisable such that a range of spatial resolutions can be explored, allowing the user to generate a landform map that is relevant to their research question and study area (Jasiewicz and Stepinski, 2013). Moreover, the pattern recognition process accounts for variation in the spatial magnitude of individual features, thus allowing features to be mapped at a range of scales (e.g. capturing both narrow and wide valleys). To our knowledge this approach has not been widely used in marine ecological studies, but when applied to bathymetry data, it provides an opportunity to investigate the potential influence of seabed topographic features on the behaviour of shelf sea predators at a spatial scale which is relevant to individual animals.

This study explores the utility of seabed geomorphological features as predictors of habitat use for highly mobile predators. Here we present a case study to: (i) employ the “geomorphon” algorithm to generate a dataset of seabed geomorphological features on a spatial scale that is relevant to the study species; (ii) examine whether inclusion of geomorphology as a covariate on state transition probabilities in a HMM applied to tracking data for three grey seals (*Halichoerus grypus*) in the southern North Sea improves the model fit over a null model (i.e. with no covariate effects); and (iii) consider to what extent this approach has the potential to provide ecological insights that will contribute information towards identifying important ecological areas for conservation management.

Grey seals are an ideal study species to explore the above research questions, as they are high trophic level predators inhabiting shelf seas of the North Atlantic. They regularly undertake multi-day foraging trips at sea, travelling up to hundreds of kilometres from terrestrial haulout sites, and thus are likely to encounter a wide range of topographic conditions (McConnell et al., 1999; Breed et al., 2009; Nowak et al., 2020). Moreover, their ecology has been studied in detail for decades (Thompson et al., 1991; McConnell et al., 1992; Russell et al., 2013), but understanding of the environmental mechanisms that underpin foraging behaviour remains incomplete. Grey seals have been model species for the development of animal movement HMM techniques (Jonsen et al., 2005; McClintock et al., 2012; Carter et al., 2020), and recent studies have begun to use HMMs to investigate the influence of environmental covariates on grey seal behaviour (van Beest et al., 2019; Nowak et al., 2020). However, no studies have examined how

different static geomorphological features might influence their foraging decisions. The North Sea is particularly important habitat for this species, with the United Kingdom (UK) coast of the North Sea alone hosting ~25% of the global population (SCOS, 2020). Yet, this area is undergoing a process of intense change with the decommissioning of oil and gas infrastructure and the large-scale construction of wind farms, which overlap with seal habitat (Russell et al., 2014; Russell et al., 2016). Grey seals are protected in the UK under specific national legislation, as well as 2019 amendments to species and habitats regulations which retained the basic requirements of the European Union (EU) Habitats Directive in UK law after Brexit in 2021. As such, grey seal populations must still be maintained in “favourable conservation status”, in line with the EU Habitats Directive. Special Areas of Conservation (SACs) have been designated around the UK (Russell et al., 2019), yet these SACs are largely centred on coastal pupping and haulout sites and adjacent coastal areas. Moreover, the foraging distribution of grey seals may be hundreds of kilometres away from breeding and haulout sites (McConnell et al., 1999; Russell et al., 2013). Delineating important ecological areas offshore in the North Sea is therefore critical for effective marine spatial planning, and understanding the environmental characteristics of key foraging grounds is a research priority.

METHODS

Tag Deployment and Study Area

The data used in this case study were from three adult grey seals tagged with Fastloc[®] GPS/GSM (Global System for Mobile Communications) devices (SMRU Instrumentation, UK) as part of a larger deployment in May 2015 ($n = 20$) at two haulout sites in Southeast England (Blakeney Point and Donna Nook) (see Russell, 2016). Seals were captured using hand nets, and anaesthetised with intravenous Zoletil100[®] (Virbac, France). The tagging procedure followed that of Sharples et al. (2012). Tags were glued to the fur on the back of the neck at the base of the skull using Loctite[®] 422[™] cyanoacrylate instant adhesive (Henkel, UK); the tags then fall off by or during the annual moult. The tags collect positional information using Fastloc[®] GPS when the seal is at the surface or on land, as well as haul-out status using a wet/dry sensor. Data are stored in the buffer memory to be transmitted when the seal enters GSM range (McConnell et al., 2004). **Table 1** outlines the tag deployment information for each seal.

The three individuals used in this case study were chosen as they had the widest ranging movements of the 20 tagged seals and thus were most likely to encounter a variety of different

geomorphological features. The spatial extent of seal tracking data is shown in **Figure 1**. All three seals were either tagged in, or visited, haulout sites within the Humber Estuary SAC (Donna Nook) for which grey seals are a qualifying feature. The habitat covered by seal tracks encompasses much of the southwestern quadrant of the North Sea; an area of shallow but variable water depth (on average ~30 m deep; bathymetry shown in **Figure 1**). This area is predominantly sandy, featuring a large sandbank (Dogger Bank), rising to ~15 m below the surface, which separates seasonally stratified deeper waters of the northern North Sea from the shallower, mixed waters of the southern North Sea (Hill et al., 1993). This division of water bodies is punctuated by the Flamborough tidal mixing front, extending eastwards from the English coast around the fringes of the Dogger Bank (Hill et al., 1993). Dominant prey species for seals in this region include sandeels (*Ammodytes* spp.), flatfish, gadids and other benthic species associated with sandy substrates [e.g. dragonet (*Callionymus lyra*) and goby] (Wilson and Hammond, 2019).

Processing of Movement Data

Location data for the three seals were cleaned to remove erroneous estimates following the protocol from Russell et al. (2015) using residual error threshold and number of satellites. Trips with < 10 observations were removed as they were unlikely to consist of foraging behaviour at sea and were more likely to be near-shore behaviour related to waiting for tidal haulout sites to become available (Thompson, 1989) (See **Supplementary Material**). Location data were regularised to a consistent time step of 1 hour using linear interpolation between pre- and post-location estimates, then any location that fell during a haul-out event was excluded, leaving only at-sea locations. For detail on the selection of a regularisation interval, see **Supplementary Material**. Any time interval for which there was a gap of > 2 hours between observed locations surrounding the interpolated point was flagged as ‘unreliable’ (Russell et al., 2015). These unreliable data points were included in the model, but the associated step lengths and turn angles were omitted. A state was assigned to these intervals by the HMM based on the Markov property, not on the state-dependent parameters, thus they did not influence the state distributions (Carter et al., 2020). See “Statistical Analysis” section below for HMM formulation. The location at the midpoint of the regularised time intervals was used for matching with environmental data (geomorphons; see below). The data were separated into trips, with the start of a trip identified by the end of a haul-out event, and the end of a trip when another haul-out event was initiated. Data within 10 km of the coast at mean high water were excluded using QGIS (QGIS Development Team, 2019) as it is impossible to distinguish

TABLE 1 | Tag deployment information.

Seal reference	Tag start date	Tag end date	Deployment Location	Mass (kg)	Sex
Seal 1	05/05/2015	27/08/2015	Blakeney	157.2	Male
Seal 2	05/05/2015	24/11/2015	Blakeney	174.6	Male
Seal 3	02/05/2015	26/12/2015	Donna Nook	150.4	Female

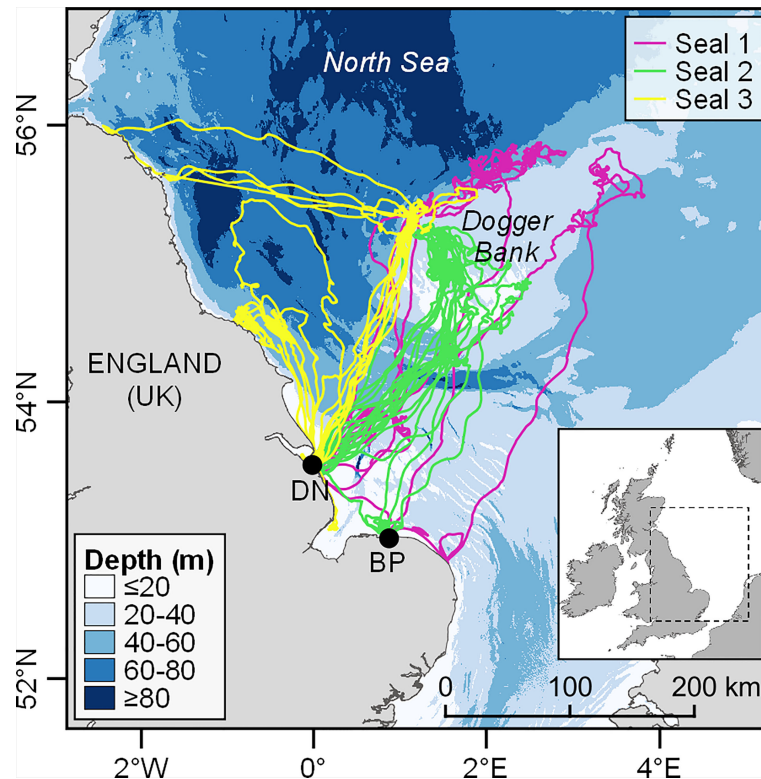


FIGURE 1 | At-sea movements of the three tagged grey seals. Black dots indicate the tagging sites (DN = Donna Nook, BP = Blakeney Point). Bathymetry data: EMODnet Digital Bathymetry (DTM) (2016).

between foraging and other near-shore behaviour (such as waiting for tidal haulout sites to become available) using location data.

Environmental Data

The “geomorphon” pattern recognition algorithm generates a raster layer of discrete landforms from DTM input data (Jasiewicz and Stepinski, 2013). A DTM for the North Sea was obtained from the European Marine Observation and Data Network (EMODnet Bathymetry Consortium, 2016) with a grid resolution of 250 m. The Geographic Resources Analysis Support System (GRASS GIS) (Neteler and Mitasova, 2007) extension *r.geomorphon* (Jasiewicz and Stepinski, 2013) was used to calculate the geomorphons in R (R Core Team, 2021). A raster was produced with grid cell values corresponding to one of the 10 landform elements which are most commonly recognisable in a typical terrestrial landscape (Figure 2). The algorithm requires three parameters to be set by the user, which can influence the geomorphology classification: (i) the maximum extent of a landform, known as the maximum lookup distance (this value needs to be relatively large for the landform elements across a range of sizes to be classified), (ii) the flatness threshold (degrees), below this value any terrain is classified as flat, and (iii) the spatial resolution of the DTM data (Stepinski and Jasiewicz, 2011). This

method uses a line-of-sight principle (Yokoyama et al., 2002) for identifying the relationship of a central cell in the DTM raster with its neighbouring cells. This line-of-sight principle allows an incremental increase in lookup distance (up to the predefined maximum value) until minimum zenith and nadir angles along the eight compass directions are obtained between the central cell and the neighbouring cells (Stepinski and Jasiewicz, 2011). These minimum zenith and nadir angles are compared by the algorithm to identify if the central cell is higher, lower or the same elevation as its neighbours and this is converted into a ternary pattern which represents the geomorphon (Stepinski and Jasiewicz, 2011). There are, theoretically, 6561 possible topographic patterns, and in order to reduce this for mapping, the patterns are grouped into the ten most common landforms: flat, summit, ridge, shoulder, spur, slope, hollow, depression, valley and footslope (Jasiewicz and Stepinski, 2013) (Figure 2). The output of this algorithm is a raster with values for each grid cell corresponding to one of the ten common landform elements mentioned above. Importantly, the algorithm allows the final lookup distance for each cell to be determined automatically, and to be self-adaptive. This means that the geomorphons are mapped at a range of spatial extents, thus allowing for the recognition of landforms of a variety of sizes (e.g., identifying both narrow and broad valleys) (Stepinski and Jasiewicz, 2011). Moreover, the option to customise algorithm parameters allows the user to produce a landform map that is

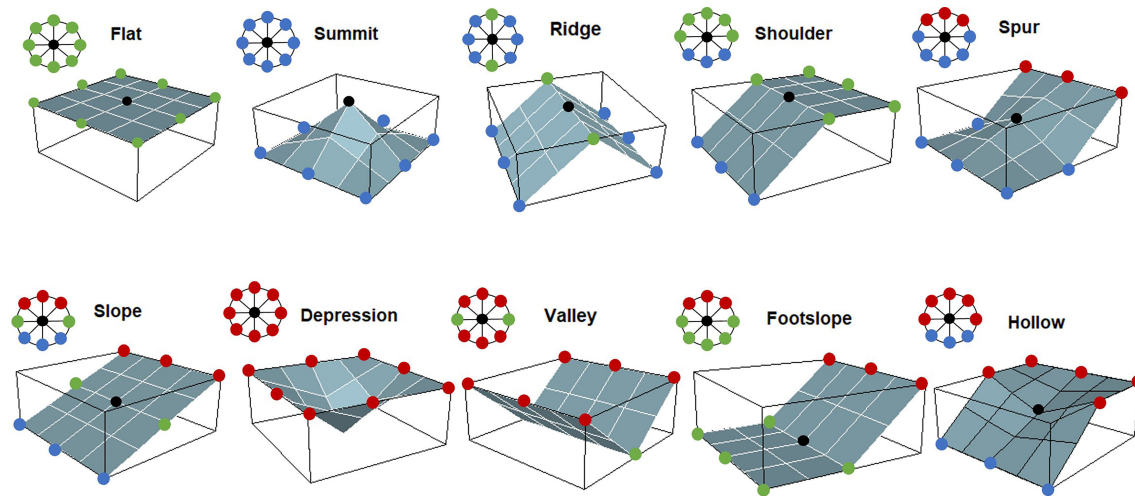


FIGURE 2 | Representative 3D morphologies and their equivalent geomorphons (ternary patterns) for the 10 most common landform elements [after Figure 3 from Jasiewicz and Stepinski (2013)]. Coloured dots indicate if the cells surrounding the central cell (black) are higher (red), lower (blue) or of the same elevation value (green) as the central cell.

relevant to their research question, depending on the spatial extent and resolution of interest.

In order to find the most suitable terrain classification for investigating how geomorphological features influence grey seal movements, a range of values for the three parameters (lookup distance, flatness threshold and spatial resolution of the DTM) were trialled. A stepwise procedure was applied by creating a matrix encapsulating all possible combinations of four distinct values for each parameter, giving a total of 64 combinations. The values in the matrix were chosen as they provided a large range in the possible geomorphology rasters; it was unknown which geomorphological scale would be most biologically relevant. Four different bathymetry resolutions were trialled (250 m, 500 m, 1000 m and 2000 m), with four different lookup distances (5 cells, 15 cells, 40 cells and 60 cells) and four different flatness thresholds (0.1, 0.25, 0.5 and 0.7 degrees). Relatively large values of lookup distance and flatness threshold would result in a terrain classification from a higher and broader viewpoint than from smaller values; smaller values would give a classification of the terrain from a finer spatial resolution and thus finer detailed features (Stepinski and Jasiewicz, 2011). Because the final lookup distance is determined automatically, and is self-adaptive, larger values of lookup distance would allow the identification of landforms of a variety of sizes (Stepinski and Jasiewicz, 2011). Higher flatness thresholds produce maps that are flatter, and the influence of this threshold increases disproportionately with coarseness of the resolution of the terrain data. Thus, values of < 1 degree were used to avoid over-classification of flat areas (Stepinski and Jasiewicz, 2011). For each combination of parameter values, a geomorphology raster was created, resulting in 64 candidate rasters. For each candidate raster, geomorphons were extracted for each seal location, and included in a HMM as a covariate effect on state transition probabilities (see “Statistical Analysis” section below). The R package *momentuHMM* (McClintock and Michelot, 2018) was

used to formulate the HMM. The best configuration of parameters for the pattern recognition algorithm was determined using model selection by Akaike Information Criterion (AIC) (Burnham and Anderson, 2002).

To allow comparison among individuals in the effect of geomorphology on behaviour, one individual (Seal 1) was used for defining the best parameters for the pattern recognition algorithm, as this seal covered the widest area and the largest variety of geomorphons (**Figure 1**). Thus, it was assumed that the scale of the geomorphology perceived by each seal would be similar. The values for the different parameters that produced the geomorphology raster with the lowest AIC score when used in the covariate HMM for Seal 1 were: a bathymetry resolution of 2000 m; a lookup distance of 15 cells and a flatness threshold of 0.1 degrees. This configuration produced the model with lowest AIC score compared to other parameter configurations (4.67 points lower than the next best model; see **Supplementary Material Table S1**). The resulting geomorphology raster is shown in **Figure 3**. This geomorphology raster was used for extracting the geomorphons for each location for each seal using the “raster” package (Hijmans and van Etten, 2021) in R.

Statistical Analysis

To test the hypothesis that there is a relationship between seabed topography and seal behaviour, a two state HMM was fitted for each seal independently with a covariate effect of geomorphology (10 level factor) acting on state transition probabilities (covariate model). This covariate model was then compared to a two state HMM for each seal with no covariate effects (null model). The covariate model was deemed superior to the null model (no covariate effects) if it resulted in a reduction in AIC score of 2 points or more (Burnham and Anderson, 2002). The package *momentuHMM* (McClintock and Michelot, 2018) was used to formulate the models in R. HMMs were fitted with step lengths

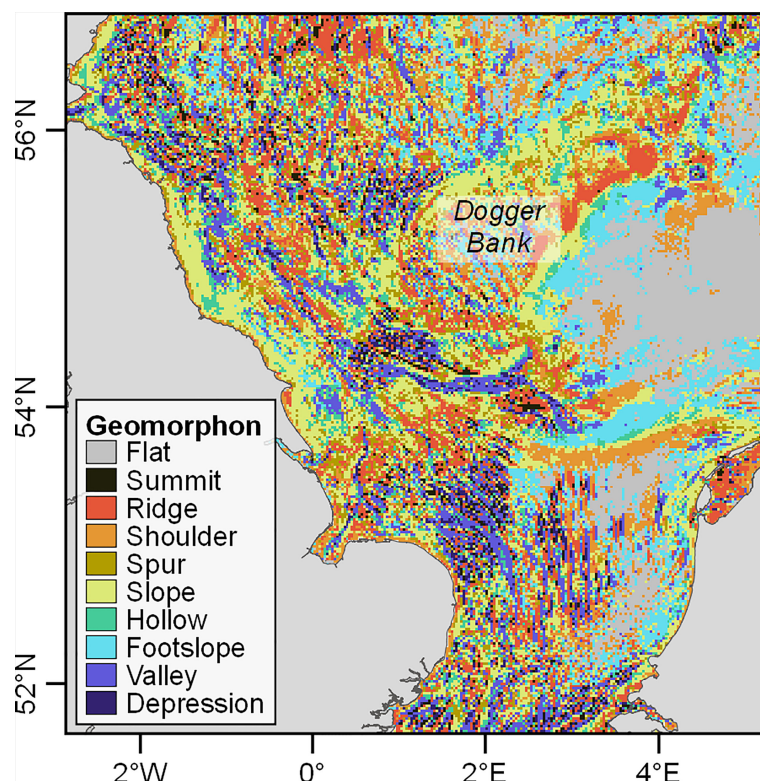


FIGURE 3 | The geomorphology raster of the southern North Sea showing the distribution of the different geomorphons.

and change in bearing (turn angle) as the state-dependent data streams, in line with other studies of grey seal behaviour (Jonsen et al., 2005; Breed et al., 2009; Russell et al., 2015; Nowak et al., 2020). Models were fitted with two discrete movement states for each individual to provide a simple framework for testing the effect of geomorphology on behavioural state. The Viterbi algorithm was used to calculate the most probable state at each time step (Zucchini et al., 2016), and states were inferred as foraging or travelling based on prior knowledge of seal behaviour, and published examples of similar models (i.e. short step lengths and high turn angles = ARS (foraging), long step lengths and low turn angles = travelling) (Carter et al., 2020; Nowak et al., 2020). A Gamma distribution was assumed for the step lengths and a wrapped Cauchy distribution was assumed for the turn angles (see Carter et al., 2020 for mathematical notation). Starting values for the state-dependent parameters (mean and standard deviation for step lengths and the wrapped Cauchy concentration parameter for turn angles) must be

specified for each state. A range of starting values for each state-dependent parameter were trialled until arriving at the global optimum for the negative log-likelihood (Michelot et al., 2016). Model validation checks were carried out by graphical checking of the pseudo-residuals (Zucchini et al., 2016), and no indication of issues relating to poor model fit were found. To facilitate a qualitative comparison of habitat use among individuals, the overall activity budgets (percentage of time spent foraging versus travelling) were estimated for each seal, alongside the percentage of total time spent per state at each geomorphon type.

RESULTS

HMMs successfully identified two discrete movement states for each seal, inferred here as foraging and travelling

TABLE 2 | AIC values for the null model and covariate model for each seal.

Seal	Null model	Covariate model	Δ AIC
1	7483.1	7465.8	-17.3
2	13405.6	13391.4	-14.2
3	8829.8	8820.2	-9.6

Δ AIC indicates the difference in Akaike Information Criterion score between the null and covariate model. Where Δ AIC < -2, the covariate model is deemed superior.

(**Supplementary Material Figure S5**). Model selection by AIC score showed clear support for the covariate model (effect of geomorphons on state transition probabilities) over the null model (no covariate effects) for all three seals (**Table 2**). The AIC score of the covariate model was substantially lower than that of the null model for all three seals ($\Delta AIC = -17.3, -14.2$ and -9.6 for Seals 1, 2 and 3 respectively; **Table 2**). **Figure 4** shows the distribution of foraging locations for each seal, as inferred from the covariate model, colour-coded by the underlying geomorphology. Foraging sites for all seals occurred either within 50–70 km of the coast, or at sites approximately 200 km away from the haulout, overlapping with a variety of geomorphons (**Figure 4**). Foraging appeared to occur mostly on the fringes of the Dogger Bank for Seals 1 and 3, and on the bank itself for Seal 2. The foraging areas of Seal 3 appeared to overlap slightly with those of Seal 1, near the northern edge of the Dogger Bank (**Figure 4**). Foraging also occurred within 20 km of the coast for Seals 2 and 3 (**Figure 4**). The number and distribution of locations inferred as foraging was similar between the covariate model and the null model for all three seals. The total percentage of state assignments which agreed between the two models was 97.8% for Seal 1, 98.1% for Seal 2 and 91.3% for Seal 3.

According to the covariate model, the activity budgets were qualitatively similar among all three seals; Seal 1 was in the putative foraging state 63% of the time, versus 61% for Seal 2 and 59% for Seal 3. **Figure 5A** and **Table 3** show the mean effect of different geomorphons on the probability of switching from travelling to foraging states with associated 95% confidence intervals (CIs). **Figure 5B** shows the percentage of time spent in each state at each of the geomorphons across the whole track for each seal, alongside the relative mean percentage of time seals are expected to be in the foraging state based on activity budgets. There was a positive effect of footslope, slope and hollow on the probability of transitioning from travelling to foraging for all three seals, but the respective effect sizes varied among individuals. While the largest effect size for Seal 1 was recorded for footslope (0.3, 0.16–0.51 95% CIs) (**Table 3**, **Figure 5A**), the seal only encountered this feature on 4.9% (83) of locations (**Table 3**), and the ratio of foraging to travelling states at this feature appeared to be proportional to the overall activity budget (**Figure 5B**). Slope was the most frequently encountered feature for all three seals, and Seal 1 appeared to show a disproportionately high amount of foraging at this feature type (**Figure 5B**). The largest effect sizes for Seal 2 were recorded for footslope (0.21, 0.1–0.38) and shoulder (0.3, 0.19–0.43) and the seal appeared to show a disproportionately high amount of foraging at these feature types. Seal 2 also encountered these two feature types more frequently than the other two seals. The largest effect sizes for Seal 3 were recorded for footslope (0.1, 0.03–0.29) and slope (0.09, 0.06–0.13). Seal 3 appeared to show a disproportionately high amount of foraging at ridges and shoulders, despite these features not having a large influence on the transition probability from travelling to foraging. There was no effect of flat on state transition probability for any of the seals, but the number of locations that overlapped with this feature type was low (**Table 3**).

DISCUSSION

This study aimed to explore the utility of a pattern recognition algorithm for classifying seabed geomorphological features (see Jasiewicz and Stepinski, 2013) to better understand the habitat use of mobile marine predators, using grey seals tagged in the southern North Sea as a case study. By modelling the seal movement data in a HMM framework with geomorphological features as a covariate acting on state transition probabilities, we found that geomorphological data improved the identification of behavioural states for the three seals studied, and offered new insights into foraging ecology which will aid the identification of important habitat.

Geomorphons impacted the state transitions for all three seals, providing evidence that seabed geomorphology does influence seal foraging behaviour. There were commonalities among the three individuals in the types of seabed geomorphology that had a positive influence on switching from travelling to foraging; slopes, footslopes and hollows were all associated with an increase in the probability of seals switching to foraging upon encountering them (**Figure 5A**). However, there was a mismatch between the feature types that were likely to increase the probability of switching from travelling to foraging, and feature types where the majority of foraging activity was concentrated. For example, Seal 3 was most likely to transition into ARS upon encountering footslopes and slopes compared to other feature types, but appeared to spend a disproportionately large amount of time foraging at ridges and shoulders (**Figure 5**). A seal travelling through the landscape towards an area of raised seabed, such as the Dogger Bank, is likely to encounter footslopes and slopes before arriving at shoulders or ridges (**Figure 3**). The mechanism underlying the influence of slopes and footslopes on the decision to switch to foraging may therefore be related to overspill of prey patches from good foraging habitat (i.e. ridges and shoulders) into surrounding areas. Similarly, the geomorphon with the largest influence on behaviour switching for Seal 1 was footslope, but the seal did not encounter this feature type frequently (only 4.9% of locations). HMMs are commonly used to understand the environmental drivers of foraging behaviour by examining covariate effects on state transition probabilities (Morales et al., 2004; Patterson et al., 2009; van Beest et al., 2019). However, our results highlight that the mechanisms that influence switching into foraging behaviour may be associated with different habitat characteristics to areas where foraging activity is concentrated. This is a key consideration when identifying important ecological areas for conservation management based on inference from covariate effects on state transitions in HMMs, particularly if the covariate is a categorical representation of habitat. We therefore recommend that habitat characteristics associated with state-switching behaviour should be considered in conjunction with the characteristics of areas where foraging activity is concentrated for a more complete understanding of the relationship between habitat and predator behaviour.

Slopes were the most frequently encountered feature type, associated with the greatest proportion of foraging activity, and had a positive effect on state transitions for all three seals

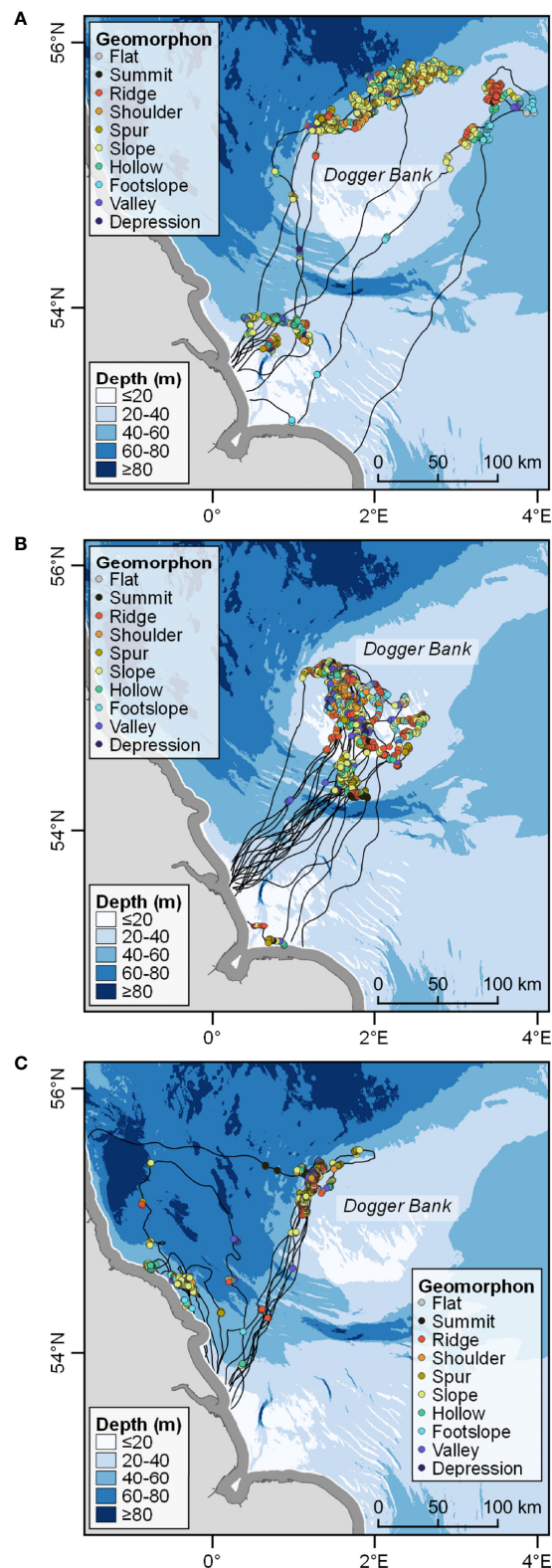


FIGURE 4 | Movement of (A) Seal 1, (B) Seal 2 and (C) Seal 3 with foraging locations classified according to the geomorphology for each location and travelling indicated by black lines. The 10 km coastal buffer within which locations were excluded is shown in dark grey. All three seals foraged in the vicinity of the Dogger Bank.

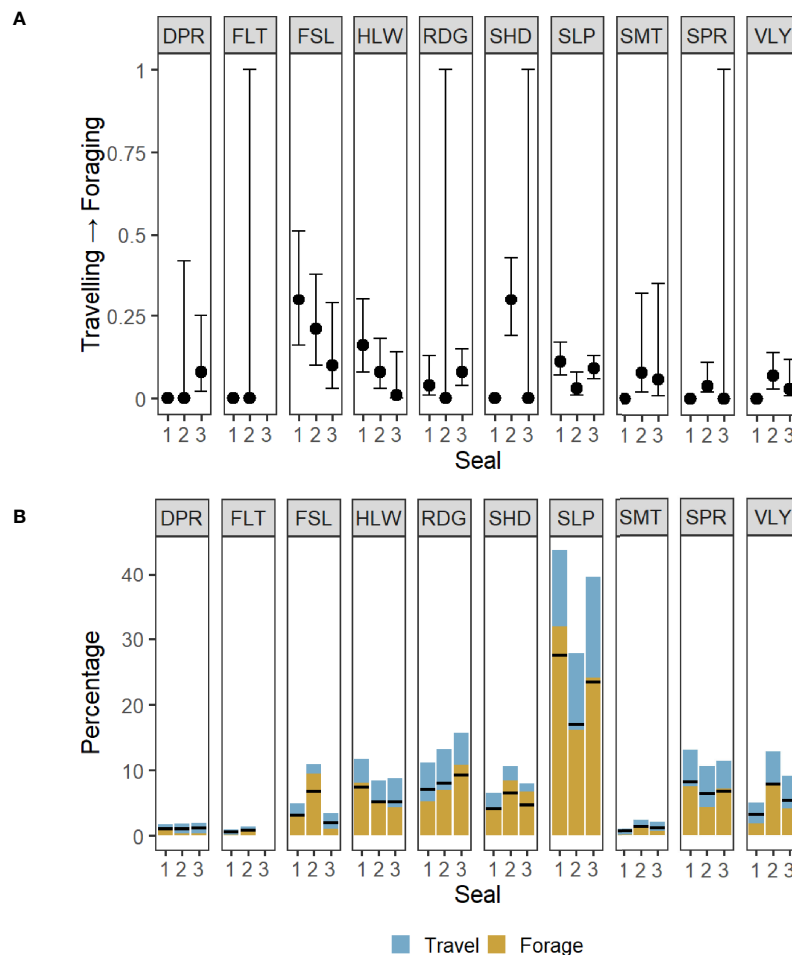


FIGURE 5 | (A) Mean transition probabilities between behavioural states inferred from the states assigned by the covariate HMM with 95% confidence intervals. There was an increased likelihood of switching from travelling to foraging for all three seals in association with the following geomorphons: footslope (FSL), slope (SLP) and hollow (HLW). Where the confidence intervals are 0, seals never transitioned out of the state they were in upon encountering that feature. But where CIs are wide (0-1), although there may have been an influence of that feature on transitioning from foraging to travel, there was no instance of the seal transitioning out of travelling upon encountering that feature. **(B)** Percentage of total time (per seal) spent in foraging or travelling state at each feature type. Horizontal black bars show the relative mean percentage of time seals are expected to be in the foraging state based on activity budgets: Seal 1 = 63%, Seal 2 = 61%, Seal 3 = 59%. A disproportionately large amount of time was spent foraging over slope features for Seal 1, footslopes (FSL) and shoulders (SHD) for Seal 2, and ridges (RDG) and shoulders for Seal 3. For all feature type abbreviations see **Table 3**.

(Figure 5). Slopes exposed to currents (e.g. on the fringes of the Dogger Bank where Seals 1 and 3 foraged) are known to produce tidal fronts and upwellings, leading to increased productivity and accumulation of plankton, and in turn, increased numbers of prey species (Ingram et al., 2007; Morato et al., 2010; Reisinger et al., 2018; Bouchet et al., 2020). Beyond the importance of slopes, there were differences among individuals in the variety of geomorphons that influenced the transition from travelling to foraging behaviour, and where foraging was concentrated (Figure 5). These differences between the seals could be caused by various factors. Firstly, individual preference has been shown to be an important factor in foraging behaviour of seals and other marine predators (Ostfeld, 1982; Tollit et al., 1998; Sargeant et al., 2005). Some individuals might have prior spatial memory of where

certain geomorphological features exist, but different individuals might also have varying prey preferences and distinct prey capture strategies. Indeed, Carter et al. (2020) found that, for grey seal pups, foraging patches encountered on initial exploration after first leaving the natal colony are re-visited in subsequent directed foraging trips throughout early life, suggesting that spatial memory plays a key role in the development of foraging habitat preferences. Maxwell et al. (2012) also found that some individual northern elephant seals (*Mirounga angustirostris*) returned to the same seamount chain in the North Pacific Ocean on discrete trips, suggesting a maintained knowledge of profitable foraging areas. As well as differences in previous experience, sex differences in diet composition have been reported for grey seals in the Northwest Atlantic, which may relate to sex differences in body size and

TABLE 3 | Effect sizes with 95% confidence intervals (CIs) for the probabilities of transitioning between travelling and foraging for each seal for each geomorphon.

Geomorphon	Seal reference					
	1		2		3	
	Effect size (CIs)	No. of locations (Forage: Travel)	Effect size (CIs)	No. of locations (Forage: Travel)	Effect size (CIs)	No. of locations (Forage: Travel)
Depression (DPR)	0 (0, 0)	30 (16:14)	0 (0, 0.42)	54 (10:44)	0.08 (0.02, 0.25)	42 (8:34)
Flat (FLT)	0 (0, 0)	17 (2:15)	0 (0, 1)	42 (30:12)	NA	0 (0:0)
Footslope (FSL)	0.30 (0.16, 0.51)	83 (55:28)	0.21 (0.10, 0.38)	328 (284:44)	0.10 (0.03, 0.29)	74 (22:52)
Hollow (HLW)	0.16 (0.08, 0.3)	199 (138:61)	0.08 (0.03, 0.18)	253 (148:105)	0.01 (0, 0.14)	191 (95:96)
Ridge (RDG)	0.04 (0.01, 0.13)	190 (90:100)	0 (0, 1)	394 (209:185)	0.08 (0.04, 0.15)	341 (235:106)
Shoulder (SHD)	0 (0, 0)	110 (73:37)	0.30 (0.19, 0.43)	317 (254:63)	0 (0, 1)	175 (146:29)
Slope (SLP)	0.11 (0.07, 0.17)	743 (543:200)	0.03 (0.01, 0.08)	834 (485:349)	0.09 (0.06, 0.13)	864 (525:339)
Summit (SMT)	0 (0, 0)	19 (2:17)	0.08 (0.02, 0.32)	71 (38:33)	0.06 (0.01, 0.35)	45 (15:30)
Spur (SPR)	0 (0, 0)	222 (127:95)	0.04 (0.02, 0.11)	316 (132:184)	0 (0, 1)	247 (156:91)
Valley (VLY)	0 (0, 0)	86 (32:54)	0.07 (0.03, 0.14)	385 (234:151)	0.03 (0.01, 0.12)	199 (91:108)

Where the confidence intervals are 0, seals never transitioned out of the state they were in upon encountering that feature. But where CIs are wide (0-1), although there may have been an influence of that feature on transitioning from foraging to travelling, there was no instance of the seal transitioning out of travelling upon encountering that feature.

metabolic strategies (Beck et al., 2007). Sex-specific diet may translate to sex-specific associations with habitat. Given that we selected three seals which show reasonably discrete foraging areas for this case study, a further study on a larger dataset is required to examine possible sex differences in habitat associations, and if features used by all three seals studied here remain important at the population level.

Our results show that categorising seabed topography using geomorphological shapes can provide a tractable static covariate to investigate marine predator habitat use across the foraging range of an individual. This covariate may also provide further insight into predator-habitat associations when considered in studies focussed on discrete known foraging areas, such as the fringes of the Dogger Bank identified here for grey seals. Given the complexity of interactions between topography and tidal currents that underpin a wide variety of mechanisms affecting prey behaviour and distribution (Cox et al., 2018), geomorphons could be combined with hydrographic data, such as tidal currents and frontal intensity, to elucidate patterns of predator behaviour and space use at fine spatial and temporal scales. Hydrodynamic features resulting from an interplay between topography and currents can be modelled at increasingly fine resolution and included in models of predator habitat associations (Embling et al., 2012; Scott et al., 2013). However, such spatially and temporally discrete features applied to movement data across the individual's foraging range are not likely to prove insightful. Moreover, although hydrodynamic features may provide important foraging habitat for aerial predators such as seabirds [as demonstrated by Scott et al. (2013)] and seals in tidally

energetic coastal channels (Hastie et al., 2016), the role of tides may be less important for benthic foragers in the southern North Sea; our results show that individual grey seals remain in certain foraging patches across multiple tidal cycles during multi-day foraging trips (**Figure 4**). This suggests that other static components of habitat (such as the potential for certain topographic features to aggregate benthic prey) may be more influential drivers of behaviour than hydrodynamic processes for grey seals. However, an assumption about the movement data in this analysis was that the seals exhibited two behavioural states at sea. Seals routinely spend prolonged periods at the surface, which may be conflated with ARS when using location data in movement models (McClintock et al., 2013; Russell et al., 2015). This surface behaviour is likely related to digestion (Sparling et al., 2007), and thus probably occurs in foraging areas. While not accounting for resting therefore likely does not impact our findings, future studies of switching from foraging to resting in relation to tidal state may provide further insight into the temporal dynamics of habitat use. Exploring the influence of geomorphons on behaviour in conjunction with other static covariates is also an important avenue for future research. For example, although we have shown that encountering a certain feature type can influence the decision for seals to switch from foraging to travelling, the role of the environment in shaping how seals navigate to these features remains unclear. It is possible that other metrics such as depth gradients or changes in substrate type may be useful in elucidating how individuals navigate to fine-scale features. Moreover, combining geomorphons with information from other static covariates such as aspect in

holistic habitat models may lead to better understanding of the functional significance of individual features.

The effect size of some of the geomorphons was small (< 0.1) and this could be related to the probability that a seal will encounter this feature type. For example, flat areas were not frequently encountered by any of the seals, and thus had no effect on foraging behaviour (Figure 5). However, large flat areas are present within the foraging range of the seals (Figure 3). To determine if certain features are preferentially selected or avoided, use of geomorphons could be modelled in a use-availability habitat preference framework (Aarts et al., 2008). Such models allow us to quantify if the use of a habitat type is proportionate to its availability within the environment accessible to the study animal (Aarts et al., 2008). However, a caveat of this approach is that it assumes that the individual has complete knowledge of their accessible environment, and thus chooses to go to certain areas despite the known existence of alternative habitat elsewhere. In reality this may not be the case. Nevertheless, combining insights from individual-focussed mechanistic studies such as ours with population level habitat preference models would be a valuable line of future investigation to understand the wider importance of different feature types and predict the location of important foraging areas.

Our case study has demonstrated the potential for this approach to provide useful information for conservation management. For example, the importance of the Dogger Bank is widely acknowledged for both commercial fisheries (Sell and Kröncke, 2013) and a range of predator species (Hamer et al., 2000; De Boer, 2010; Hammond et al., 2013; Gilles et al., 2016), yet the mechanisms influencing predator behaviour and distribution are less well understood. Our results suggest that slopes and slope-like features on and around the bank may be especially important for seals. The southern North Sea (and Dogger Bank in particular) is an area of rapid offshore wind development, with numerous large turbine arrays currently at various stages of planning, consenting, construction and operation. The impact of such developments on important prey species, and the implications for grey seal foraging habitat remain unknown. Russell et al. (2014) found that some individual harbour (*Phoca vitulina*) and grey seals repeatedly forage at established wind turbines and other anthropogenic structures, suggesting that novel foraging habitat is created due to artificial reef effects that arise from placing a solid structure in an otherwise sandy or soft sediment environment (Wright et al., 2020). However, artificial reefs may concentrate prey that would otherwise be distributed elsewhere, leading to increased competition and vulnerability to over-exploitation (Pickering and Whitmarsh, 1997). Moreover, seals are known to exhibit short-term avoidance of areas during pile driving for wind turbine installation (Russell et al., 2016), but it is unclear what the fitness consequences of such disturbance might be. The continued expansion of offshore anthropogenic structures in the North Sea may therefore have complex implications for marine predator foraging behaviour, as well as trophic dynamics and species interactions in the wider ecosystem. Further research is needed to understand the environmental

characteristics of important foraging habitat, and the possible long-term consequences for predator populations of modifying such habitat.

CONCLUSION

This study found that incorporating seabed geomorphology into behavioural models improved predictions of habitat use by a marine predator in the southern North Sea and provided new insights into foraging behaviour. Although originally developed for terrestrial applications, we demonstrate how the geomorphon algorithm can be used to provide geomorphology datasets for shelf seas using bathymetry data, where other datasets (e.g. Harris et al., 2014) are not resolved to detect discrete seabed features. Metrics such as slope and aspect have been used to explore the environmental drivers of foraging in cetaceans (e.g. Hastie et al., 2003), seals (e.g. Maxwell et al., 2012) and seabirds (e.g. Suryan et al., 2006; Carpenter-Kling et al., 2020), and although these studies have provided some key insights into how predators exploit seabed terrain, habitat selection may be influenced by specific patterns beyond the presence and gradient of slope. Moreover, in highly heterogeneous environments such as shelf seas, a more complex representation of the seabed topography than simple gradient metrics may be necessary to understand its relationship to predator activity (Bouchet et al., 2020). Furthermore, where gradient computation requires a single user-defined scale to be set, the geomorphon algorithm allows flexibility in the size of mapped landforms, identifying landforms at the most appropriate scale for the habitat and study species (Stepinski and Jasiewicz, 2011). This provides a more tractable representation of the habitat, allowing better visualisation of the seabed terrain that individual animals encounter, and facilitating biological interpretation of movement models. When used in conjunction with other metrics, this approach may reveal key insights about scale-dependence of habitat associations and further our understanding of how predators interact with, and respond to, their environment. Our study highlights an avenue for future research to gain more ecological understanding of the mechanistic influence of seabed terrain on marine predator behaviour and distribution, and aid the identification and delineation of important habitats. Improving our understanding of what features characterise important predator foraging habitat is essential in assessing how marine ecosystems will be affected by changes caused by anthropogenic habitat modification, overfishing and climate change (McCauley et al., 2015). Moreover, better identification of important foraging areas for marine predators will lead to more effective marine spatial planning and conservation management for the wider ecosystem.

DATA AVAILABILITY STATEMENT

Sources of environmental data are outlined in the methods section. Other data are available upon request from the authors. Requests to access these datasets should be directed to Dr Debbie Russell (dr60@st-andrews.ac.uk).

ETHICS STATEMENT

The animal study was reviewed and approved by the University of St Andrews Ethics Committee. Capture, handling and tagging of seals was carried out under UK Home Office project licence 60/4009 under the Animals (Scientific Procedures) Act 1986. The capture of seals was conducted under licence from the Marine Management Organisation (England) with necessary approvals from Natural England for work on designated sites.

AUTHOR CONTRIBUTIONS

Designed the experiment: LB, DJFR, MIDC, HMEW. Collected the data: DJFR. Processed the data: HMEW, MIDC. Analysed the data: HMEW. Wrote the manuscript: HMEW and MIDC. Edited the manuscript: DJFR and LB. All authors reviewed the final version of the manuscript and gave consent for submission.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.818635/full#supplementary-material>

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The Beat Goes On: Humpback Whale Song Seasonality in Antarctic and South African Waters

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Little is known of the movements and seasonal occurrence of humpback whales (*Megaptera novaeangliae*) of South Africa and the Antarctic, populations once brought to near extinction by historic commercial whaling. We investigated the seasonal occurrence and diel-vocalizing pattern of humpback whale songs off the west coast of South Africa (migration route and opportunistic feeding ground) and the Maud Rise, Antarctica (feeding ground), using passive acoustic monitoring data collected between early 2014 and early 2017. Data were collected using acoustic autonomous recorders deployed 200–300 m below the sea surface in waters 855, 1,118 and 4,400 m deep. Acoustic data were manually analyzed for humpback whale vocalizations. While non-song calls were never identified, humpback whale songs were detected from June through December in South African waters, with a peak in percentage of acoustic occurrence around September/October in the austral spring. In Antarctic waters, songs were detected from March through May and in July (with a peak occurrence in April) where acoustic occurrence of humpback whales was negatively correlated to distance to the sea ice extent. Humpback whales were more vocally active at night than in the day at all recording sites. Detection range modelling indicates that humpback whale vocalizations could be detected as far as 18 and 45 km from recorders in South African and Antarctic waters, respectively. This study provides a multi-year description of the offshore acoustic occurrence of humpback whales off the west coast of South Africa and Maud Rise, Antarctica, regions that should continue to be monitored to understand these recovering populations.

Keywords: seasonal occurrence, humpback whales, passive acoustics, diel-vocalizing patterns, Antarctica, South Africa, songs

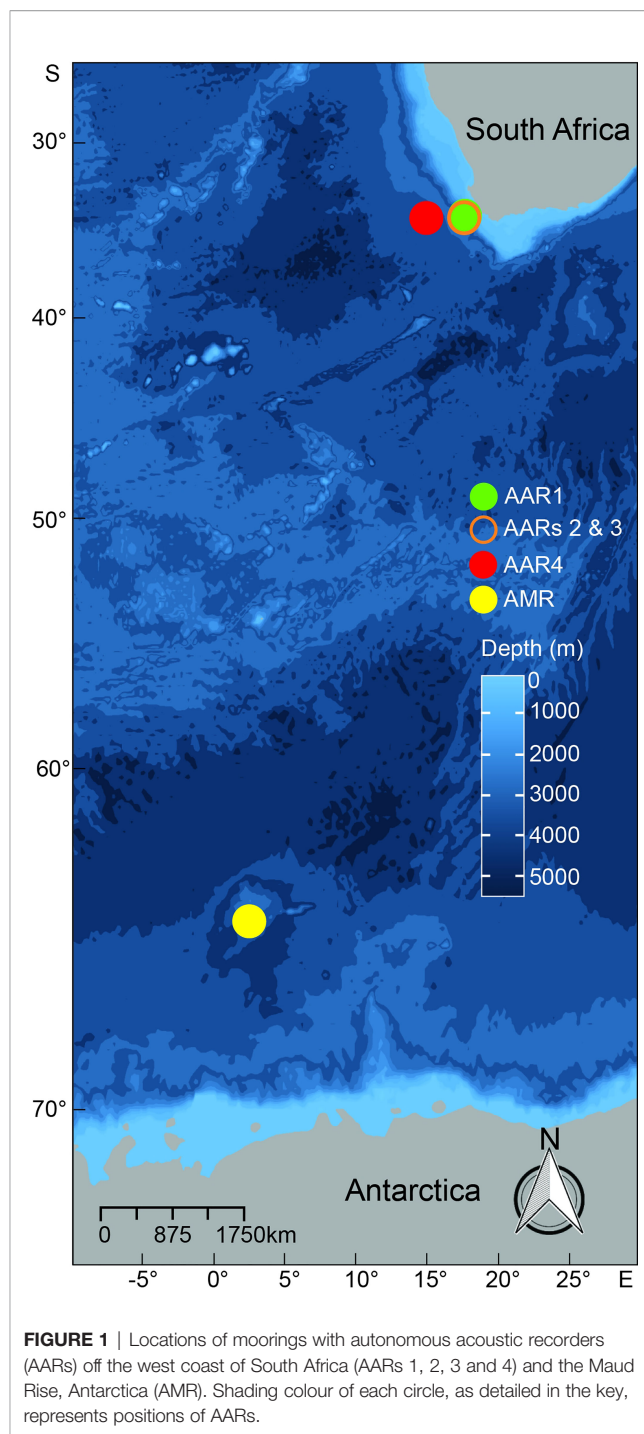
INTRODUCTION

Southern Hemisphere humpback whales (*Megaptera novaeangliae*) perform impressive seasonal migrations between their austral summer feeding grounds in Antarctica and their winter breeding and calving grounds in low latitudes. The distribution and migration of humpback whales are believed to be driven by food availability, suitable environmental conditions, and reproductive

status (Matthews, 1938; Lockyer, 1984; Best et al., 1995; Brown et al., 1995; Pomilla and Rosenbaum, 2005; Purdon et al., 2020; Dey et al., 2021; El-Gabbas et al., 2021; Reisinger et al., 2021; Schall et al., 2021a; Schall et al., 2021b). Off the west coast of South Africa, current knowledge on humpback whale occurrence is based on whaling data (Olsen, 1914; Mackintosh, 1942; Best, 2007; Best and Allison, 2010), sighting data (e.g., Best et al., 1995; Findlay and Best, 1995; Barendse et al., 2010; Barendse et al., 2011; Barendse et al., 2013; Purdon et al., 2020), and one coastal (i.e., adjacent to the coast and shallower than 100 m water depth) acoustic study (Ross-Marsh et al., 2021). In the Southern Ocean, the known seasonal occurrence of humpback whales is based on whaling data (e.g., Mackintosh, 1942), sighting data (e.g., Thiele et al., 2004) and five acoustic studies (McKay et al., 2004; Van Opzeeland et al., 2013; Schall et al., 2020; Schall et al., 2021a; Schall et al., 2021b). There is a general knowledge gap in spatio-temporal occurrence of humpback whales in both these regions since whaling data is dated, sighting data are mainly limited to spring and summer, and acoustic studies have been limited to inshore waters or ice edge regions to the marginal ice zone. More research is required in both Antarctic and South African waters to improve our knowledge of humpback whale movements and distribution and how the species adapts to ecological variabilities over time. As the species continues to recover from the impacts of historic whaling, this information is critical to understanding their trends in occurrence that can inform management and mitigations for multiple populations.

Humpback whales are vocally active making them ideal for passive acoustic monitoring (PAM). Their vocalizations can be categorized into non-song and song (Payne and McVay, 1971; Dunlop et al., 2007; Dunlop et al., 2008; Cholewiak et al., 2013). Non-songs are produced by males, females, and calves throughout the year and are used for a wide range of purposes including foraging and social interaction (e.g., Stimpert et al., 2007; Parks et al., 2014; Videsen et al., 2017; Fournet et al., 2018). In addition to non-song calls, male humpback whales produce complex rhythmic songs and singing can last for several hours (e.g., Payne and McVay, 1971; Cholewiak et al., 2013). Songs are made up of units, phrases, and themes, and a series of repeated songs makes up a song session (Cholewiak et al., 2013). Whales within the same breeding ground sing a rendition of the same song, and songs change through time and can spread across different regions *via* social learning (e.g., Dunlop et al., 2007; Garland et al., 2013; Garland et al., 2017). Songs are a largely seasonal reproductive display produced prolifically on the breeding grounds, as well as during migration, and on feeding grounds pre- and post-migration (Edds-Walton, 1997; Dunlop and Noad, 2016; Gridley et al., 2018; Kowarski et al., 2021; Ross-Marsh et al., 2021). Song notes can range in frequency from approximately 20 Hz to above 24 kHz (Au et al., 2006; Stimpert et al., 2007; Zoidis et al., 2008; Cholewiak et al., 2013).

Here, we use PAM to monitor the acoustic occurrence of humpback whales over long-periods of time in regions difficult to monitor regularly by visual techniques. PAM was employed in two regions of known ecological significance: the west coast of South Africa and the Maud Rise Seamount (**Figure 1**). Humpback whales off the west coast of South Africa belong to the Breeding Stock B1



(Best, 2011), Breeding Stock B2 (Rosenbaum et al., 2004; Rosenbaum et al., 2009), and possibly Breeding Stock C (Findlay et al., 2017) that breed in Angola, Congo, Gabon, Gulf of Guinea, Namibia or Mozambique (Best et al., 1995; Best and Allison, 2010; Best, 2011). Whales off the Maud Rise belong to Breeding Stocks B, C and D (Amaral et al., 2016; Schall et al., 2021b). Both regions are positioned within the boundaries of the International Whaling Commission (IWC) Southern Hemisphere Management Area III

(Donovan, 1991). The west coast of South Africa (**Figure 1**) is found in the southern Benguela ecosystem, an area which is characterized by the strong wind-driven upwelling regime of the Benguela Current (Shannon, 2009). Cold, nutrient rich waters of the Benguela ecosystem support the occurrence of high numbers of marine mammals (Best, 2007; Shabangu et al., 2019; Shabangu et al., 2020a; Shabangu and Andrew, 2020; Shabangu et al., 2021; Letsheleha et al., 2022). Humpback whales have been observed off the west coast of South Africa feeding opportunistically on euphausiids (possibly *Euphausia lucens*), amphipods (*Themisto gaudichaudi*), copepods and clupeid fish such as sardine (*Sardinops sagax*) and anchovy (*Engraulis encrasicolus*) (Olsen, 1914; Matthews, 1938; Best et al., 1995; Findlay et al., 2017). The Maud Rise (**Figure 1**) is a seamount in the eastern Weddell Sea characterized by topographically induced upwelling of relatively warm ($>1^{\circ}\text{C}$), nutrient-rich deep water, which enhances phytoplankton blooms and breaks sea ice in winter to form polynyas and initiates sea ice melt in spring (e.g., Comiso and Gordon, 1987; Hellmer, 2007; Gordon, 2009). Due to phytoplankton blooms, large swarms of Antarctic krill *Euphausia superba* are usually present around the Maud Rise (Everson, 2000). As a result, krill-eating predators, such as seals, blue whales, and humpback whales, return to the Maud Rise annually (e.g., Matthews, 1938; Shabangu et al., 2017; Shabangu and Rogers, 2021).

No offshore description of the acoustic occurrence of humpback whales exists in South African waters, and likewise, humpback whale occurrence has not previously been studied off the Maud Rise, Antarctica. We aim to fill this knowledge gap by studying PAM data collected between 2014 and 2017. Estimates of detection ranges of humpback whale vocalizations are provided for the recording sites based on acoustic propagation modelling. Results of this study are placed within the context of other baleen whale acoustic occurrence previously described from these same recordings. This information on seasonal occurrence and behavior of humpback whales can inform the assessment of the ecology and the appropriate management of breeding stocks in Antarctic and South African waters.

MATERIALS AND METHODS

Data Collection

Acoustic recordings were collected between early 2014 and early 2017 from four PAM stations off the west coast of South Africa,

and the Maud Rise, Antarctica (**Figure 1**) as part of the South African Blue Whale Project (SABWP; Shabangu et al., 2019). We used autonomous acoustic recorders (AARs) of Autonomous Underwater Recorder for Acoustic Listening-Model 2 version 04.1.3 (Multi-Électronique Inc., Canada). AARs were deployed on oceanographic moorings (Shabangu et al., 2019) in three locations off the west coast of South Africa, and on an acoustic mooring off the Maud Rise, Antarctica (**Figure 1**). Settings and sampling protocols for each AAR are detailed in **Table 1**.

For diel analysis, hourly sun altitude data were required. Since all AARs off the west coast of South Africa were on the same latitudinal position, we used hourly sun altitudes for each day of the year from $34^{\circ} 22' \text{ S}$, $17^{\circ} 37' \text{ E}$ for all AAR locations. For the Maud Rise, we used the exact location of the seamount ($65^{\circ} 00' \text{ S}$, $2^{\circ} 50' \text{ E}$). We obtained data on sun altitudes from the United States Naval Observatory Astronomical Applications Department (<http://aa.usno.navy.mil>). Daylight regimes (daytime, night-time, and twilight) were classified according to the geometrical position of the centre of the sun relative to the horizon as detailed in Shabangu et al. (2020a) and Shabangu and Andrew (2020).

For Antarctica, monthly sea ice extensions were sourced from the data set ID: G02135 (Fetterer et al., 2016) at the National Snow and Ice Data Centre data pool server: <ftp://sidacs.colorado.edu/DATASETS/NOAA/G02135/shapefiles/>. The distance of the nearest sea ice edge to the AAR off the Maud Rise (AMR) mooring position was measured from the monthly sea ice extents to determine the effects of sea ice on the acoustic occurrence of humpback whales off the Maud Rise. Daily sea ice concentrations (%) were obtained from the satellite sea ice concentration product of the Advanced Microwave Scanning Radiometer-2 with a 3.1 km grid resolution (Spreen et al., 2008; Beitsch et al., 2014).

Humpback Whale Acoustic Occurrence Analysis

All acoustic files were reviewed by an experienced acoustic analyst (FWS) to the Nyquist frequency of each AAR recordings (1,024 Hz for AMR; 2,048 Hz for AARs 1 and 2; 4,096 Hz for AARs 3 and 4). Acoustic data were inspected *via* spectrogram analysis in Raven Pro (Center for Conservation Bioacoustics, 2019). The aim of acoustic analysis was to identify humpback whale vocalizations and subsequently categorized them into songs and non-songs using guidelines from published literature (e.g., Payne and McVay, 1971;

TABLE 1 | Summary of deployment details and recording settings of the five autonomous acoustic recorders (AARs) used in this study.

AAR ID	Latitude (S)	Longitude (E)	Water depth (m)	AAR depth (m)	Sampling rate (Hz)	Sampling protocol (min h ⁻¹)	Hydrophone sensitivity (dB re 1 V/ μPa)	Start recording date	Stop recording date
AMR	65° 00.00'	2° 50.00'	1,267	250	2,048	25	-164.10	12/01/2014	17/09/2014
AAR1	34° 22.21'	17° 37.69'	855	200	4,096	30	-164.20	24/07/2014	01/12/2014
AAR2	34° 23.64'	17° 35.66'	1,118	300	4,096	20	-163.90	16/09/2014	01/12/2015
AAR3	34° 23.64'	17° 35.66'	1,118	300	8,192	25	-164.10	04/12/2015	01/01/2017
AAR4	34° 30.36'	14° 58.81'	4,481	200	8,192	25	-164.20	04/12/2015	13/01/2017

AARs deployed in South African waters are numbered according to order of their chronological deployment. ID stands for identification. Hydrophone sensitivities are from factory calibrations of the HTI-96-MIN (High Tech Inc.) hydrophones.

Stimpert et al., 2012; Cholewiak et al., 2013; Kowarski et al., 2019). Song complexity, in terms of level of hierarchy and repetition of phrases, occurs on a spectrum ranging from the repetition of phrases and sub-phrases over minutes to five or more themes repeated in sequence for hours. To manage this spectrum of complexity, Kowarski et al. (2019) broadly divided songs into full songs, where at least three themes are repeated, and song fragments, which can be as simple as a repeated phrase. Such differentiation of full songs and song fragments can be challenging when working with duty-cycled data or faint acoustic signals and was beyond the scope of the present work. Therefore, the definition of song applied here encompasses both full songs and song fragments where any organization of units into a sequence of phrases or themes was categorized as song. Readers should be mindful of this inclusive definition when interpreting results. Vocalizations not organized into phrases or themes would have been categorized as non-songs, but acoustic signals falling within this definition were never identified. Humpback whale acoustic presence or absence was scored for each acoustic file. The time between which acoustic data were recorded demarcated the sampling session of each AAR (Table 1).

Monthly percentages of humpback whale occurrence for each AAR were calculated as the number of sound files with presence of songs per month divided by the total number of sound files per month. To establish the seasonal diel pattern of humpback whale acoustic occurrence, we divided the number of sampling sessions with humpback whale songs for each hour of the day for that season by the total number of sampling sessions recorded for each hour of the day for that season. Austral seasons were used: summer (December to February), autumn (March to May), winter (June to August), and spring (September to November). Given that time of day is a circular variable, the pattern of diel occurrence of humpback whale songs per season were smoothed through penalized cyclic cubic regression splines (Wood, 2017) in generalized additive models (Guisan et al., 2002). Pearson's correlation (r) was used to determine the relationship between the percentage of humpback whale occurrence and distance to the sea ice extent.

The SABWP acoustic monitoring program was initiated with the aim to study acoustic occurrence of Antarctic blue whales (*Balaenoptera musculus intermedia*). Since then, the acoustic occurrence of Antarctic minke (*B. bonaerensis*), fin (*B. physalus*), southern right (*Eubalaena australis*), and sperm (*Physeter macrocephalus*) whales have been described (Shabangu et al., 2019; Shabangu and Andrew, 2020; Shabangu et al., 2020b; Shabangu et al., 2021; Letsheleha et al., 2022). Humpback whale acoustic occurrence results are interpreted using the current knowledge on both humpback whales and the previously analyzed species in the monitoring areas.

Detection Range Estimation

The objective of detection range estimation was to determine the distance at which humpback whale songs were likely to be detected by our recorders, allowing us to better interpret any variation in occurrence results across recording sites. We used

Detection Range Modelling (DRM) software (JASCO) previously described by Warren et al. (2021) and Delarue et al. (In Press) and summarized here. DRM uses the following inputs to model the detection range of humpback whales at different sites: recorded ambient noise, bathymetry, sound speed profiles, geoacoustic properties, and characteristics of humpback whale vocal behaviour. Ambient sound levels were input in the form of sound pressure levels averaged over one min in each decade band of the recorded data (International Organization for Standardization, 2017; Ainslie et al., 2018; Martin et al., 2019). Bathymetry information for the modelled sites was collected from the SRTM15+ grid (Smith and Sandwell, 1997; Becker et al., 2009). Sound speed profiles were derived from the U.S. Naval Oceanographic Office's Generalized Digital Environmental Model V 3.0 (Teague et al., 1990; Carnes, 2009). Geoacoustic properties for the modelled sites were classified as volcanic rock for the Maud Rise (Huang and Jokat, 2016) and sandy mud for the west coast of South Africa (Birch, 1977). For humpback whale vocalization parameters, we input information on songs as that was the only type of acoustic signal identified during manual analysis (as opposed to non-song calls which have different source levels). Song source levels were modelled at 171.5 dB re 1 μPa^2 (standard deviation of 5.7; Girola et al., 2019). We modelled from 100–1,000 Hz to capture the predominant frequencies in which humpback whale songs occur and assumed the vocalizing source depth to be between 10 and 30 m. We modelled out to a 50 km distance of the recorders, with the option of extending further if results indicated the full detection range was not captured within 50 km. DRM used the aforementioned parameters and the Marine Operations Noise Model (Matthews and MacGillivray, 2013) to estimate the probability of acoustically detecting humpback whales under different noise conditions.

DRM was performed on AAR2, AAR4, and AMR for the month of May. AARs 1, 2, and 3 were not more than 5 km apart (Figure 1), so these recorders would be expected to have a similar detection range and AAR2 was selected to represent them. One month (May) was selected because 1) it was an achievable timeframe over which modelling could be performed, 2) South Africa does not undergo dramatic seasonal fluctuations, thus a single month is likely representative of the entire year in terms of sound propagation, 3) for Antarctica, May is one of the few months humpback whales were confirmed present and 4) May was a time when there was little interference from ocean current-induced mooring noise across the sites. Low frequency mooring noise was a particular issue for AAR1 and AAR4, with the greatest impact under 100 Hz and spanning to 500 Hz (Shabangu et al., in preparation). Manual analysis of humpback whale songs was still effective above 100 Hz and analysts could make out signals through the noise, therefore, because humpback whale vocalization detection was undergone manually (rather than an automated method) we are confident that mooring induced noise did not significantly impact our humpback whale occurrence results, but it was more of a concern for DRM and therefore mooring noise should be considered when interpreting DRM results.

RESULTS

Seasonal Acoustic Occurrence

A total of 1,567 hours were recorded from AAR1, 3,490 hours from AAR2, 3,982 hours from AAR3, and 4,096 hours from AAR4, which yielded a total of 13,135 hours of acoustic recordings from the South African waters (Table 2). A total of 2,479 hours of acoustic data were recorded off the Maud Rise, Antarctica (Table 2). All detected humpback whale vocalizations were classified as songs (Figure 2) from the 15,614 hours of data analyzed. Non-song calls were never confidently identified, though these signals may have been missed amongst the songs, particularly when there were multiple singers. Off the Maud Rise,

the highest number of days and hours with humpback whale songs present were in autumn with few detections in winter (Table 2). In contrast, off the west coast of South Africa, the number of days and hours with detections were high in spring and low in winter with few detections in summer and no detections in autumn (Table 2). With an average of 25% of hours with humpback whale acoustic presence across months, AAR2 had the highest percentage of hours with acoustic occurrence; AARs 3 and 4 had the second highest percentage of hours (20%) with humpback whales while AAR1 had the lowest percentage of hours (15%) with detections (Table 2).

Percentage of humpback whale acoustic occurrence from AMR had a single peak of 71.40% in April, and the lowest

TABLE 2 | Seasonal number and percentage of hours and days containing male humpback whale songs off the west coast of South Africa and the Maud Rise, Antarctica.

AAR ID	Season	Hours recorded	Hours with humpback whale songs	% of hours with humpback whale songs	Number of days recorded	Number of days with humpback whale songs	% of days with humpback whale songs
AMR	Summer	481	0	0	48	0	0
	Autumn	927	281.82	30.40	92	51	55.43
	Winter	927	0.42	0.05	92	1	01.09
	Spring	164	0	0	17	0	0
AAR1	Summer	10	0	0	1	0	0
	Autumn	–	–	–	–	–	–
	Winter	465	12.50	2.69	39	7	17.95
	Spring	1,092	465	42.58	91	65	71.43
AAR2	Summer	715	0	0	91	0	0
	Autumn	729	0	0	92	0	0
	Winter	729	209.88	28.79	92	51	55.44
	Spring	1,317	953.70	72.42	167	140	83.83
AAR3	Summer	1,211	1.26	0.10	120	1	0.83
	Autumn	927	0	0	92	0	0
	Winter	927	275.52	29.72	92	64	69.57
	Spring	917	481.32	52.49	91	64	70.34
AAR4	Summer	1,324	7.56	0.57	132	4	03.03
	Autumn	927	0	0	92	0	0
	Winter	927	156.24	16.85	92	22	23.91
	Spring	917	586.74	63.98	91	68	74.73

– represents period without passive acoustic monitoring effort.

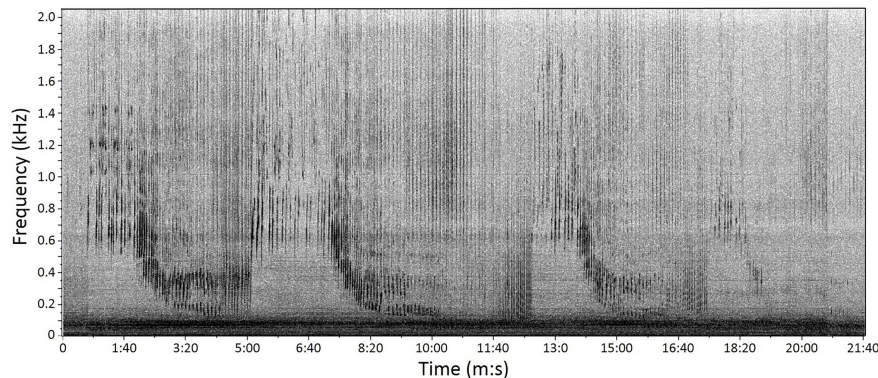


FIGURE 2 | Example of humpback whale song recorded off the west coast of South Africa from AAR2 on 7 July 2015. Spectrogram parameters: frame size 2.32 s, 90% overlap, discrete Fourier transform size 16,384 samples.

percentage of occurrence was 0.13% in July (**Figure 3**). Sea ice concentration was 0% within 3.1 km of the AAR position from 12 January to 20 April 2014 but increased to 50% by the end of April. The AMR mooring position was submerged under sea ice from the beginning of May through mid-September when the recorder stopped working, with sea ice concentrations around 80% at beginning of May and 100% by mid-May through mid-September. Humpback whale songs were first detected in March and continued to be detected even when the AAR mooring position was submerged under sea ice. Percentage of humpback whale occurrence had a weak negative correlation (Pearson's $r = -0.31$) with the distance to the sea ice extent, indicating that the acoustic occurrence decreased with increasing distance to the sea ice extent.

For AARs 1 and 2, the percentage of humpback whale acoustic occurrence peaked in October and were complementary during periods of recording overlap (from September through November 2014), whereas AAR3 peak in acoustic occurrence was in September 2016 (**Figure 3**). AAR4 had a bimodal peak of acoustic occurrence in June and October 2016 (**Figure 3**).

Humpback whale songs were detected from late winter through spring in South African waters, and no humpback whale songs were detected from autumn until mid-winter (**Figure 3**). Songs were detected from August through November for AAR1. For AAR2, songs were detected from September through November in 2014 and from June through November in 2015. Songs were detected in December 2015 and from June through November 2016 for AAR3 (**Figure 3**). For AAR4, songs were detected in December 2015, between June and July, and from September through November in 2016. The seasonal occurrence of songs did not change inter-annually between AARs 2 and 3 that were deployed on the same location (**Figure 3**).

Observed Diel-Vocalizing Pattern

Diel percentages of occurrence of humpback whale songs were lowest between 06h00 and 16h00 in winter and spring for South African waters and in autumn for Antarctic waters (**Figure 4**). Diel percentages of acoustic occurrence were highest between 18h00 and 04h00 for autumn, winter and spring (**Figure 4**). Due to few hours with songs in summer (**Table 3**), no diel occurrence

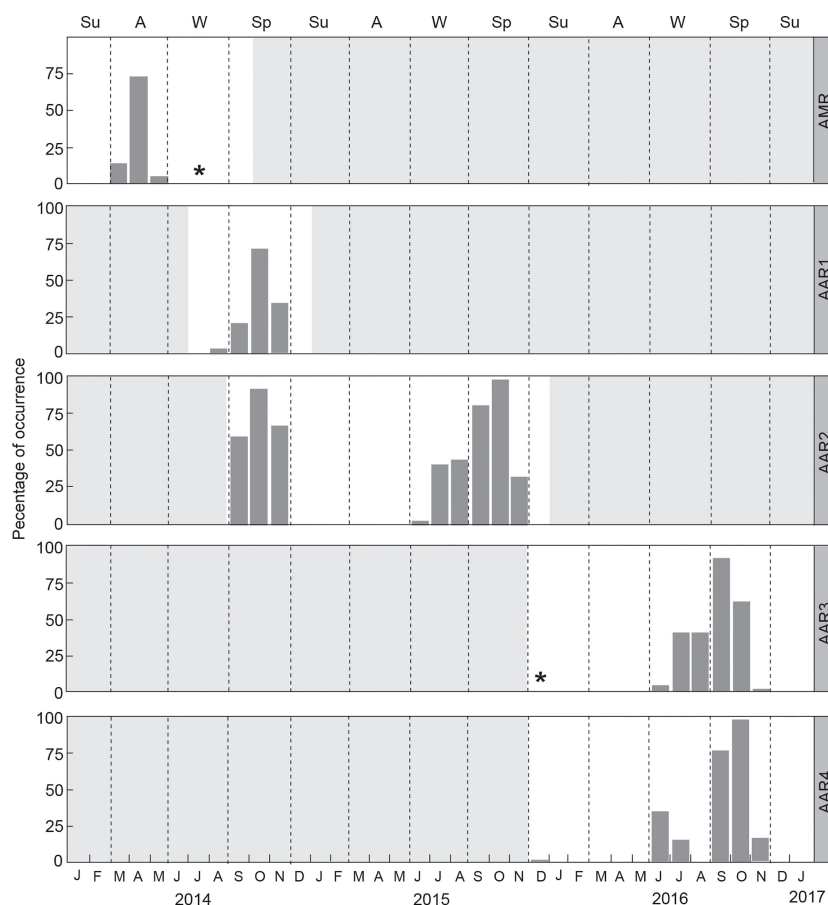


FIGURE 3 | Monthly percentage of acoustic occurrence of male humpback whale songs off the west coast of South Africa and Maud Rise, Antarctica. Asterisks represent cases when the monthly percentage of acoustic occurrence was less than 0.5%. Gray shaded areas designate periods without passive acoustic monitoring effort. Su is summer, A is autumn, W is winter, and Sp is spring are shown on the top axis and defined by dashed lines, and years are stated on the bottom axis.

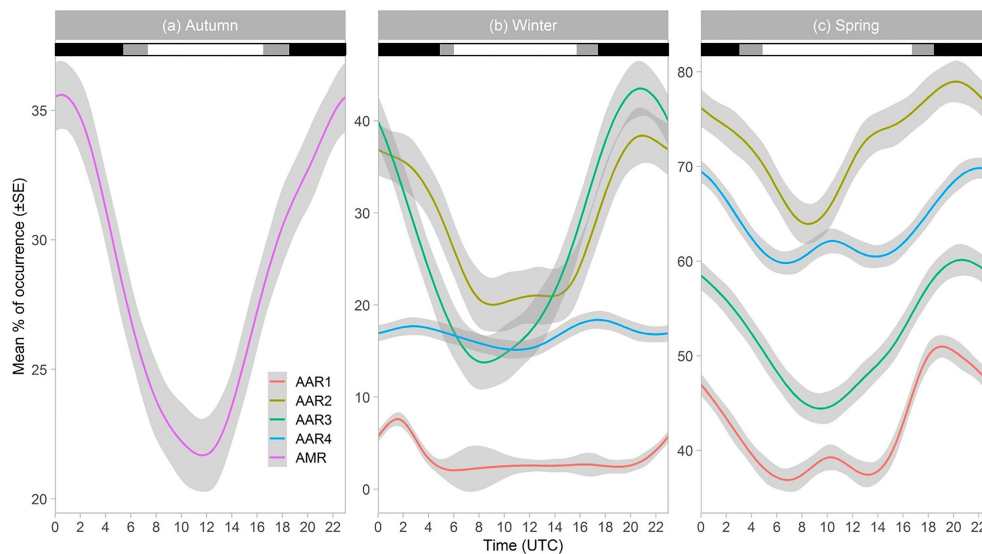


FIGURE 4 | Diel percentage of acoustic occurrence per season for humpback whales off the west coast of South Africa (AARs 1, 2, 3 and 4) and Maud Rise, Antarctica (AMR). Note different y-axes scales. Horizontal bar shadings indicate daylight regime: black represents the average nighttime hours; grey represents average twilight hours; white represents average daytime hours. Grey shading around line plots indicates the standard error (SE). Autumn daylight regime is from the Maud Rise since there was no pattern for South African waters, and remaining daylight regimes are from South African waters since there was no presence data for the Maud Rise. Coordinated Universal Time (UTC) is used.

TABLE 3 | Detection ranges (km) of male humpback whale vocalizations in May around AAR2, AAR4 and AMR.

Recorder	Percentile noise	P_d conditional		
		$P_d=0.1$	$P_d=0.5$	$P_d=0.9$
AMR	NL ₁₀	30.0 – 44.8	5.9 – 15.8	2.0 – 2.2
	NL ₅₀	18.3 – 33.8	4.1 – 7.4	1.5 – 1.6
	NL ₉₀	10.3 – 20.2	2.8 – 3.1	1.1 – 1.3
AAR2	NL ₁₀	8.2 – 18.0	2.2 – 2.3	1.0 – 1.2
	NL ₅₀	2.8 – 11.9	1.6 – 1.7	0.6 – 0.6
	NL ₉₀	1.9 – 2.0	0.8 – 0.9	0.1 – 0.1
AAR4	NL ₁₀	3.0 – 3.6	2.3 – 2.9	0.9 – 1.0
	NL ₅₀	3.0 – 3.5	1.3 – 2.1	0.8 – 0.8
	NL ₉₀	2.8 – 3.1	1.0 – 1.1	0.6 – 0.7

P_d is probability of detecting humpback whale vocalization of 0.1, 0.5, and 0.9, which is based on the source level. The source level is high at 0.1, average at 0.5, and low at 0.9. NL is noise level given in the 10th (NL₁₀), 50th (NL₅₀), and 90th (NL₉₀) percentile.

pattern was established for all sites (Figure 4). Likewise, no diel occurrence patterns were established for AARs 1–4 in autumn and for AMR in winter and spring due to few hours with songs (Figure 4).

Detection Ranges

Quiet noise conditions (NL₁₀) resulted in longer detection ranges, whereas very noisy conditions (NL₉₀) resulted in shorter detection ranges (Table 3). In average noise conditions (NL₅₀) and detection probability ($P_d=0.5$), humpback whales were modelled to be detected at a range of approximately 1 to 8 km from the recorder (Table 3). This detection range is likely an underestimate as a portion of the sound levels in the

humpback whale vocalization band were high due to mooring noise, but manual analysis of spectrograms allowed for songs to be observed through this noise or in the frequencies above this noise.

DISCUSSION

Here, we provide the offshore seasonal and diel acoustic occurrence of male humpback whales off the west coast of South Africa and the Maud Rise, Antarctica. Humpback whales were acoustically present offshore the west coast of South Africa from June through December and off the Maud Rise from March through May and in July. Given that all acoustic data were analyzed manually, the presence results can be considered a reliable representation of the acoustic occurrence of humpback whales in the data. Though, some considerations should be taken when interpreting the present results.

Detectability

Maximum detection ranges were modelled to be limited for some recording sites, particularly for the more offshore station (AAR4). The short detection ranges are likely a reflection of elevated mooring noise which influenced the modelling outputs. Detection range results indicate that, off South Africa's west coast, detected humpback whale songs were produced by animals near the recorder and acoustic signals from more distant animals could have been missed. Detections at these sites should therefore be considered a minimum. For the Maud Rise, which had lower ambient and mooring noise, the detection range

estimation of 40 km likely captures most vocal animals in the region. Low sampling rate used for AMR, AARs 1 and 2 that yielded recordings with Nyquist frequencies below 2,048 Hz could have, in some cases, negatively biased the detection of some songs and song notes that reside above this frequency. Such instances are expected to be rare given that most humpback whale song notes reside, at least in part, below 2,000 Hz and these lower frequencies would propagate further. Mooring noise below 500 Hz (likely generated by mooring strumming during high ocean current speeds) could have masked some songs below this frequency during strong weather events. The impacts of mooring noise were mitigated by analyzing the data manually, where humans are more sensitive to visually identifying partially masked signals than automated techniques. In addition to the above considerations, it must always be considered that PAM techniques will only capture vocally active animals in the region. We currently do not have a quantitative estimate of the above errors, but these recordings provide a good opportunity to estimate the acoustic occurrence of humpback whales and the overarching trends are certainly accurate.

Offshore South Africa's West Coast

Acoustic occurrence of humpback whales off the west coast of South Africa was observed from June through December, which is in conjunction with the humpback whale breeding season and seasonal high productivity of the Benguela ecosystem (Best, 2007; Shannon, 2009; Dey et al., 2021). The high humpback whale song detections from early to mid-spring (i.e., September through October) correspond with high sighting rates of the species at this time of the year in coastal waters where whales were observed moving in both southerly and northerly directions (Best et al., 1995; Barendse et al., 2010; Barendse et al., 2011; Barendse et al., 2013; Findlay et al., 2017). Shore based sightings indicate that humpback whales are present year-round off the Saldanha Bay on the west coast of South Africa, designating some form of inshore residency (Barendse et al., 2010; Barendse et al., 2011). Bimodal peaks (June and October) in humpback whale catches were reported from the Hangklip and Dankegrat Whaling Stations off the west coast of South Africa (Best and Allison, 2010). Our acoustic efforts only detected one peak of acoustic occurrence around September/October for most recording sites except for AAR4 that had a small peak in June and a bigger peak in October, suggesting that humpback whales present off the west coast of South Africa around June were less vocally active, were outside the detection ranges of our AARs, or that the whales changed their migration behavior since the end of the whaling era.

The lack of humpback whale songs between January and May from the offshore locations of our South African AARs was somewhat unexpected given recent indications of inshore residency on the west coast of South Africa by Barendse et al. (2011); (2013). The lack of detections could be due to low numbers of whales in the area (Findlay and Best, 1995; Barendse et al., 2011; Barendse et al., 2013), as call numbers (which are used to calculate call rates) of other baleen whales have been found to increase with whale numbers (e.g., Shabangu et al., 2017).

Alternatively, whales could have been less frequently vocalizing because it was not the breeding season associated with singing or because the residency observed by Barendse et al. (2011, 2013) was dominated by females. Moreover, whales could have migrated out of the South African waters to higher latitudes if environmental conditions and food availability were limiting.

Where there were recordings at the same location over multiple years (AARs 2 and 3), the seasonal occurrence trends were similar, confirming the region is regularly frequented by this species. Coastal acoustic recordings in False Bay, off the west coast of South Africa, similarly detected humpback whale songs in September and October (Ross-Marsh et al., 2021). The coastal song detections of Ross-Marsh et al. (2021) correspond to the peak acoustic occurrence from AARs 1, 2 and 3; indicating that whales may have passed through the offshore stations on their way to coastal areas or vice versa since these locations are about 70 km apart. Off the Walvis Ridge, Namibia, humpback whale non-songs and songs were detected from May through January (Thomisch et al., 2019), which is comparable to our documented offshore acoustic occurrence of the species.

Humpback whale acoustic occurrence was similar between the closely spaced (5 km apart) AARs 1 and 2 during periods of recording overlap, which is different to that observed for other baleen whales such as Antarctic blue and fin whales (Shabangu et al., 2019) and southern right whales (Shabangu et al., 2021) that have different detections between AARs 1 and 2 even though the recorders were only 5 km apart. The difference in percentage of acoustic occurrence between AARs 1 and 2 for both blue and southern right whales was associated with varying AAR depths relative to the thermocline depth, whale vocalizing depth and noise levels between recording sites (Shabangu et al., 2019; Shabangu et al., 2021; Letsheleha et al., 2022). Humpback whales produce sounds from the sea surface to as deep as 175 m (Stimpert et al., 2012), our recorders deployed at different depths were well positioned to equally record vocalizations of these whales. Thus, the difference in acoustic occurrence of humpback whales from this study and whale species from other studies might be caused by different ecological use of the region and differences in vocalizing depths of different whale species.

In August 2016, humpback whales were not detected at AAR4 but were present 240 km away at AA3. Correspondingly, Antarctic minke and sperm whale acoustic signals were also more common at the more inshore stations and simultaneously detected between AARs 1 and 2 but differently detected between AARs 3 and 4 during periods of overlap (Shabangu et al., 2020a; Shabangu and Andrew, 2020). The difference in humpback whale signal detection between AARs 3 and 4 during the period of overlap is due to the great distance between them (i.e., 240 km) and indicates a preference for the more inshore AAR3 waters. Peak humpback whale acoustic occurrence was in October for AARs 1, 2 and 4, suggesting that most humpback whales arrive in the South African west coast around that month or they sing more often during that month. The peak acoustic occurrence for AAR3 was September (spring), indicating that

arrival of whales is slightly early in some years. Barendse et al. (2010) also observed a mid-spring peak of whale occurrence from shore-based observations off Saldanha Bay. Furthermore, difference in peak occurrence between AARs 3 and 4 during time of recording overlap might indicate that whales in the 1,100 and 4,400 m water depths transitioned back and forth between the two sites.

Maud Rise

Off Antarctica, the highest percentage of acoustic occurrence of humpback whales was in April with few detections in May and July, which supports findings of previous studies that showed humpback whales can sometimes inhabit ice-infested areas as they occasionally provide suitable year-round feeding conditions and inhabitable overwintering conditions (e.g., Van Opzeeland et al., 2013; Schall et al., 2020; Schall et al., 2021a; Schall et al., 2021b). The peak occurrence at mid-autumn relates to the high Antarctic krill abundance dominated by large sized zooplankton in late summer (Hewitt et al., 2004), which could indicate that whales were feeding in that region by then. Humpback whales present in Antarctica during winter could be few males that do not migrate to mid- and low latitudes to reproduce (Brown et al., 1995) in efforts to conserve energy associated with migration and reproduction (Lockyer, 1984). Van Opzeeland et al. (2013) detected humpback whale non-songs produced by males and females year-round off the Ekström Ice Shelf, eastern Weddell Sea, and attributed such presence of whales in sea ice-infested waters to food availability and presence of polynyas in that area.

Antarctic blue whales (Shabangu et al., 2020a), Antarctic minke whales (Shabangu et al., 2020b), and crabeater seals (*Lobodon carcinophaga*) (Shabangu and Charif, 2021) were detected acoustically off the Maud Rise during periods of high sea ice concentration. Humpback whales seems to show a different pattern by having little to no detections when sea ice concentration increased above 80% (hence negative correlation with distance to the sea ice extent), likely to avoid resource competition with Antarctic blue and minke whales that increased their acoustic presence with increasing sea ice concentration (Shabangu et al., 2020a; Shabangu et al., 2020b). Additionally, limited acoustic presence could be due to humpback whales moving on with their migration.

Unfortunately, there was little overlap in recording periods between the Antarctic site and South African sites, making it difficult to interpret movements between the areas. Nonetheless, these acoustic detections provide useful information about acoustic occurrence in these regions. The Maud Rise has been shown to be a useful habitat for other marine mammals such as Antarctic blue and fin whales (Shabangu et al., 2020a), minke whales (Shabangu et al., 2020b), crabeater seals (Shabangu and Charif, 2021), and Ross seals (*Ommatophoca rossii*) (Shabangu and Rogers, 2021). Thus, the Maud Rise is likely an important summer foraging habitat for humpback whales given their elevated percentage of acoustic occurrence in austral autumn. It is conceivable that songs were produced while feeding (Stimpert et al., 2012; Gridley et al., 2018). Equally, humpback whales have been observed to sing outside of their breeding grounds in the Southern Ocean IWC Management Area V

between ~68°S and 166°E (Garland et al., 2013). Furthermore, studies around the world have found humpback whales singing outside of breeding grounds (Au et al., 2000; Parks et al., 2014; Kowarski et al., 2017; Kowarski et al., 2019; Kowarski et al., 2021; Martin et al., 2021), and our results from South Africa and the Maud Rise support the notion that this pattern is true for all migratory humpback whale populations. Humpback whales were observed to sing extensively in IWC Management Area II during the years, 2011–2013, but not in 2015–2016, but again in 2017–2018, most likely in relation to El Niño Southern Oscillation (Schall et al., 2021a). It would therefore be informative to collect more long-term data for the Maud Rise and South Africa to investigate the effects of climate variabilities on humpback whale acoustic ecology.

Diel Trends

The increase in humpback whale song detection during nighttime off the west coast of South Africa and the Maud Rise, Antarctica, suggests that humpbacks are more vocally active at night. Likewise, humpback whale songs were modelled to vocalize more at nighttime in the coastal area of False Bay on the west coast of South Africa (Ross-Marsh et al., 2021). To our best knowledge, the diel pattern of humpback whale songs was previously unknown for the Maud Rise although Schall et al. (2020; 2021a) found no diel vocalizing patterns of humpback whale non-songs and songs from multi-year data for sites close to the Maud Rise. Humpback whales have also been observed elsewhere to vocalize more at night; for example, off Angola (Cerchio et al., 2014) and eastern Canada (Kowarski et al., 2017; Kowarski et al., 2019). Parks et al. (2014) showed that humpback whales tagged with multi-sensor acoustic tags in the Gulf of Maine, western North Atlantic, were more vocally active at nighttime while performing relatively shallower dives. In contrast, bottom dives during daytime were not accompanied by sound production when whales were observed with a conspecific nearby (Parks et al., 2014). Sound production during nighttime dives may allow whales to maintain aural contact with conspecifics when visual contact is limited (Au et al., 2000). Likewise, other baleen whales (Antarctic blue, fin, minke and southern right whales) studied from this data were also more vocally active at night (Shabangu et al., 2019; Shabangu et al., 2020a; Shabangu et al., 2020b; Shabangu et al., 2021; Letsheleha et al., 2022).

CONCLUSIONS

We provide the first description of the offshore seasonal occurrence and diel-vocalizing behavior of humpback whales off the west coast of South Africa and the Maud Rise, Antarctica, which both seem to be important regions for this species. High percentages of acoustic occurrence were detected in spring (September/October) off the west coast of South Africa, which corresponds to the breeding season and elevated Benguela Current upwelling activities. Off the Maud Rise, the high percentage of whale acoustic occurrence in mid-autumn

(April) matches the high abundance of Antarctic krill at the end of summer. Whales were more vocally active at nighttime in both regions, potentially to maintain acoustic communication with conspecifics when visual contact was not possible. We found the simultaneous acoustic occurrence of humpback whales between two AARs during time of recording overlap to be different to other baleen whale acoustic occurrence previously described from these same recordings given their vocalizing depths and ecological use of the west coast of South Africa. This study contributes essential knowledge towards improving our understanding of the seasonal occurrence and diel-vocalizing behavior of humpback whales in both regions, which is crucial for understanding their occurrence trends which can inform appropriate management of these breeding stocks. Future work should expand upon the present PAM program to observe trends over extended timeframes, understand movements, and identify critical habitats.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

FS conceived the original idea. FS and KAK designed the study. FS processed the acoustic data, performed the statistical data

analysis, and lead in writing the manuscript. KAK conducted the sound propagation modelling. KAK provided critical feedback and helped shape the research, analysis and manuscript. All authors contributed to the article and approved the submitted version.

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Predicting Foraging Habitat of European Shags - A Multi-Year and Multi-Colony Tracking Approach to Identify Important Areas for Marine Conservation

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Human activity in the coastal zone is increasing worldwide, putting a number of seabird species under pressure. Norway is no exception to this development, and with > 35% of the NE Atlantic population of the currently declining European shag (*Gulosus aristotelis*) population, Norway has an international responsibility for the conservation of this species, and its important foraging habitats during breeding. We analysed tracking data from shags breeding in five colonies along the Norwegian coast spread over a latitudinal gradient of > 1700 km. We identified foraging locations and associated environmental characteristics. Using model cross-validation, we assessed the transferability of habitat models, both spatially (across colonies) and temporally (within colonies and across years), based on three modelling approaches: Training datasets consisted either of the data from one year at one colony, all years at one colony, or all years from all colonies except the testing colony. Across colonies, foraging activity was associated with shallow depths, proximity to colony, and the presence of kelp forests, while sea surface temperature and sea surface height contributed little to model fit. Transferability of habitat use across colonies was low when based on the training data from only one year and one colony and improved little when using several years of data from one colony for training the models. Transferability was very high for all colonies if the training dataset consisted of data from all years and all colonies except the one to be predicted. Our results highlight the importance of multi-year and multi-colony studies and show that it is possible to make sound fine-scale predictions of important foraging areas for breeding shags without the need to track birds in every colony. This facilitates much needed management of coastal marine ecosystems and the protection of the most important feeding areas for breeding shags.

Keywords: expectation-maximization binary clustering (EMBC), Norwegian coastal zone, kelp forest, bathymetry, foraging range, sea surface temperature, sea surface height, model transferability

INTRODUCTION

Coastal zones, although widely acknowledged to be of high ecological and economic value, are also highly vulnerable and impacted by a multitude of human activities (Crain et al., 2008; Brown et al., 2018). These impacts have profound effects on entire food webs, from primary producers to top-predators (Worm et al., 2006; Worm et al., 2009; Poloczanska et al., 2013). Marine spatial planning, and the creation of Marine Protected Areas (MPAs) are increasingly used to counteract the potential detrimental effects of human activities on marine ecosystems (Edgar et al., 2014; Halpern et al., 2015).

Seabirds are among the most threatened taxonomic groups of birds, facing a multitude of mostly anthropogenic stressors (Dias et al., 2019). These range from oil exploration (Votier et al., 2005; Votier et al., 2008), establishment of wind farms (Garthe and Hüppop, 2004; Furness et al., 2013; Peschko et al., 2020), kelp harvesting (Lorentsen et al., 2010; Christensen-Dalsgaard et al., 2020), bycatch (Anderson et al., 2011; Žydelis et al., 2013), ship traffic (Dehnhard et al., 2020a) and fisheries (Cury et al., 2011; Saraux et al., 2020) to various impacts of climate change (e.g. Grémillet and Boulinier, 2009; Keogan et al., 2018), but also include predation by introduced predators (Craik, 1997). Although these stressors affect seabird species differently, and their impact varies geographically, many of them act to make seabird foraging areas particularly relevant for protection (e.g. Davies et al., 2021). Previous approaches to identify important foraging areas for breeding seabirds have largely been based on an existing toolkit by BirdLife International (2010). Where feasible, tracking data, ideally collected over several years, should be used to identify important foraging areas (e.g. Lascelles et al., 2016). Since it is highly unrealistic to track individuals of all species in all colonies, the next best alternative has been to use a standardised foraging range radius around each colony to define the areas most likely used by the seabirds (BirdLife International, 2010; Thaxter et al., 2012). The foraging radius approach is, however, likely to result in the inclusion of substantial areas that are not regularly used by birds for feeding (Thaxter et al., 2012; Soanes et al., 2016). A refinement of this approach, using for example additional environmental covariates such as depth has been suggested (Soanes et al., 2016). An alternative solution could be to predict important foraging areas for a given population based on tracking information from birds in other colonies. This approach has so far been attempted only for a few pelagic seabird species, with varied success (e.g. see Torres et al., 2015; Péron et al., 2018; Fauchald et al., 2021), but to the best of our knowledge not for coastal seabird species.

The European shag (*Gulosus aristotelis*, hereafter: shag) is a coastal benthic foraging seabird with an all-year coastal distribution. In Norway, which had approximately 28,000 breeding pairs in 2013 (Fauchald et al., 2015), constituting about 35% of the NE Atlantic population (Mitchell et al., 2004), shags breed in hundreds of colonies scattered all along the entire western and northern coastlines (Figure 1). While information about critical foraging habitats is highly relevant for

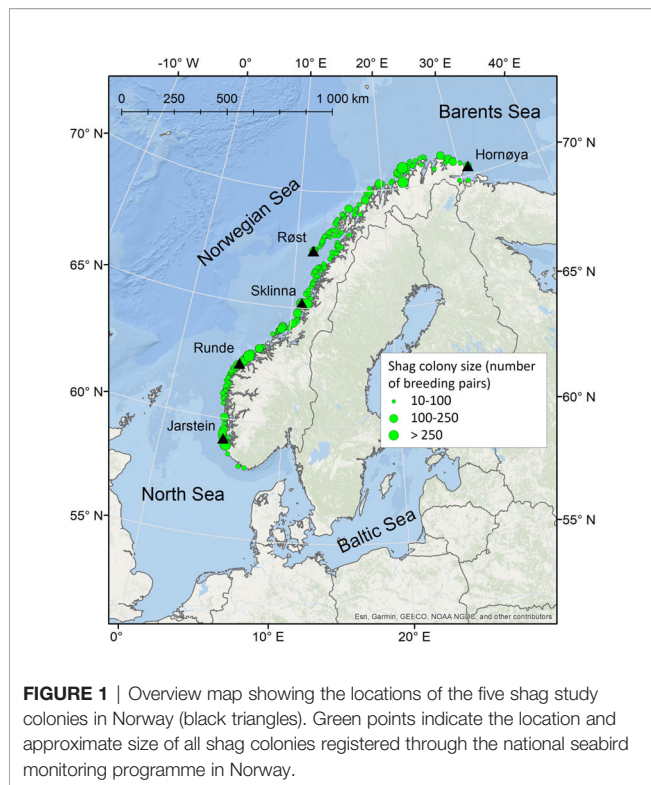
management purposes, it remains an unrealistic task to track shags from every colony. The species therefore represents an ideal case to test whether important foraging areas can be accurately identified for one colony based on habitat use in another colony.

Shags primarily feed on fish (e.g. Hillersøy and Lorentsen, 2012; Howells et al., 2018) and typically show shallow diving patterns in the range of about 15–20 m, although they can dive down to 60 m (Wanless et al., 1997; Evans et al., 2016; Christensen-Dalsgaard et al., 2017). As other seabirds, the species exhibits a typical central-place foraging behaviour during the breeding period (Bell, 1990) with a maximum foraging range of about 20–40 km around their colonies (Bogdanova et al., 2014; Lorentsen et al., 2019). Shags are vulnerable to disturbance by boats (Velando and Munilla, 2011), and incidental mortality in gillnet fisheries (Žydelis et al., 2013; Christensen-Dalsgaard et al., 2019). Furthermore, kelp harvesting in areas used by shags for foraging has the potential to affect foraging success (Christensen-Dalsgaard et al., 2020). Finally, aquaculture installations can easily lead to a reduction in available coastal marine habitat, increased boat traffic and therefore higher disturbance effects, and shags are perceived as a pest by the aquaculture industry (Beveridge, 2001). Licences to cull (shoot) shags are issued on such grounds where shags are expected to cause damage (BirdLife International, 2016).

We tracked breeding shags with GPS loggers in five colonies spread along the Norwegian coast (Hornøya, Røst, Sklinna, Runde and Jarstein; Figure 1). The overarching goal of this study was to identify the foraging areas and associated environmental characteristics in all five colonies and assess the transferability of models of habitat use within colonies (across years; temporal transferability) and across colonies (spatial transferability). Model transferability is a central issue in conservation ecology (Yates et al., 2018; Matthiopoulos et al., 2022), and in the context of our study transferability both within and across colonies is key to sound protecting of foraging areas utilised by shags without having to track birds each year or from each colony.

We first (aim 1) investigated the habitat characteristics and variability in fine-scale (< 1 km) habitat use of shags breeding in the different colonies. Since variability in habitat use within colonies might have confounding effects on the transferability of results from one colony to another, we assessed if the data from one year could be used to predict the habitat use in another year within the same colony (i.e. ‘transferability within colonies’). Aim 2 was to assess the predictability of fine-scale habitat use in a given colony based on environmental habitat characteristics in one or several other colonies (‘transferability across colonies’). With this in mind, we set up three different modelling approaches with different training datasets, in order to find the approach that delivered the best results for transferability across colonies.

We hypothesised that distance to colony would be an important variable in the models describing foraging habitat use, but that foraging range would differ across colonies, e.g. due to inter-colony differences in the number of breeding pairs sharing the foraging grounds (e.g. Jovani et al., 2016). Based on



previous studies (Christensen-Dalsgaard et al., 2017; Grémillet et al., 2020), we further expected that foraging habitats would be characterised by shallow depths and the presence of kelp forests or sandy bottom, representing the habitat preferences of their main prey; gadids (e.g. Hillersøy & Lorentsen, 2012) and sandeel (*Ammodytes* spp., Howells et al., 2018), respectively. Spatial variation in sea surface temperature (sst) and sea surface height (ssh) are typically associated with frontal zones and eddies in the pelagic environment (e.g. Kostianoy et al., 2004; Mason et al., 2014), and upwelling plumes over continental shelves (e.g. Ainley et al., 2009). These variables tend to be important to characterise the habitat of pelagically foraging seabirds (e.g. Pinaud and Weimerskirch, 2005), but we expected them to be less important variables to characterise foraging habitats of the coastal-feeding shags. Finally, we hypothesised that – similar to findings in other seabirds (Péron et al., 2018) – shags breeding in colonies located closer to each other would be more similar in their habitat use compared to colonies further away, and thus that across-colony transferability of the models would decrease with distance between colonies.

METHODS AND MATERIAL

Fieldwork was conducted at Hornøya (70°23'N, 31°09'E; 630 breeding pairs in 2012), Ellefsnyken/Røst (67°27'N, 11°55'E; 345 breeding pairs in 2020), Heimøya/Sklinna (65°12'N, 10°59'E; 2000 breeding pairs on average in 2011–2020), Runde (62°23'N,

5°36'W; 150 breeding pairs in 2020), and Jarstein (59°09'N, 5°10'E, 274 breeding pairs in 2020). These five colonies (**Figure 1**) together represent approximately 10–15% of the total Norwegian shag population and are focal study colonies for the species in the long-term monitoring and mapping programme for Norwegian seabirds, SEAPOP (www.seapop.no/en). Notably, at Hornøya, Røst and Jarstein there are additional, neighbouring shag colonies, located within the foraging ranges of the above-listed study colonies. We do not have exact population numbers for these other shag colonies, but the approximate total number of shag breeding pairs sharing the foraging area was 1000 at Hornøya, 1000 at Røst and 600 at Jarstein. A colony was here defined as an aggregation of more than 10 nests at a given location (e.g. on a single island).

Shags were equipped with either a GPS logger or a combination of a GPS and a temperature-depth (TDR) logger (**Table S1.1, Supplement 1**). The logger types used were I-gotU GT-120 GPS loggers (Mobile Action Technology, modified and re-fitted in heat shrink tubes, 24 g) and remote-downloading solar-driven PathTrack GPS loggers (PathTrack nanoFix® GEO +RF, 21.8 g), as well as G5 TDR-loggers (CEFAS Technology, 6.5 g). I-gotU loggers were programmed to record data at either 30 or 60 second intervals (**Table S1.1, Supplement 1**). PathTrack loggers were programmed to record data on a solar-power-based schedule at either ≥ 30 sec (only a short trial in 2020 at Sklinna) or ≥ 5 min intervals (majority of deployments), with a download frequency of 30 min or less *via* UHF to a fixed base-station positioned within 500 m of the nests. The GPS sampling rates of PathTrack loggers thus automatically downsampled when batteries got depleted (e.g. from 5 min to 10 min, and subsequently 15 min, 20 min, 25 min and so on). Averaged across colonies and years, PathTrack loggers obtained GPS fixes at intervals every 11.75 ± 30.1 min (average \pm SD). TDR loggers recorded data at 1 or 2 second intervals. I-gotU and TDR loggers were joined with tape prior to the deployment and attached to 3–4 middle tail feathers using strips of Tesa tape. PathTrack loggers were also attached to the middle tail feathers, using a thin plastic-plate and a combination of tape and cable ties. Those birds that were equipped with both a PathTrack logger and a TDR, were fitted with a plastic leg-ring to which the TDR-logger was attached. GPS and TDR loggers combined weighed at maximum 31 g, corresponding to $< 1.7\%$ and $< 1.9\%$ of the mean body mass of males and females, respectively.

The nests used in this study were randomly selected among those nests that had approachable adults, and attempts were made to capture equal numbers of males and females when sampling the individuals. Adults were caught on the nest by hand or a noose pole, and sex was determined by size and vocalization (cf. Cramp and Simmons, 1977). The majority of shags deployed with GPS loggers were rearing chicks when loggers were deployed, but some were still in the late phase of incubation (**Table S1.1, Supplement 1**). Birds deployed with I-gotU loggers were recaptured after 1–3 days to recover the devices, and the same happened with the trial birds deployed with PathTrack loggers programmed at the ≥ 30 sec schedule in 2020 at Sklinna. Birds deployed with PathTrack loggers and TDR loggers (combined deployment only at Sklinna) with GPS fixes ≥ 5

min were recaptured after 14–18 days to retrieve the TDR-loggers, but the PathTrack loggers remained attached until they fell off when tail feathers were moulted. Birds deployed with only PathTrack loggers (without TDRs) were not recaptured, and loggers remained attached until the birds moulted their tail feathers. Deployments with I-gotU loggers usually did not take longer than 3 min, while those with PathTrack loggers usually took less than 10 min.

Subsequent GPS Data Analyses

We obtained data from a total of 550 GPS deployments (**Table S1.1, Supplement 1**). Following Lorentsen et al. (2019), we excluded locations within 500 m of their nest sites at all colonies, since these locations are mostly associated with resting and preening activities as well as washing dives. As such, this near-colony habitat is important for the shags but does not represent important foraging habitat. Similarly, any roosting places at or near foraging sites were removed, i.e. when GPS locations were located on land and not at sea. GPS data after the chicks were fledged was excluded from the analysis, assuming a fledging age of 57 days, based on Daunt et al. (2007). Apparent locational outliers were removed using a speed filter with a maximum speed of 30 m/s, and a speed filter of 15 m/s on strongly curvaceous flight paths, as described in Lorentsen et al. (2019).

Following Lorentsen et al. (2019), we defined foraging trips as movement paths ≥ 5 min ≥ 500 m away from the colony. For comparing foraging trip metrics across colonies, we excluded incomplete foraging trips: i.e. trips where 1) locations at the colony were not available either before or after the trip, 2) gaps of > 30 minutes (to account for the GPS-intervals of PathTrack loggers) existed between the last and or first location in the trip and the next or previous location at the colony, and 3) gaps of > 60 minutes existed between locations during the trip. Due to the inability of GPS loggers to acquire locations when submerged (i.e. when the bird is diving), trips recorded by both logger types frequently included gaps between GPS locations. The one-hour cut-off to define incomplete trips was chosen as a conservative measure based on average trip duration (see **Table 1**) and the obtained GPS-intervals.

We identified likely foraging locations of shags based on expectation-maximization binary clustering (EMbC) of the GPS locations (Garriga et al., 2016b). EMbC uses velocity and turning angle to classify movement data into four different clusters aligned with likely behavioural states: low velocities and low turns (LL; “resting”), low velocities and high turns (LH; “intensive search”), high velocities and low turns (HL; “travelling”) and high velocities and high turns (HH; “extensive search”) (Garriga et al., 2016b). EMbC has been shown to be useful across a broad range of species (e.g. Cecere et al., 2020; De Pascalis et al., 2020; Dehnhard et al., 2020b) and comes with the advantage of requiring less supervision, less a-priori assumptions and less computational power than other approaches (Garriga et al., 2016b).

GPS data were analysed in the R-package *EMbC* (Garriga et al., 2016a), using the stack clustering function (*stbc*), which accounts for potential among-individual behavioural differences

by annotating behavioural states for each individual. The stack clustering function was run pooled for all data from all colonies and all years, in order to guarantee the same cut-offs across colonies and years. The pre- and post-smoothing options were set to zero.

To test the performance of our EMbC-based approach to identify foraging locations, we used known diving locations from the colonies and years where TDR data were available (**Supplement 1**). Summary statistics of dive depth and dive duration are presented in **Table S1.2, Supplement 1**. We found a high spatial overlap between the known dive locations and EMbC-states LL (“resting”) and LH (“intensive search”): More than 81% of known dive locations were spatially close (within 200 m) or identical to locations that the EMbC algorithm identified as LL and LH (see **Table S1.3, Supplement 1**). All GPS time-stamps with EMbC states LL and LH were thus defined as foraging locations in further analyses. By doing so, we might characterise some fixes as foraging locations that in fact were not foraging locations, but which still represent an area birds were commuting through.

Environmental Variables

To characterise the habitat use of the shags, we selected five environmental variables, all of which have previously been shown to be important determinants of foraging areas for this species (Christensen-Dalsgaard et al., 2017; Grémillet et al., 2020): bathymetry, slope, kelp presence, sst and ssh. We downloaded bathymetry data from GEBCO (https://www.gebco.net/data_and_products/gridded_bathymetry_data/; spatial grid of 450x450m). Sea bottom slope (in degrees) was calculated from the bathymetry data as the maximum change from the cell to its eight closest neighbours using the raster package in R (Hijmans, 2021). Kelp data were obtained from The Norwegian Environmental Agency (<https://geocortex01.miljodirektoratet.no/Html5Viewer/?viewer=naturbase>). Daily sst and ssh data were obtained from the Norkyst800m model (at a spatial resolution of 800x800m; Albretsen et al., 2011). These data were provided by the Norwegian Meteorological Institute on request for the entire study period, and were obtained from a model version that produced consistent results over this period of time (see Asplin et al., 2020). Instead of working with daily sst and ssh values, which would have substantially complicated our modelling approach, we calculated their means and temporal variances over the period 1st of June – 15th of July for each year. These dates correspond on average to a period of 2 weeks before the first GPS deployment and up to – for most sites and years – the retrieval of the last GPS loggers/data (see **Table S1.1, Supplement 1**), and were consistently used for all colonies. The two-week period prior to the (on average) first deployment was chosen since sst and ssh may affect prey availability and distribution over a longer period of time, and thus may have a lagged effect.

Sea bottom substrate data, which have been proven an important environmental covariate for shag foraging habitats (Grémillet et al., 2020), were downloaded from the European Marine Observation and Data Network (EMODnet) (<http://gis.ices.dk/geonetwork/srv/eng/catalog.search#/metadata/01bf1f24-fdc4-4ee7-af8b-e62cf72fe2f9>). Unfortunately, data quality in the

TABLE 1 | Foraging trip metrics per colony and year obtained from complete foraging trips (see Methods).

Colony & Year	N	Average max trip distance from Colony (km) \pm SD	Max distance from colony reached (km)	Average trip duration (min) \pm SD	Max trip duration (min)
Hornøya 2011	157 (32)	11.5 \pm 5.4	18.79	88 \pm 109	781
Hornøya 2012	113 (23)	7.7 \pm 4.5	17.32	81 \pm 111	721
Røst 2019	590 (7)	2.5 \pm 1.5	7.39	168 \pm 267	1561
Røst 2020	42 (3)	3.4 \pm 2.2	8.64	216 \pm 260	1561
Sklinna 2011	70 (35)	15.7 \pm 9.1	36.29	165 \pm 189	240
Sklinna 2012	33 (26)	18.0 \pm 7.6	27.92	242 \pm 229	1201
Sklinna 2013	75 (26)	18.1 \pm 7.2	26.44	223 \pm 209	1081
Sklinna 2014	167 (53)	9.9 \pm 8.5	27.77	126 \pm 125	901
Sklinna 2015	74 (27)	14.1 \pm 8.2	28.83	178 \pm 171	1021
Sklinna 2016	87 (35)	15.5 \pm 8.0	26.31	174 \pm 138	901
Sklinna 2017	199 (58)	14.5 \pm 8.1	27.09	121 \pm 87	841
Sklinna 2018	148 (38)	14.9 \pm 9.3	27.17	138 \pm 115	600
Sklinna 2019	153 (49)	10.4 \pm 8.7	28.02	130 \pm 135	841
Sklinna 2020	646 (57)	13.2 \pm 8.4	38.89	140 \pm 146	1081
Runde 2017	16 (5)	4.5 \pm 3.7	12.26	131 \pm 169	1741
Runde 2020	1668 (11)	4.2 \pm 2.1	24.64	110 \pm 202	721
Jarstein 2019	568 (7)	2.9 \pm 2.9	21.12	49 \pm 154	3122
Jarstein 2020	458 (9)	3.4 \pm 2.2	15.70	47 \pm 73	3122

N gives the number of trips with the number of individuals in brackets.

coastal areas were poor and for 57% of the likely foraging locations, the substrate type was unknown. We therefore refrained from including sea bottom substrate into our analyses.

Definition of Available Habitat - Creation of Random Points

We followed the approach of Christensen-Dalsgaard et al. (2017) and defined available habitat as the area within reach for breeding birds around their colonies, and thus created a circular buffer around each colony. The radius of this buffer was set as the maximum distance between a foraging location and the colony, which was largest for Sklinna (40 km), followed by Runde (25 km), Jarstein (22 km), Hornøya (19 km) and Røst (9 km). To create a representative sample of available habitats within these areas, five point locations were created randomly for each GPS fix defined as a foraging location within the defined available area, using the R-package *sp* (Pebesma and Bivand, 2005; Bivand et al., 2013). As we include temporal environmental variables in the model, the process was done separately for each year. Land areas within the circular buffers were removed before generating random locations. All foraging locations and random locations were intersected with the environmental layers using the function “extract” in R-package *raster*.

Modelling Approach

All statistical procedures were carried out in R (R Development Team, 2020). To assess if maximum foraging distance differed across colonies, we ran a linear mixed-effects model (LMM) using function *lmer* from package *lme4* (Bates et al., 2015). The LMM contained maximum trip distance from the colony (only for complete foraging trips) as dependent variable, and colony as explanatory variable (factor). Bird ID was included as a random factor, nested within year and colony. We further present marginal and conditional R^2 values as calculated from the R-package *performance* (Lüdtke et al., 2021) and to identify

differences among colonies, we ran a Tukey *post-hoc* test (R-package *multcomp*; Hothorn et al., 2008).

To investigate marine habitat preferences (aim 1), we ran generalised additive models (GAMs) with a binomial distribution (1 = foraging locations, 0 = availability, i.e. random locations). GAMs were run using the R-package *mgcv* (version 1.8-38; Wood, 2017) with a logit link function. Generalised additive models allow the fitting of non-linear responses to predictor variables, which is a major advantage, as animals rarely respond linearly to their environment (Aarts et al., 2008; Dehnhard et al., 2020b). Similarly to Christensen-Dalsgaard et al. (2017), GAMs were fitted using thin plate regression smoothing (Wood, 2017). We initially set the maximum number of knots for smooth terms to 5 in order to avoid overfitting, and used the functions “gam.check” to check whether models with more knots had a better fit. We followed a forward-stepwise approach to add environmental covariates, and modelled the environmental habitat preferences separately for each colony. The initial models therefore contained year (as a fixed factor), and one environmental covariate, either as fixed factor (kelp) or as smooth term (depth, slope, distance to colony, sst mean, sst variance, ssh mean, ssh variance). After identifying the best-performing smoothed environmental variable, we assessed the inclusion of kelp, and then subsequently of a second and third smoothed environmental variable. To avoid collinearity among environmental covariates, we only included those that had a Spearman’s rank correlation of ≤ 0.5 . Model selection was based on AIC, and we did not attempt to fit more than three smooth terms into the final model to avoid over-fitting. We calculated Akaike weights (w_i) for all models following Burnham & Anderson (2002).

After identifying the best model structure for each colony, we investigated the transferability of the results within colonies and across colonies. We used model cross-validation, and the dataset was divided into a training dataset to fit the model, and a testing dataset to assess its performance. We used the area under the receiver curve (AUC; pROC package; Robin et al., 2011) to assess performance of models. AUC values <0.7 were considered poor,

0.7 to 0.9 reasonable, and >0.9 very good model performance. To investigate transferability across years within the same colony, the testing dataset consisted of one year of data, and the training dataset of another year of data from the same colony, similarly as performed by Péron et al. (2018). For Sklinna, where we had ten years of data, we also assessed if transferability across years could be improved by training the dataset with nine years of data (instead of only one) and using the remaining year as test dataset (similar to Fauchald et al., 2021). When assessing the transferability across colonies (aim 2), we applied three different strategies to train models in order to see which one would deliver the best results, and whether increasing the variation within the training dataset could improve the between-colony transferability.

Firstly (“**individual colony and year approach**”), both the training and the testing dataset consisted of data from one colony and one year each, and AUC values were calculated for all combinations of colonies and years. This approach thus followed the same strategy as that by Péron et al. (2018). The best fitting model for the training dataset was chosen as model structure. With this approach, we thus attempted to predict the foraging habitat of the birds in one colony during one specific year based on the model structure based on the habitat use of birds in another colony during one year (same or different year).

Secondly (“**individual colony approach**”), the training and the testing dataset consisted of all data from all years of a given colony, and AUC values were calculated for all combinations of test colonies. The model structure was based on the best fitting model for the training dataset (i.e. as in the individual colony and year approach). With the individual colony approach, we thus attempted to predict the foraging habitat of the birds in one colony across several years based on the model structure, data and habitat use of birds in another colony during 2+ years.

Thirdly and lastly (“**all colonies approach**”), the training dataset consisted of all data from all colonies and years, with exception of the testing colony, and AUC values were calculated using each colony as a test colony once. Since the environmental predictors retained in the best model varied between colonies (Table 2), we had to use a simplified model structure, and only included kelp, depth and distance to colony in the models (i.e. those static variables that were consistently supported in the models for all colonies), but none of the temporally variable environmental variables (i.e. means or variances in sst and ssh). The motivation for the all colonies approach was to test if a larger and more diverse training dataset from four colonies with 2+ years of data each would be suitable to predict the habitat use in a fifth colony. This approach was based on the assumption that the temporally variable environmental covariates (see Supplement 2) would not contribute much to explain the habitat use across colonies compared to the temporally static ones (kelp, depth and distance to colony).

RESULTS

We found strong evidence that maximum distance from colony and thus foraging range differed among colonies (LMM: $F_{4,5265} = 35.05$, $P < 0.001$, $R^2_{\text{mar}} = 0.332$, $R^2_{\text{con}} = 0.784$; Figure 2; Table 1).

Foraging range was largest at the largest colony, Sklinna, followed by Hornøya, while there was no evidence that foraging range differed among Røst, Runde and Jarstein (Figure 2).

Environmental Habitat Preferences Per Colony

Across colonies, depth or distance to colony were the single best explanatory environmental variables and explained alone at least 22% of deviance (Table 2). Both were supported in the final model for all colonies except Røst, where depth correlated with distance to colony and therefore only distance to colony was included in the final model (Table 2). The probability for foraging declined steeply in all colonies with increasing depth (Figure 3A) and approached zero for all colonies at a depth of 100 m or more. The probability for foraging also declined steeply with increasing distance from colony (Figure 3B), and approached zero at a distance of 10 km for birds from Røst and Runde. Birds from Sklinna showed a second peak in foraging probability at 20 km distance, and similarly for Hornøya there was a slight increase at this distance.

The inclusion of kelp was supported in the final models for all colonies (Table 2). There was very strong evidence that the presence of kelp increased the foraging probability of shags at all colonies except at Hornøya (z -values ≥ 16.16 , $p < 0.001$ in the best models for Røst, Sklinna, Runde and Jarstein; Hornøya: $z = 0.128$, $p = 0.898$). In addition, ssh mean was included in the final models for Sklinna, Hornøya and Jarstein, and ssh variance in the models for Røst and Runde. However, by adding ssh to the models, the adjusted R^2 value increased by at maximum 0.05 (Table 2), reflecting a relatively minor importance of ssh for the characterisation of shag foraging habitat. The final models explained between 53.5% and 81.5% of the deviance, reflecting a good to very good fit (Table 2).

Transferability Within and Across Colonies

Transferability across years within the same colony was highly variable and ranged between 0.50 and 0.98, when both the training and the testing dataset consisted of data from one year each (Supplement 3). Transferability across years at Sklinna was considerably higher for all years when the training dataset consisted of nine years of data, i.e. all years except the testing year (AUC range: 0.96–0.98) compared to when the training dataset consisted of one year only (AUC range: 0.51–0.98).

Following the “**individual colony and year approach**” (i.e. both the training and the testing dataset consisted of the data from one colony and one year each), transferability across colonies was variable and ranged between 0.45 and 0.99, with an average AUC of 0.73 ± 0.11 (Supplement 3). Thus, predictability could be excellent in some cases (e.g. using the Jarstein 2019 data to predict the foraging locations of birds at Runde in 2020, with an AUC of 0.99; see Supplement 3), or poor in other cases (e.g. data from Røst 2020 predicting the foraging locations of birds at Hornøya in 2011, with an AUC of 0.46; Supplement 3).

With the “**individual colony approach**” (i.e. the training and the testing dataset consisted of all data from all years of a given

TABLE 2 | Summary of the model selection process.

Model	Fixed effects	adj. R ²	Dev	AIC	ΔAIC	w _i
Hornøya						
HoM_best	year + kelp + s(depth) + s(sshmean) + s(distcol)	0.65	70.2%	20035	0	1
HoM_2nd	year + kelp + s(depth) + s(sshmean)	0.52	59.3%	27385	7349	< 0.01
HoM_3rd	year + kelp + s(depth)	0.49	57.3%	28385	8349	< 0.01
HoM3	year + s(depth)	0.49	57.2%	28786	8751	< 0.01
HoM8	year + s(sshmean)	0.31	36.9%	42391	22356	< 0.01
HoM5	year + s(distcol)	0.17	22.3%	52254	32219	< 0.01
Røst						
RøM_best	year + kelp + s(distcol) + s(sshvar)	0.54	53.5%	38554	0	1
RøM_2nd	year + kelp + s(distcol)	0.52	50.1%	41374	2820	< 0.01
RøM5	year + s(distcol)	0.50	48.9%	42390	3836	< 0.01
RøM3	year + s(depth)	0.21	25.5%	61747	23193	< 0.01
RøM4	year + s(sshvar)	0.23	21.3%	65217	26663	< 0.01
RøM7	year + s(sstvar)	0.14	15.4%	70150	31596	< 0.01
Sklinna						
SkM_best	year + kelp + s(depth) + s(distcol) + s(sshmean)	0.73	70.8%	320177	0	1
SkM_2nd	year + kelp + s(depth) + s(distcol)	0.73	70.8%	320925	748	< 0.01
SkM_3rd	year + kelp + s(depth)	0.52	53.3%	512315	192138	< 0.01
SkM3	year + s(depth)	0.52	53.0%	516366	196189	< 0.01
SkM5	year + s(distcol)	0.26	30.0%	768513	448336	< 0.01
SkM1	year + kelp	0.24	20.5%	872171	551994	< 0.01
Runde						
RuM_best	year + kelp + s(distcol) + s(depth) + s(sshvar)	0.84	81.5%	24583	0	1
RuM_2nd	year + kelp + s(distcol) + s(depth)	0.83	81.0%	25182	599	< 0.01
RuM_3rd	year + kelp + s(distcol)	0.66	63.2%	48850	24268	< 0.01
RuM5	year + s(distcol)	0.66	63.0%	49155	24572	< 0.01
RuM3	year + s(depth)	0.51	54.5%	60417	35834	< 0.01
RuM9	year + s(sshvar)	0.17	27.2%	96643	72060	< 0.01
Jarstein						
JaM_best	year + kelp + s(distcol) + s(depth) + s(sshmean)	0.80	78.8%	11206	0	1
JaM_2nd	year + kelp + s(distcol) + s(depth)	0.75	74.2%	13659	2452	< 0.01
JaM_3rd	year + kelp + s(distcol)	0.69	65.4%	18277	7070	< 0.01
JaM5	year + s(distcol)	0.63	58.0%	22166	10960	< 0.01
JaM3	year + s(depth)	0.46	48.8%	27032	15826	< 0.01
JaM8	year + s(sshmean)	0.34	40.5%	31410	20204	< 0.01

For each colony, the model structure of the sex best fitting models, including the best additive models (M_best, M_2nd, M_3rd) is given. Models are ranked by AIC, and we further present the adjusted R² values, the explained deviance, ΔAIC and Akaike weights (w_i). distcol = distance to colony.

colony), the transferability across colonies remained highly variable (AUC ranged between 0.36 to 0.98, mean 0.76 ± 0.16 ; **Table 3**). For example, Jarstein was poor in predicting the foraging locations for all colonies but Runde. The Sklinna dataset, on the other hand, predicted the foraging locations at all other colonies comparatively well (AUC range of 0.85-0.98). Transferability was not necessarily higher between colonies located closer to each other, e.g. transferability was better from Røst to Runde and Jarstein, than from Røst to Hornøya and Sklinna, and transferability from Runde to Jarstein was the lowest overall (**Figure 1**, **Table 3**).

Finally, with the “all colonies approach” (i.e. the training dataset consisted of all data from all colonies and years, with exception of the testing colony), transferability across colonies was highest and least variable (AUC range: 0.91-0.97; **Table 3**). The prediction maps based on this final model highlighted the shallow, near-shore areas as the most important foraging habitat for the shags (**Figure 4**). The foraging locations based on the GPS tracking data were mostly located within the predicted areas, although foraging locations were often closer to the colonies than the range predicted by the models (**Figure 4**).

DISCUSSION

Environmental Habitat Preferences

As expected, we found that distance to colony, depth and the presence of kelp were the most important variables to characterise foraging habitat across all colonies. Sea surface temperature (sst) was not supported in the final models to characterise foraging habitat, while sea surface height (ssh) was supported in the models, but was of comparatively minor importance.

As expected for a benthic diving species, models suggested that foraging activity increased with shallower depth. This also matched with the dive data obtained in this study, with average dive depths at all colonies being in the range of 7-13 m, and no dive being deeper than 63 m (**Table S1.2**, **Supplement 1**). Further, matching our prediction, foraging probability increased in the presence of kelp. Only at Hornøya could we not find evidence for shag foraging activity increasing in the presence of kelp forests, although kelp was still supported as a factor in the models. Kelp forests, with *Laminaria hyperborea* being the dominating species, typically occur in water depths down to 30 m depth, and on rocky substrate (Bekkby et al., 2009), thus not all shallow marine habitats

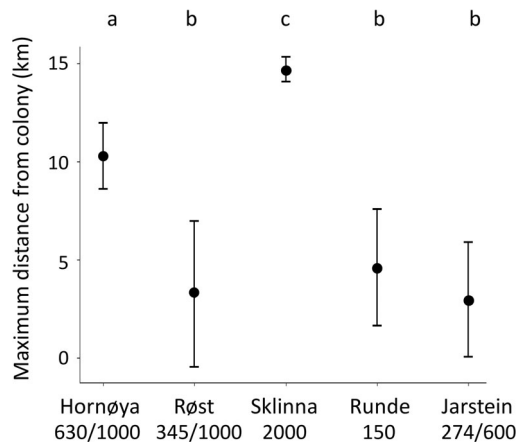


FIGURE 2 | Predicted values of foraging range between the five study colonies based on the LMM results (mean \pm CI). Only complete foraging trips were considered. Letters at the top correspond to the results of Tukey *post-hoc* tests based on the LMM (see *Methods and Material*). Different letters indicate strong evidence for colony-specific differences in foraging range (all $z \geq 3.4$; $P \leq 0.005$), same letters indicate no evidence for such differences (all $z \leq 0.773$, $P \geq 0.930$). Colony sizes (number of breeding pairs) are given below the colony names. Numbers behind the dash (/) give the approximate total number of breeding pairs within the maximum foraging range of the focal colony, in case of neighbouring colonies.

are colonised by kelp. Around Hornøya and many other areas in northern Norway, kelp forests are very sparse or absent after a collapse in the 1970s and 1980s due to overgrazing by the green sea urchin (*Strongylocentrotus droebachiensis*) (Christie et al., 2019). As such, only 8% of the likely foraging locations around Hornøya were associated with the presence of kelp, compared to 51% in the other colonies. The low availability of kelp forests thus likely explained the lower importance of this habitat type for Hornøya compared to the other colonies. Our results are – not surprisingly – in agreement with earlier studies from Norway (based partly on the same GPS data), showing that kelp forests are of high importance around Sklinna, while data for kelp presence was lacking until recently for the area around Hornøya and could thus not be included into earlier analyses (Christensen-

Dalsgaard et al., 2017). Depth, on the other hand, was of importance at both Sklinna and Hornøya also in the previous study (Christensen-Dalsgaard et al., 2017), and in Normandy, France (Grémillet et al., 2020), where shags in fact used much shallower habitats with an apparent preference at about 10 m depth. In distribution models for shags around the British Isles, depth was not retained as important variable, possibly due to the coarser spatial scale of the models, and the inclusion of non-foraging locations (Wakefield et al., 2017). In contrast, and in agreement with our results, in an analysis of habitat use by shags around the Isle of May, Scotland, shags tended to avoid areas with water depths exceeding 60m (Daunt et al., 2012).

The lack of importance of sst and ssh parameters to characterise foraging locations of shags is maybe less surprising given the benthic foraging behaviour of this species and thus the strong preference for shallow foraging areas. Instead of indicating distinctions in water masses and thus frontal zones, eddies or upwelling plumes, respectively (e.g. Kostianoy et al., 2004; Ainley et al., 2009; Mason et al., 2014), we found mean sst and mean ssh but also temporal variance in sst and ssh to increase from pelagic towards coastal habitats, reaching highest levels in near-shore areas (Supplement 2). Sea surface temperatures also reflected the negative trend towards lower temperatures with increasing latitude. Furthermore, both mean sst and mean ssh showed some annual variation, with distinct gradients in the coastal zones in some but not all years (Supplement 2). Quite possibly, the variation across years also contributed to lower across-year and across-colony transferability of models containing ssh. Sea surface height and sst, albeit retained in models, also seemed to be of lower importance for shags in Normandy (Grémillet et al., 2020) and in the British Isles (sst only; Wakefield et al., 2017).

Besides the environmental covariates, distance to colony was an important variable in the models for all colonies. This is in agreement with the study by Wakefield et al. (2017), who found distance to colony as well as the number of conspecific breeders to be of strong importance in shag distribution models. In accordance with this, we found foraging range to be largest for the biggest colony, Sklinna with 2000 breeding pairs, where shags foraged up to 40 km away from their breeding location, and smallest at Røst, with 345 breeding pairs in the study colony (and approximately 1000 pairs in the entire 20 x 10 km² archipelago),

TABLE 3 | AUC results of models based on the individual colonies approach (top) and the all colonies approach (below).

Training dataset	Testing dataset				
	Hornøya	Røst	Sklinna	Runde	Jarstein
Individual colony approach					
Hornøya	-	0.8995	0.768	0.712	0.869
Røst	0.647	-	0.756	0.935	0.945
Sklinna	0.947	0.849	-	0.978	0.952
Runde	0.635	0.761	0.609	-	0.362
Jarstein	0.683	0.508	0.665	0.916	-
All colonies approach					
all except testing dataset	0.964	0.906	0.969	0.953	0.953

In the individual colony approach, the training and the testing dataset consisted of all data from all years of a given colony each, and the model structure being the best fitting model for the training dataset, whereas in the all colonies approach, the training dataset consisted of all data from all colonies and years, with exception of the testing colony, and the model contained only the static environmental covariates kelp, depth and distance from colony.

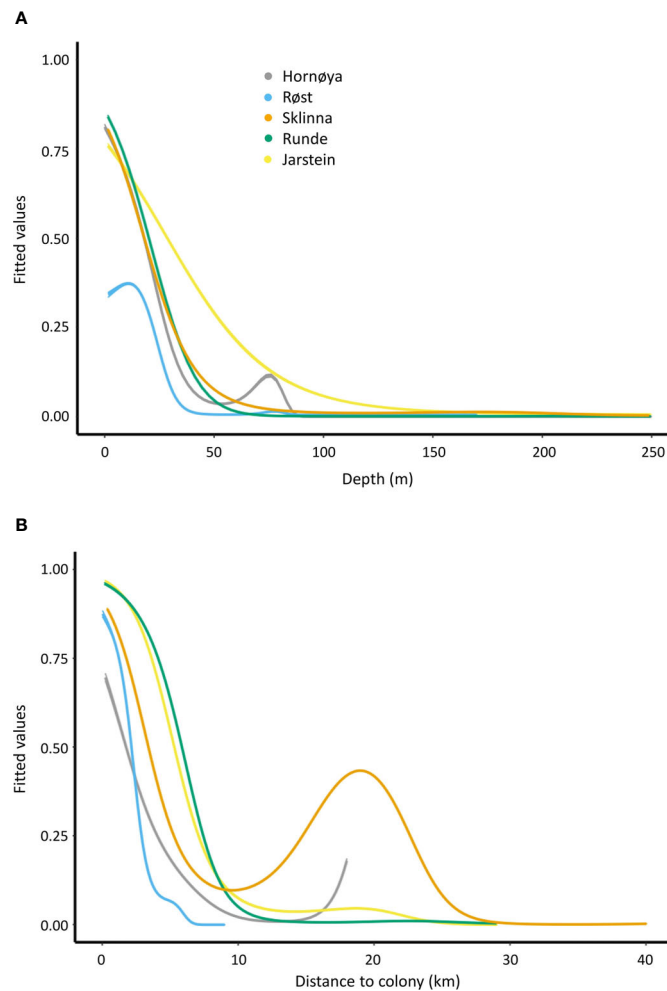


FIGURE 3 | Model response curves (fitted values \pm SE) showing the predicted foraging probability in response to depth **(A)** and distance from colony **(B)** for the different colonies. Fitted values were extracted from the individual models per colony (e.g. for the Hornøya colony model HM3 and HM5; see **Table 3**).

where foraging occurred within a radius of 9 km from the colony. However, given the size of our dataset (only 5 colonies) and uncertainty about colony sizes in the direct vicinity of our study colonies, we did not test for a relationship between colony size and foraging range.

Transferability Within and Across Colonies

Transferability of foraging habitats across colonies differed depending on which of the three modelling approaches was used. With the individual colony and year approach, transferability was overall low, and the results in many instances unsatisfactory. The individual colony and year approach was also used to assess transferability across years within colonies. Even within the same colony, the transferability was poor across years. Noteworthy, transferability was low across colonies and years, and thus not an artefact of few individuals tracked (or a low number of foraging trips recorded) at a given colony in a given year (cf. between-year transferability based on Hornøya 2011 data (AUC = 0.552; N = 31 individuals, 157 complete trips) and Sklinna 2014

data (AUC = 0.608–0.954; average: 0.772; N = 55 individuals, 167 complete trips) being very low compared to the high across-year transferability based on the Røst 2020 data (AUC = 0.908; N = 7 individuals, 42 complete trips). While transferability across years within the same colony was on average in the same range as for across-year transferability of breeding season habitat of Scopoli's shearwaters (*Calonectris diomedea*; Péron et al., 2018), we had more extreme values to both ends. Transferability across years increased substantially for the Sklinna dataset when nine years of data were used in the training dataset, to predict the habitat use in the tenth year. Unfortunately, given that we only had two years of tracking data at all other colonies, we could not test if this pattern was universal.

With transferability across years within the same colony being limited when the training dataset consisted of only one year, it was not surprising to also find low transferability across colonies. In a management perspective, using the tracking data from only one year and one colony to predict habitat use by birds around another colony, increases the risk of focussing on an area

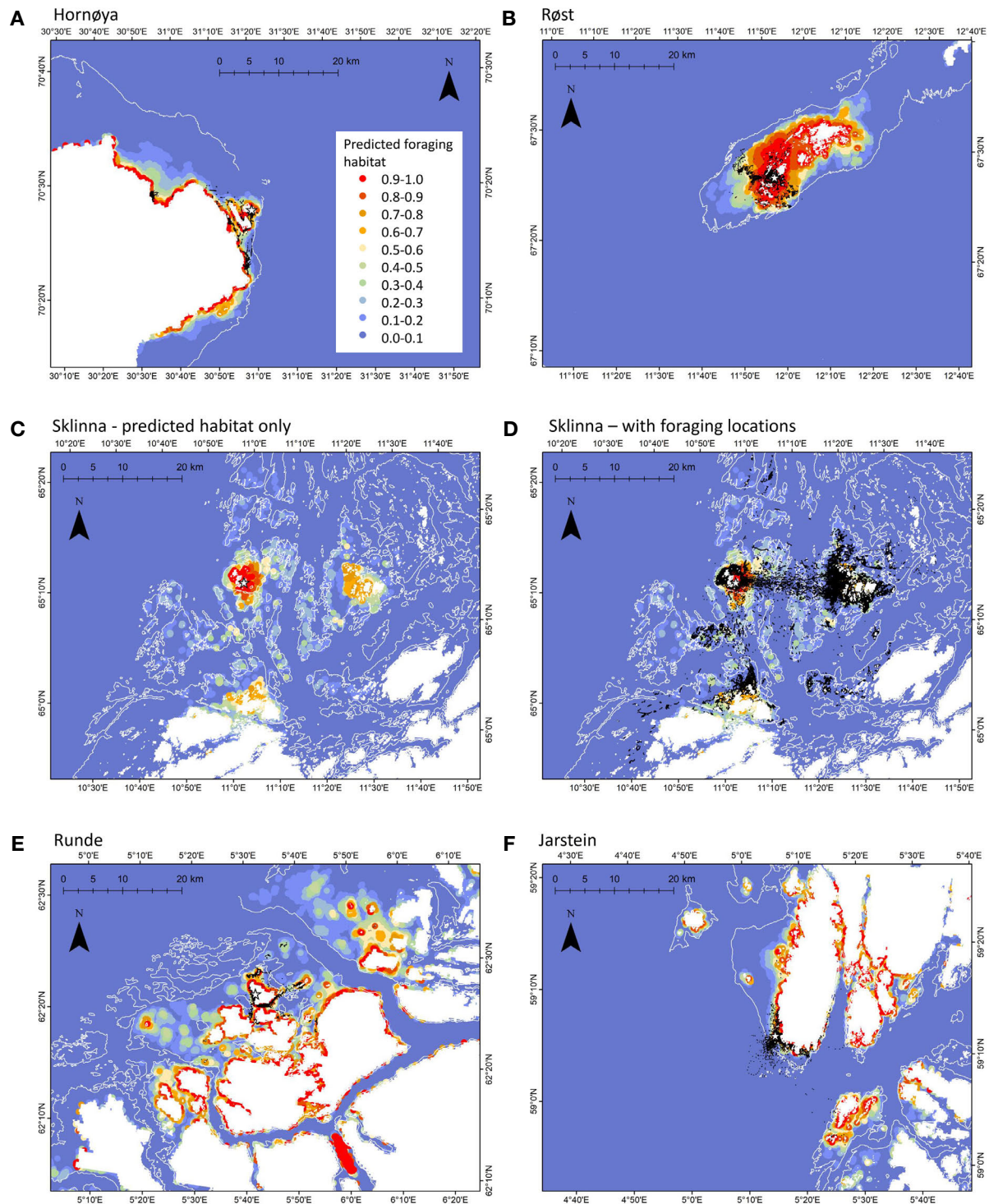


FIGURE 4 | Predicted habitat maps based on the “all colonies approach” models, i.e. data from all other colonies and years was used to predict the foraging habitat around the shown (focal) colony. The location of the colony is marked with a white star. The probability for the area to be used as foraging habitat is shown in colours from blue (low) to red (high), as detailed in the legend. White lines show the 100m bathymetry line, land areas are depicted in white. Foraging locations based on the EMBC algorithm are shown as black dots (**A, B, D–F**). Due to the high data amount, foraging locations for Sklinna are shown in a separate plot (**D**) than the predicted foraging habitat (**C**).

that is of only minor importance, and – worse – not protecting the really important habitat.

The individual colony approach yielded slightly better outcomes regarding the transferability across colonies than the individual colony and year approach. Thus, pooling the data from each colony together in the training dataset helped to improve predictability. However, the results were still variable. Against our expectation, and in contrast to previous findings (Péron et al., 2018; Fauchald et al., 2021), transferability across colonies was not higher for those colonies being relatively more closely located. Thus, the dataset from Runde was poor to predict foraging habitat characteristics at either Sklinna (located 400 km away) or Jarstein (located 360 km away), while the Hornøya dataset was good in predicting the foraging habitat characteristics at both Runde (1420 km away) and Jarstein (1730 km away). Possibly, the actual distances between our study colonies (all ≥ 250 km) were still too large to allow good transferability at a high spatial scale. In fact they were larger than for those colonies with good transferability in the work by Péron et al. (2018) on breeding Scopoli's shearwaters. Although Fauchald et al. (2021) found high transferability of winter distribution for colonies located less than 500 km away from each other, seabirds are much less restricted in habitat use during winter than during the breeding season (Bell, 1990), and their study was also based on six pelagic seabird species, and not coastal-bound shags. Rather than relative proximity between colonies playing a role for transferability, similarity of foraging habitat between specific colonies, or availability of prey may be factors affecting transferability. Shags are fish specialists, and availability of fish is obviously a key determinant of where and what shags are feeding. Unfortunately, we do not have a complete overview of the diet for all of our study colonies, but there is some clear variation between the colonies: Young age classes of saithe (*Pollachius virens*) are the dominating prey at Sklinna and Røst (Hillersøy and Lorentsen, 2012; Lorentsen et al., 2018; Anker-Nilssen unpublished data), whereas lesser sandeel (*Ammodytes marinus*) is the main prey, followed by gadoids, including saithe, at Hornøya (Barrett et al., 1990). Shags at Runde fed on a mix of gadoids, including saithe as well as sandeel (Graham, 2019), while we had no diet information from Jarstein. Based on the diet, one could thus have expected higher transferability between Sklinna and Røst as well as between Hornøya and Runde, but poorer transferability between Sklinna and Hornøya, Sklinna and Runde, Røst and Hornøya, as well as Røst and Runde, respectively. Evidence for this was rather mixed, though (Table 2).

Overall, it rather seemed that some datasets were better to train models than others, which was the case particularly for the Sklinna dataset. This again may not be too surprising given that Sklinna was the only colony for which we had more than 2 years of data, and many more individuals were tracked in this colony than from other colonies. The importance of multi-year tracking of shags to capture the full range of utilised habitats has been highlighted earlier by Bogdanova et al. (2014). In addition, shags are known to show individual segregation in foraging space use (Morgan et al., 2019), and thus a dataset that holds multiple foraging trips from more individuals likely covers a wider range

of environmental habitats than the same number of trips obtained from fewer individuals (as e.g. for the Røst 2020 dataset). The Sklinna dataset was therefore in a way more diverse and the large foraging range at this colony in addition to the 10 years of tracking may have contributed to covering a broader range of environmental variables than at other colonies, possibly making this dataset more suitable for predictions.

Finally, the all colonies approach, i.e. the approach based only on the temporally static environmental variables (depth, distance and kelp), and pooling all data from all colonies except for the testing colony, performed best and transferability across colonies was very high for all five colonies. This high performance may have several non-exclusive reasons: Firstly, dropping the spatio-temporally variable covariates ssh mean and ssh variance and only including temporally stable environmental covariates into the training model may have improved transferability. At individual colonies it was either ssh mean or ssh variance that was supported in the models. As such, including e.g. ssh mean in a model when predicting the utilised habitat at a colony for which ssh variance was supported (as was the approach in the individual colony and year approach and the individual colonies approach) would in fact likely not improve model fit and thus transferability. In this context, it is further noteworthy that ssh mean and ssh variance, even though supported in the models to characterise foraging habitats, were of generally lower importance than the temporally non-variable environmental covariates (i.e. depth, distance to colony and kelp presence) that remained included in the models of the all colonies approach. Secondly, using a very diverse training dataset, consisting of four colonies with at least 2 years of data each, very likely also contributed to improving model fit and transferability of the results from one colony to another. This would be a similar effect as discussed above as a possible reason for why the Sklinna dataset in the individual colony approach performed best to predict utilised habitat in all other colonies, and also why within-colony transferability increased for Sklinna when the training dataset contained nine years instead of only one. Importantly, while Sklinna performed well as a training dataset with the individual colony approach, the data from the other colonies performed on average poorly to predict the utilised habitat of the shags around Sklinna. In contrast, with the all colonies approach, the utilised habitat was predicted very well also around Sklinna. Therefore, our results clearly highlight that with a solid database, consisting of at least 2 years of tracking data from several different colonies, it is possible to predict important habitat around another shag colony – even when working across large spatial scales.

It remains open to which degree our data can be used to predict the foraging hot-spots of shags in other parts of their breeding range, and we advocate strongly against blindly predicting key foraging habitat outside of Norway based on our data. Shags are geographically widespread and as pointed out above, variability in diet across colonies as well as availability of habitat around colonies contribute to differences in foraging habitat use. Despite the variable diet across the colonies, we were able to predict the habitat use of shags at all colonies with high precision with our complete dataset. Possibly, this was helped by

the comparatively similar bathymetry along the Norwegian coastline, with relatively shallow zones near-shore along the coast (around the often many islands and skerries) inside of a much deeper continental shelf. However, our models may not function equally well in areas with other habitat compositions, for example if all available habitat around a colony was characterised by comparatively shallow sandy bottom as was the case in Normandy (Grémillet et al., 2020).

CONCLUSIONS

Our in-depth analyses of habitat use of shags in five different colonies along the Norwegian coast reflects the importance of collecting data over several years and in several colonies, and shows the value of comprehensive datasets in modelling and predicting important foraging areas. Our study is the first to test transferability of fine-scale habitat models in shags, and the first study assessing transferability of habitat models across colonies based on different approaches. Our dataset and modelling approach puts us in the unique position to be able to predict important foraging habitat around any shag colony along the Norwegian coast, likely with a reasonably high level of accuracy, without the need to track birds in additional colonies. Our models on foraging habitat included distance to colony, thus the transferred predictions sometimes highlighted areas as important that were further away from the colony than those used by the tracked birds (cf. **Figure 4**). This will require some more fine-tuning of predictions about the foraging range around colonies, possibly by combining our method with the foraging radius approach as part of the BirdLife International (2010) toolbox, or using also the relationship between colony size and foraging range, as successfully performed by Wakefield et al. (2017).

Shags have or are experiencing population declines in most parts of their distribution range (BirdLife International, 2021). In Norway, population sizes showed substantial inter-decadal variation over the past 40 years, and a regional decline in the Barents Sea, while the overall population number appears relatively stable (Fauchald et al., 2015). With about 35% of the NE Atlantic population (Mitchell et al., 2004), Norway has a special responsibility for the conservation of shags. Consequently, information on the most suitable foraging areas for shags should always be at hand for management authorities to consider proper measures when anthropogenic pressures have the potential to substantially reduce their quality as foraging habitat or hinder birds access to such areas.

The UN decided in 2015 that, by 2030, 30% of the marine environment, including coastal zones, should be protected. We are, however, still far from reaching that goal, both globally, regionally (Europe and North America) and nationally (Maestro et al., 2019). This is also true for Norway, which by 2020 had only protected 3.5% of its territorial waters (Statistics Norway, 2021). On the contrary, Norway's coastal industries like fisheries and, in particular, aquaculture are expected to increase fivefold by 2050 (Olafsen et al., 2012), including plans for opening of additional, large areas to kelp harvesting (Steen et al., 2020).

In such times of increasing anthropogenic pressures on coastal marine habitats and the rising need for better management of wildlife, our work delivers important knowledge for ecosystem-based management decisions, which could contribute to reach the UN goals for 2030.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by The Norwegian Food Safety Authority (Mattilsynet).

AUTHOR CONTRIBUTIONS

Conceptualization: SC-D and S-HL. Funding acquisition and project management: SC-D. Data were collected by ND, TA-N, S-HL, and SC-D. Analyses were completed by ND, with contributions from JM, and AT. Writing was led by ND, with contributions from all other authors. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.852033/full#supplementary-material>

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Variability in Foraging Range and Direction Among Colonies in a Widespread Seabird, the Magellanic Penguin

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Most seabirds forage far from land, making them hard to observe when foraging. Satellite tracking of seabirds shows where they come into conflict with human uses of the ocean, and whether they use protected areas. Because tracking data are expensive, data from one colony and/or year are sometimes used to design marine protection for a species across its range. Two assumptions commonly made are that foraging distance increases with colony size and individuals are uniformly distributed around colonies. We tested these assumptions using Magellanic penguins *Spheniscus magellanicus* as an example. We used a large tracking dataset of 338 penguins foraging for chicks at 10 colonies in Argentina from 1996 to 2019. Foraging distance increased with population size among colonies, but predicted distances would not cover foraging areas for all colonies. There was no relationship between population size and foraging distance within colony among years for colonies with ten and 23 years of data. Penguins were not uniformly distributed around colonies. Penguins used ~24% (12–40%) of the ocean available within the colony's maximum foraging distance. We also show that overlap between penguin foraging areas and marine protected areas (MPA) and hydrocarbon concessions varied among colonies partly because of variation in how far offshore penguins forage. Overlap with MPAs was low (0% – 20%) for seven of the ten colonies and high (23% – 100%) for the other three. Overlap with a large area permitted for hydrocarbon exploration (seismic surveys) was relatively high (23% – 81%) for seven colonies where penguins forage offshore. Data from one colony are unlikely to indicate the most effective marine spatial planning for all colonies. Our data show that to be effective, marine planning should consider the temporal and spatial dynamics of ocean conditions and the response of marine wildlife to these changes. Climate variability is predicted to increase, making knowledge of foraging-location variation among colonies and years critical to conservation planning.

Keywords: *Spheniscus magellanicus*, marine protected area, MPA, hydrocarbon exploitation, colony size, at-sea distribution, foraging radius, seismic survey

INTRODUCTION

Penguins are important components of marine food webs in the Southern Hemisphere (Brooke 2004), and economically important as a basis for wildlife tourism (Lewis et al., 2013; Raya Rey et al., 2017; Wagner et al., 2020). Penguins are also among the most threatened groups of species (Trathan et al., 2014; Ropert-Coudert et al., 2019). Nine of eighteen species of penguins are vulnerable or endangered (IUCN, 2021), facing a variety of threats at sea, especially pollution, prey depletion by overfishing, bycatch in fishing gear, and climate change (Trathan et al., 2014; Dias et al., 2019). Effective conservation requires protection of penguins and their prey at sea, requiring knowledge of their seasonal use of areas and habitats.

Most penguin species breed in multiple, widely distributed colonies. Colony size varies over orders of magnitude within species (García Borboroglu and Boersma, 2013). Some species breed over wide ranges of latitude, and some occur in more than one ocean basin. Oceanographic conditions and prey fields vary among colony foraging areas (Lescroël and Bost, 2005; Boersma et al., 2009; Ratcliffe and Trathan, 2011; Santora et al., 2020), and foraging distance often varies among colonies of the same species (Boersma et al., 2009; Santora et al., 2020). Spatial use of the ocean by penguins also varies among seasons and years (Boersma and Rebstock, 2009; Bost et al., 2015; Horswill et al., 2017).

Identification of priority areas for protection of penguins requires data on the locations or habitats they use at sea. Data on overlap between foraging areas and the locations of threats, as well as existing and proposed marine protected areas (MPAs), are pressing needs for conservation of penguins (Critchley et al., 2018; Baylis et al., 2021; Yorio et al., 2021). Tracking data and at-sea surveys are the two typical sources of at-sea distribution data, but many species have not been tracked at all colonies or in all regions. These data are expensive and logistically challenging to obtain.

When data do not exist for colonies, space use is often modeled using tracking data from other colonies (Soanes et al., 2016). Models range from simply using the maximum foraging distance for one colony, to complex models including population size of each colony and habitat preferences (Grecian et al., 2012; Handley et al., 2020). The 'Foraging Radius Approach' (Soanes et al., 2016) is frequently used when tracking and survey data are not available (Grecian et al., 2012; Handley et al., 2020). In this method, circles or arcs are drawn around colonies with no at-sea data using a foraging distance from available data for the species. Soanes et al. (2016) recommend using the mean maximum distance (mean of the maximum distance for each individual). Population size of colonies and habitat preferences can be included, when known (Soanes et al., 2016).

A common assumption of the models is that foraging distance increases with population size (Grecian et al., 2012; Soanes et al., 2016). Colonial central-place foragers, including most seabirds, may deplete prey near the colony, with larger populations depleting prey more than smaller populations. This forces individuals from larger colonies to forage farther from breeding sites than those from smaller colonies (Ashmole, 1963; Lewis et al., 2001; Weber et al., 2021).

A second common assumption is that foraging individuals spread out uniformly around the colony (Grecian et al., 2012; Soanes et al., 2016), as it is assumed that this behavior reduces competition for prey (Bolton et al., 2018). Individuals from each colony should forage closer to their colony than to other colonies, resulting in no overlap among colony foraging areas (Cairns, 1989). Birds from smaller colonies may avoid the foraging areas of larger colonies, modifying the uniform distribution (Bolton et al., 2018). A uniform distribution is the null hypothesis, and may be the only reasonable hypothesis in the absence of knowledge of foraging areas and foraging habitats.

Variation in foraging distances among families, species, and colonies of seabirds makes spatial scales of MPAs an important consideration (Oppel et al., 2018). Variation among colonies also makes predicting interactions between foraging seabirds and spatially explicit threats at sea difficult (Bolton et al., 2018). In addition, including data on threats and resources along with tracking data makes tracking studies more useful for conservation (Hays et al., 2019).

The goals of the study were to 1) test the two common assumptions of the Foraging Radius Approach, colony-size-dependent foraging distance and uniform distribution, and 2) determine how variation in foraging behavior among colonies affects penguins' overlap with MPAs and threats at sea. Our goal was to show the effects of variation in foraging behavior among colonies, not to determine optimal boundaries for marine protection. We used a large dataset for Magellanic Penguins *Spheniscus magellanicus* tracked at ten colonies in Argentina to test the assumptions, and used hydrocarbon industry concessions as an example of a spatially explicit threat.

Specifically, we tested whether colony size predicted foraging distance among colonies and whether interannual variation in colony size predicted interannual variation in foraging distance within colonies. We tested three predictions of the uniform-distribution assumption. First, a histogram of bearings to foraging locations (trip endpoints) should be uniformly distributed. Second, penguin locations should occupy most of the area within the foraging range for each colony. Third, if penguins deplete prey around large colonies more than around small colonies, penguins from large colonies should spread out more (increase the range of bearings) than penguins from small colonies, resulting in a positive relationship between colony size and the percentage of available foraging area that penguins used. Alternatively, if penguins from large colonies swim farther, but do not spread out more than penguins from small colonies, there should be no relationship between colony size and the percentage of available foraging area used. Finally, to help policy makers and stakeholders understand the effects of variation in foraging behavior among colonies, we compared penguins' spatial use of the continental shelf of Argentina with the locations of MPAs and hydrocarbon industry concessions and seismic survey areas.

MATERIALS AND METHODS

Magellanic penguins breed in colonies along the coasts of Argentina and Chile, and dispersed along the coasts of the

Falkland/Malvinas Islands. The Atlantic population winters at sea off northern Argentina, Uruguay, and southern Brazil (Boersma et al., 2013). They lay two eggs in October or November, which hatch in November or December. Chicks are brooded for about a month and fledge in January or February (Boersma et al., 2013). Magellanic penguins are offshore foragers (Croxall and Davis, 1999; García Borboroglu and Boersma, 2013), especially during incubation and the post-brood stage of breeding (Boersma and Rebstock, 2009). Their primary prey is small pelagic fish, especially anchovy *Engraulis anchoita* in northern colonies in Argentina and sprat *Sprattus fuegensis* farther south. They also eat juvenile hake *Merluccius hubbsi*, squid, and crustaceans (Wilson et al., 2005; Boersma et al., 2013).

Tracking Data

We tracked Magellanic penguins at ten colonies, spread along 1240 km of coastline, most of their latitudinal range in Argentina, between 1996 and 2019 (Table 1; Figure 1). We used data for penguins rearing chicks > 30 days of age (post-brood), when they forage at intermediate distances from the colony compared to incubation and when chicks are younger (Boersma and Rebstock, 2009). We tracked one member of each pair except in 2019 at Punta Tombo, when we tracked mated pairs. Most (92%) of tracked penguins were males. We combined the data for males and females as their foraging distances were similar during the breeding season (Boersma and Rebstock, 2009; Blanco et al., 2022). We left tags on for multiple trips by each penguin. We tracked two penguins in more than one breeding season at El Pedral, five at Cabo Dos Bahías, and 40 at Punta Tombo. We used three models of Argos satellite transmitters (PTTs) and three models of GPS archival tags (Table S1). Tag type did not affect foraging-trip duration or distance (Boersma et al., 2009).

We smoothed the tracking data and estimated locations every 30 minutes using the state-space model *crawl* (Johnson et al., 2008) (Table S1). We chose 30 minutes as a compromise between location intervals for GPS tags (23 ± 94 minutes, mean \pm SD) and Argos satellite transmitters ($62 \pm$

151 minutes). Foraging trips averaged 2 ± 2 days, giving us 96 locations per trip on average. Prior to running the models, we removed duplicate locations, locations on land more than 5 km from the colony, and locations that represented a large movement away from the track line followed by an immediate return. We retained locations on land near the colony as they helped the model predict a location at the colony, which we used to define a trip. We added sightings of the tracked individual in the colony or on the beach for the same reason, and set the error estimates to the lowest values for each tag type, so the model would treat the locations as highly accurate.

We defined a trip as at least eight consecutive locations away from the colony, with at least one location at the colony before and after the trip. Eight locations was the minimum needed for a track in the shape of a trip (2-3 locations in each part of the trip, outbound, foraging, and inbound). Additionally, fewer locations likely represented trips to the beach for bathing. For each trip, we defined trip distance as the straight-line distance between the colony and the location farthest from the colony. For each colony and breeding season, we calculated the mean trip distance (mean distance of all trips of all penguins), the mean maximum distance (the mean of the longest trip distance for each penguin), and the maximum distance (the distance of the longest trip for any penguin). We calculated the bearing to each penguin location as the angle between the colony and the location, where north = 0°.

We have published some of the tracking data (Boersma and Rebstock, 2009; Boersma et al., 2009; Rebstock et al., 2022). We present some unpublished data and new analyses in this paper.

Kernel Analysis

We projected the tracking data using the Lambert Azimuthal Equal-Area projection prior to conducting a kernel analysis (Baylis et al., 2021). We calculated the 50% and 90% UD kernel areas from penguin locations at sea (at least 5 km from the nest) using the *adehabitatHR* package in R. We calculated one kernel for each breeding season for each colony, and

TABLE 1 | Colony and tracking details for Magellanic penguins at 10 colonies in Argentina.

Colony	Location	Size (year estimated)	N penguins (N trips)	Years tracked
Complejo Islote Lobos	41° 26' S, 65° 1' W	4,700 (2011) ¹	4 (66)	2010
Estancia San Lorenzo	42° 5' S, 63° 51' W	57,000 (2003) ²	6 (25)	2003
El Pedral	42° 56' S, 64° 20' W	675 (2013) ¹	18 (320)	2011, 2012, 2014
Punta Tombo	44° 2' S, 65° 11' W	209,000 (2012) ³	238 (1783)	1996-2010, 2012-2019
Cabo Dos Bahías	44° 54' S, 65° 32' W	12,300 (2010) ¹	48 (565)	2002-2010, 2013
Isla Leones	45° 3' S, 65° 36' W	46,000 (2009) ¹	5 (51)	2009, 2010
Isla Chaffers	47° 46' S, 65° 52' W	13,700 (1992) ²	5 (36)	2003
San Julián	49° 18' S, 67° 42' W	37,000 (1993) ²	5 (30)	2003
Monte León	50° 22' S, 68° 53' W	32,000 (1994) ²	6 (64)	2003
Cabo Virgenes	52° 22' S, 68° 24' W	89,000 (1994) ²	3 (12)	1997

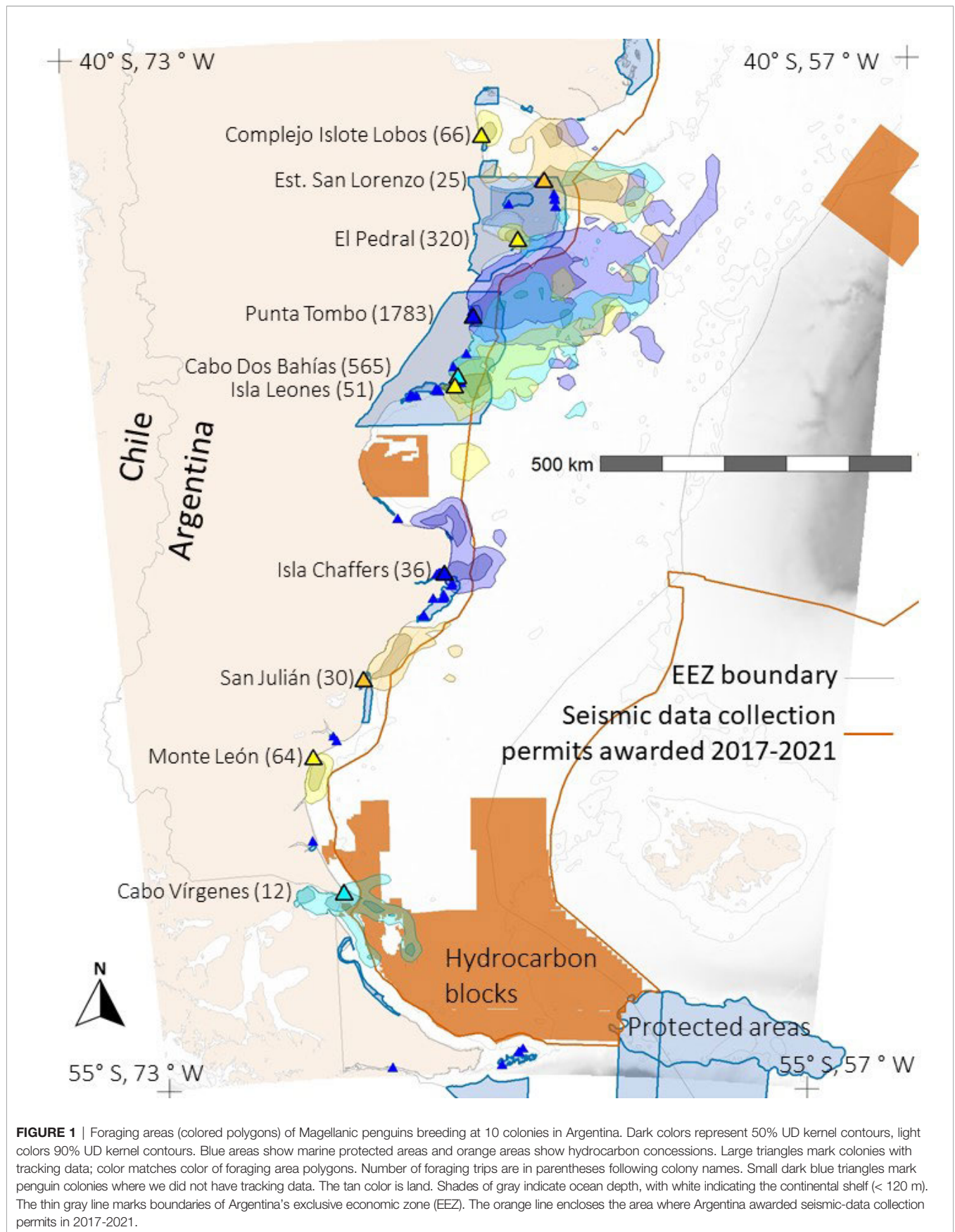
Size of each colony is number of pairs or number of active nests, using the estimate closest to the tracking year. N penguins is the number of penguins tracked, with the number of trips in parentheses. Year is the calendar year of the start of the breeding season (Sept-March). Tags were deployed in December of the year listed or January of the following calendar year.

Sources for population estimates are shown in the footnotes.

¹(Pozzi et al., 2015).

²(Boersma et al., 2013).

³(Rebstock et al., 2016).



combined (*st_union*, *sf* R package) the kernel contours for each colony where we tracked penguins in more than one year. The 50% UD kernel area represents the core area that penguins swim through and forage in (Soanes et al., 2013). The 90% UD kernel area represents most of the area penguins use. We chose a percentage less than 100 so that the total area would not be influenced by a few penguins that made abnormally long trips. We compared the kernel polygons to coastline polygons and removed land area using the *sf* package. We downloaded coastlines as country shapefiles from www.diva-gis.org/gdata.

Kernel polygon sizes depend on the smoothing parameter (*h*) selected (Kie, 2013). Dias et al. (2018) recommended setting *h* = 7 for penguin tracking data. We compared kernel polygons created with *ad-hoc* *h* and with *h* = 7, and selected *h* = 7 (Appendix 1; Table S2; Figure S1).

Colony Population Estimates

For all colonies except Punta Tombo and Cabo Dos Bahías, we used the population estimates in Pozzi et al. (2015) or Boersma et al. (2013) (Table 1). We used the estimate closest to the tracking year if multiple estimates were available (e.g., Estancia San Lorenzo). We tracked penguins in 2009 and 2010 at Isla Leones, but only had a population estimate from 2009 (Pozzi et al., 2015). We tracked penguins in 2011, 2012, and 2014 at El Pedral, and had population estimates for 2011, 2012, and 2013 (Pozzi et al., 2015). El Pedral grew exponentially from 2009 through 2013 (Pozzi et al., 2015), and was presumably larger in 2014. Foraging distance did not increase over the three years of tracking (see Results), so we selected the 2013 estimate to represent the population.

We tracked penguins at Punta Tombo for 23 years and at Cabo Dos Bahías for 10 years. We conducted population surveys at Punta Tombo (Rebstock et al., 2016) from 1987 through 2019 and at Cabo Dos Bahías from 1992 through 2019, estimating nest density in 100-m² circles around 22 fixed locations 100 m apart at Punta Tombo and 24 fixed locations 33 m apart at Cabo Dos Bahías. To convert from nest density to a population estimate at Punta Tombo for each year that we tracked penguins, we used the population estimate from a stratified-random survey in 2012 (Rebstock et al., 2016). We divided the 2012 population estimate by the nest density from our 22-circle survey in 2012. We multiplied the result by the nest density from each year's 22-circle survey to obtain a population estimate for each year, rounding to the nearest 50. Similarly, for Cabo Dos Bahías, we used our nest density estimates and the population estimate for 2010 from Pozzi et al. (2015).

Testing Assumptions of Foraging Distance and Uniform Distribution

To compare foraging distance and population size among colonies, we used each colony once. We tracked penguins at six colonies in only a single year. Therefore, for this analysis, we used one population estimate and one foraging distance for each colony. If we tracked penguins in more than one year at a colony, we combined all trips for all years at that colony to calculate the mean, mean maximum, and maximum distances. We used

ordinary least squares (OLS) regression with log-transformed foraging distance as the response and log-transformed population size as the predictor (*n* = 10 colonies), and found predicted foraging distances and 95% confidence intervals for each colony. We back-transformed the predicted distances and 95% confidence intervals to express them in kilometers. We report the results for the mean maximum distance for each year. Conclusions were the same using mean distance and maximum distance.

For Punta Tombo and Cabo Dos Bahías, we estimated population size for each year of tracking, as described above. We regressed (OLS) log-transformed foraging distance on log-transformed population size (*n* = 23 years for Punta Tombo and 10 years for Cabo Dos Bahías).

We used the 90% UD polygons to determine if colony foraging areas overlapped (Cairns, 1989; Bolton et al., 2018). We did not quantify the overlap, but determined its presence visually (Figure 1). We also determined visually whether penguins always foraged closer to their own colonies than to other colonies, as predicted by the hinterland model (Cairns, 1989).

We tested for uniform distributions of penguin locations around colonies using the G-test (log-likelihood ratio test) on a histogram of the bearings to the endpoints of trips for each colony. The G-test is more reliable than χ^2 when some cells contain small or zero counts. Most colonies had gaps in bearings because land to the west prevents foraging, and histograms were bimodal. To eliminate the bimodal distributions, we subtracted 360 from bearings between 200 and 360, essentially shifting the axes so that the gap fell beyond the tails rather than in the center of the distribution. We estimated the range of bearings available for foraging around each colony as the range of bearings covered by water at the maximum foraging distance from the colony. To make the histograms, we used the range of foraging bearings available at each colony (excluding bearings to land) and a bin width of 15°. The G-test compares the distribution of counts in each bin with the expected count under a uniform distribution (the same count in each bin). We used the same number of trips for each penguin at a colony (the minimum number of trips for any penguin at the colony; Table 2), to prevent a penguin with more trips than others from influencing the outcome. At San Julián, we excluded one penguin with one trip and used the first five trips for the remaining four penguins. We did not have enough trips at Cabo Virgenes to test the distribution (three penguins with one, three, and eight trips).

In addition, we estimated the available foraging area for each colony as the area covered by ocean with a radius around each colony equal to the maximum foraging distance by any penguin from that colony. We used the maximum rather than the mean maximum to define the available area because many penguins foraged beyond the mean maximum distance (37.8% of penguins at Punta Tombo and 43.8% of penguins at Cabo Dos Bahías), and UD kernel polygons extended beyond the mean maximum distance for some colonies. We estimated the area used by penguins from each colony as the area enclosed within the 90% UD kernel polygons. We compared the area used by

TABLE 2 | Foraging locations of Magellanic penguins breeding at 9 colonies in Argentina were not uniformly distributed around colonies.

Colony	Trips per penguin	Penguins	Total trips	G	df	p
Complejo Islote Lobos	10	4	40	45.5	12	<0.0001
Estancia San Lorenzo	2	6	12	40.9	23	0.01
El Pedral	2	18	36	62.1	20	<0.0001
Punta Tombo	1	238	238	456.5	13	<0.0001
Cabo Dos Bahías	1	48	48	96.5	20	<0.0001
Isla Leones	4	5	20	42.0	19	0.002
Isla Chaffers	3	5	15	28.0	16	0.03
San Julián*	5	4	20	48.9	11	<0.0001
Monte León	7	6	42	51.1	10	<0.0001

We did not have enough data to test the distribution of foraging locations at one colony, Cabo Virgenes. The test compared counts from a histogram of foraging-location bearings with expected counts for a uniform distribution. G is the log-likelihood ratio test statistic, df is degrees of freedom (number of bins -2), p is the probability of G.

*We excluded one penguin with one trip and tested the remaining four penguins at San Julián.

penguins from each colony with the available area for that colony. To test whether penguins from larger colonies fanned out more than penguins from smaller colonies, we regressed (OLS) the percentage of area used on log-transformed colony size. We expected a positive relationship if penguins spread out more around larger colonies than around smaller colonies. We also considered no relationship to be likely because the area of a circle or arc increases with distance from the colony but the percentage of a circle covered by an arc of a given range of angles is constant for circles of any radius.

Overlap With Marine Protected Areas and Hydrocarbon Concessions

We downloaded marine protected area polygons from protectedplanet.net (UNEP-WCMC and IUCN) and projected them to match the tracking data. We calculated the percentage of the 50% and 90% UD kernel polygons that are within one or more MPAs for each colony.

Argentina is currently offering tax incentives and 30-year concessions for developing its offshore oil and gas basins (Nievas El Makte et al., 2021). We obtained shapefiles for the Argentine hydrocarbon concessions and permit areas from the Secretaría de Energía of Argentina (see <https://sig.se.gob.ar/visor/visorsig.php?t=4> for data visualization), and projected them to match the tracking data. Permits were awarded for seismic data collection over most of the continental shelf of Argentina and beyond in 2017–2021. We calculated the percentage of the 50% and 90% UD kernel polygons

that overlap this area for each colony. Penguins from one colony, Cabo Virgenes, used areas within other concessions, including areas with current extraction activities. We calculated the percentage of the 50% and 90% UD kernel polygons for Cabo Virgenes that are within these concessions.

Statistics and GIS Analyses

For the maps, we downloaded exclusive economic zone (EEZ) polygons from MarineRegions.org (Flanders Marine Institute, 2021) and bathymetric data from the U.S. National Oceanic and Atmospheric Administration's ETOPO1 database (Amante and Eakins, 2009; NOAA National Geophysical Data Center, 2009). We made all maps and conducted GIS analyses in R 3.6.3 (R Development Core Team, 2020). We ran statistical tests in Stata/IC 11.2 (StataCorp LP, College Station, TX) or R. We wrote custom queries in Microsoft SQL Server Management Studio for all filters and pre-model processing and ran the *crawl* state-space models in R.

RESULTS

Assumption That Colony Size Predicts Foraging Distance

Foraging distance was positively related to colony size (Table 3; Figure 2 Top; $F_{1,8} = 22.4$, $p = 0.002$, $R^2 = 0.70$, $n = 10$). Confidence intervals were large relative to foraging distances, however.

TABLE 3 | Foraging distances for Magellanic penguins breeding at 10 colonies in Argentina.

Colony	Mean (km)	SD	Mean maximum (km)	Maximum (km)
Complejo Islote Lobos	25	10	46	52
Estancia San Lorenzo	92	51	145	228
El Pedral	16	6	26	39
Punta Tombo	90	55	164	466
Cabo Dos Bahías	34	44	118	458
Isla Leones	48	61	175	289
Isla Chaffers	74	30	115	125
San Julián	85	37	127	177
Monte León	40	15	63	88
Cabo Virgenes	64	42	118	149

Mean is the mean foraging-trip distance for all trips of all individuals in all years at the colony. Mean maximum is the mean of the maximum distances for each individual. Maximum is the maximum foraging distance for all trips at the colony.

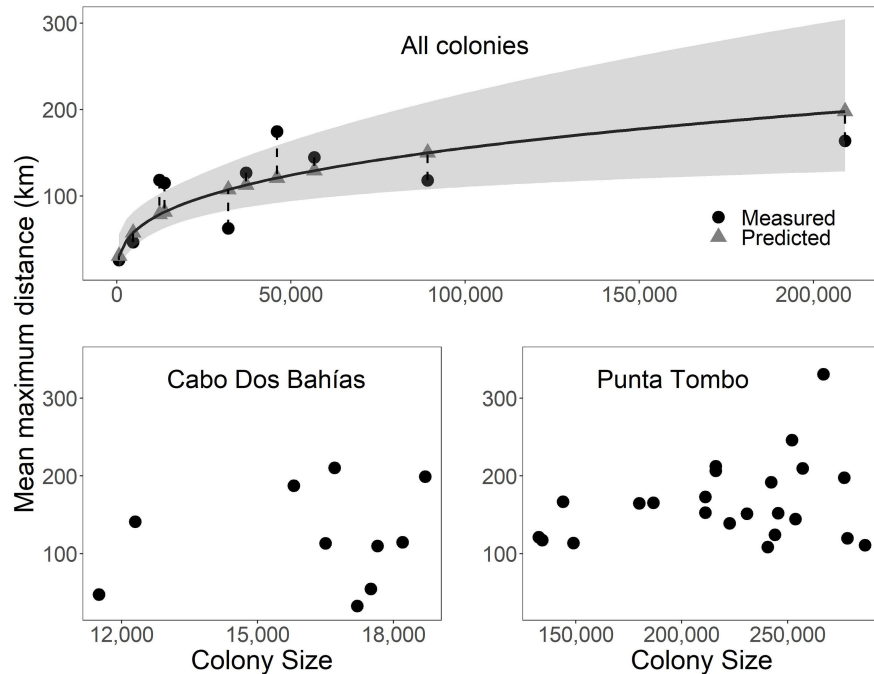


FIGURE 2 | The relationship between colony size (pairs or active nests) and foraging distance in Magellanic penguins at 10 breeding colonies in Argentina was significant (curved solid line, $p = 0.002$, $R^2 = 0.70$), but not predictive for several colonies (vertical dashed lines connect predicted and measured distances; gray ribbon represents 95% confidence intervals) (Top). Colony size was not significantly related to foraging distance within colony among years for Cabo Dos Bahías ($p = 0.60$, $R^2 < 0.01$; Bottom left) or Punta Tombo ($p = 0.39$, $R^2 < 0.01$; Bottom right). Mean maximum distance is the mean of the maximum distances for each individual.

Predicted mean maximum foraging distance differed from measured distance by 11%–72% (**Figure 2** Top). Predicted mean foraging distance differed from measured distance by up to 43% and predicted maximum foraging distance differed from measured distance by as much as 100% (not shown). The spread between upper and lower 95% confidence intervals around predicted foraging distances ranged from 40 km to 175 km. The smallest colony had a predicted foraging distance of 30 km with confidence intervals of 17 km and 56 km. The largest colony had a predicted foraging distance of 198 km with confidence intervals of 128 km and 305 km.

Contrary to the assumptions that each colony has a distinct foraging area, and birds forage closer to their own colony than to other colonies, we found overlap among colonies. Foraging areas for penguins from four colonies, Estancia San Lorenzo, Punta Tombo, Cabo Dos Bahías, and Isla Leones overlapped (**Figure 1**). Penguins from smaller colonies (e.g., Cabo Dos Bahías) did not always avoid foraging areas of larger colonies (e.g., Punta Tombo). Among these four colonies, penguins from colonies farther south often foraged closer to colonies farther north than to their own colonies.

Within colonies among years, there were no significant relationships between foraging distance and population size. The population at Cabo Dos Bahías ranged from 11,500 active nests in 2013 to 18,700 in 2002 (**Figure 2** Bottom left; $F_{1,8} = 0.3$, $p = 0.60$, $R^2 < 0.01$, $n = 10$). Mean maximum foraging distance ranged from 33 km in 2009 to 210 km in 2003. The population at

Punta Tombo ranged from 132,600 active nests in 2016 to 286,400 in 2012 (**Figure 2** Bottom right; $F_{1,21} = 0.8$, $p = 0.39$, $R^2 < 0.01$, $n = 23$). Mean maximum foraging distance ranged from 109 km in 2015 to 331 km in 1997. We had too few years ($n = 3$) to test interannual variation at El Pedral, but mean maximum foraging distance was least in 2014 when the colony size was largest (**Table 4**).

Assumption of Uniform Distributions

Penguin foraging areas (trip endpoints) at sea were not uniformly distributed around colonies (**Table 2**; **Figure S2**; $p \leq 0.03$). Penguins used a quarter of the available ocean area around their colonies, on average, based on 90% kernel UD contours ($23.9 \pm 10.1\%$, **Table 5**; **Figure 1**). The maximum amount of available area used was 39.6%, at Complejo Isote Lobos. In colonies with limited tracking data, these numbers may be underestimates, but at Punta Tombo, with 23 years of data and almost 1800 trips, the penguins used only 15.6% of the area at sea where they could forage.

Colony size and the percentage of available foraging area that penguins used were correlated ($F_{1,8} = 6.4$, $p = 0.03$, $R^2 = 0.38$, log-scale estimate = -4.1 ± 1.6). The relationship was negative, however, opposite the direction predicted if penguins from larger colonies spread out more than penguins from smaller colonies. This result also contradicts the prediction that penguins from larger colonies have a similar range of bearings but still fan out more than penguins from smaller colonies (because the

TABLE 4 | Foraging distance of Magellanic penguins tracked at El Pedral, Argentina, did not increase monotonically with an exponentially growing population.

Year	Population size (pairs)	Mean maximum distance (km)
2011	90	24.7
2012	240	29.6
2014	1640	22.2

Population size for 2011 and 2012 are from Pozzi et al. (2015), and the size for 2014 was calculated using the growth rate in that paper. Mean maximum distance is the mean distance of the longest trip for each penguin in each year.

available area of a section of circle increases with the radius of the circle).

The amount of available space used by penguins also varied among years (**Figure S3**). At Cabo Dos Bahías, penguins used between 0.4% and 6.7% of available ocean, depending on year ($n = 10$ years). At Punta Tombo, they used 2.0%-7.4% of the area at sea ($n = 23$ years).

Overlap With MPAs

Penguin foraging areas overlapped with 12 marine protected areas in Argentine waters, but for most colonies, especially southern colonies, overlap was minimal (**Figures 1, 3**). The two southernmost colonies reported here (Monte León and Cabo Virgenes) have no marine protection for the penguins' foraging areas. The two large biosphere reserves, Peninsula Valdés and Patagonia Azul (**Table S3; Figure 4**), accounted for most of the overlap. For Cabo Dos Bahías and Isla Leones, 50% UD kernel contours overlapped with MPAs much more than 90% UD kernel contours did, because most of the MPA areas are close to shore and most of the 90% UD kernel contours are farther from shore (**Figures 1, 3**).

Overlap With Hydrocarbon Concessions

The area permitted for seismic data collection covers most of the Argentine continental shelf, offshore of provincial waters, and extends over deeper waters north of the Falkland/Malvinas Islands, covering 1,090,454 km² (**Figure 4**). Seismic surveys have already been carried out over extensive areas (**Figure S4**). The area where seismic surveys are permitted overlaps areas used by penguins from all except three of the 10 colonies (**Figures 3, 4**).

Penguins at Complejo Islote Lobos and El Pedral foraged within gulfs that are not included in the seismic-data-collection area, and penguins at Monte León foraged closer to shore than the area extends. The 90% UD kernel contours extend farther offshore than the 50% UD kernel contours for Cabo Dos Bahías, Isla Leones, and Cabo Virgenes, accounting for the higher overlap with 90% UD kernel contours than for the 50% UD kernel contours.

Penguins from Cabo Virgenes also overlapped with other hydrocarbon concessions, with 18% of the 50% kernel UD contour and 22.2% of the 90% kernel UD contour being inside currently exploited concessions. In addition, 13% of the 50% kernel UD contour and 26.2% of the 90% kernel UD contour are inside concession blocks that are offered, in bidding, or awarded (**Figure 4**).

DISCUSSION

Although foraging distance of Magellanic penguins increased with colony size among ten colonies, variation not explained by colony size meant that MPAs based on the predicted distances would not protect foraging areas adequately at several colonies. In addition, there was no relationship between breeding population size and foraging distance within colony among years. We found no support for the assumption that penguins spread out uniformly around colonies to forage. Foraging habitats depend on oceanographic features that occur in specific locations on the Patagonian Shelf (Acha et al., 2004; Boersma et al., 2009). Overlap between penguin locations and MPAs in Argentina was low for most colonies, as penguins forage farther offshore than coastal MPAs extend, and some colonies do not benefit from any currently implemented marine protection. The foraging area of only one colony overlapped with an area of current hydrocarbon extraction. Based on areas designated for seismic exploration, however, the potential future overlap between penguins foraging at sea and hydrocarbon activities is high. Most of the continental shelf is now open for seismic surveys. The low-frequency sounds produced likely impact the nearshore waters where surveys are not permitted, and can cause avoidance behavior and lower breeding success in penguins (Pichegru et al., 2017).

TABLE 5 | Foraging area used by Magellanic penguins from 10 colonies in Argentina.

Colony	50% UD area (km ²)	90% UD area (km ²)	Available area (km ²)	% Available area used
Complejo Islote Lobos	527	1,760	4,441	39.6
Estancia San Lorenzo	5,368	20,895	96,989	21.5
El Pedral	484	1,303	3,490	37.3
Punta Tombo	14,406	54,001	346,646	15.6
Cabo Dos Bahías	3,952	40,981	347,209	11.8
Isla Leones	2,559	21,057	149,762	14.1
Isla Chaffers	3,793	10,301	31,187	33.0
San Julián	1,778	6,583	44,727	14.7
Monte León	964	2,578	9,369	27.5
Cabo Virgenes	2,322	10,659	43,900	24.3

50% and 90% UD areas are the areas within the 50% and 90% kernel UD contours, respectively. Available area is the area covered by ocean within the maximum foraging distance from each colony. % available area used is the area of the 90% UD kernel polygon for each colony divided by the available area, times 100.

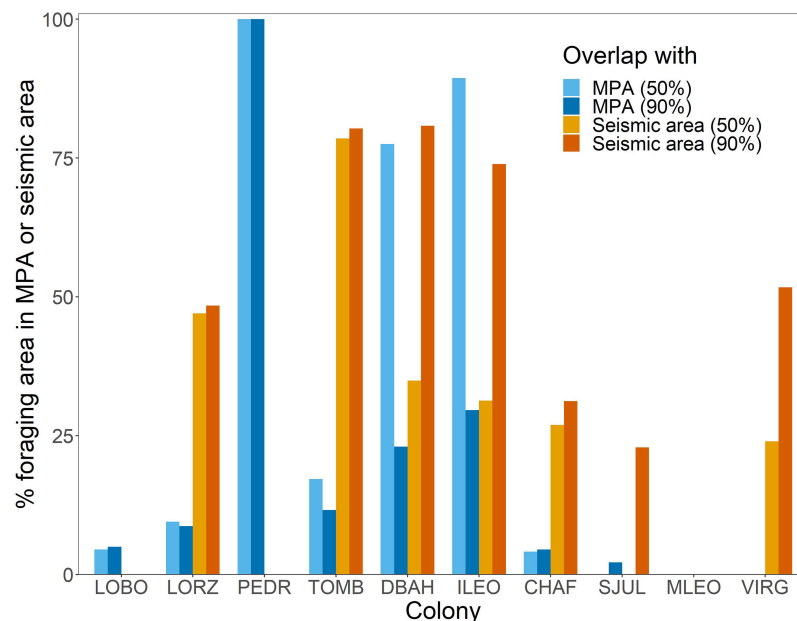


FIGURE 3 | The percentage of Magellanic penguin foraging area contained within marine protected areas (MPA) or seismic-survey areas (Seismic area) varied among colonies in Argentina. 50% = overlap of 50% UD kernel contours with MPAs or seismic-survey areas; 90% = overlap of 90% UD kernel contours with MPAs or seismic-survey areas. LOBO, Complejo Islote Lobos; LORZ, Estancia San Lorenzo; PEDR, El Pedral; TOMB, Punta Tombo; DBAH, Cabo Dos Bahías; ILEO, Isla Leones; CHAF, Isla Chaffers; SJUL, San Julián; MLEO, Monte León; VIRG, Cabo Vírgenes. See **Table S3** for MPAs that overlap each colony's foraging area and **Figure 4** for locations of MPAs.

Assumption That Colony Size Predicts Foraging Distance

Habitat and foraging behavior can vary across small spatial scales (10s to 100s of km), leading habitat use to vary among colonies in marine central-place foragers (Baylis et al., 2019). Gentoo penguins *Pygoscelis papua* at three colonies of similar small size, 20–55 km apart, in the Kerguelen Archipelago had almost as much variation in foraging distance as the species showed across its entire range (Lescroël and Bost, 2005). Oceanographic features that concentrate prey (Weimerskirch, 2007; Scales et al., 2014) influence penguin foraging locations in Argentina (Boersma et al., 2009), accounting for much residual variation in the population size-foraging distance relationship we found.

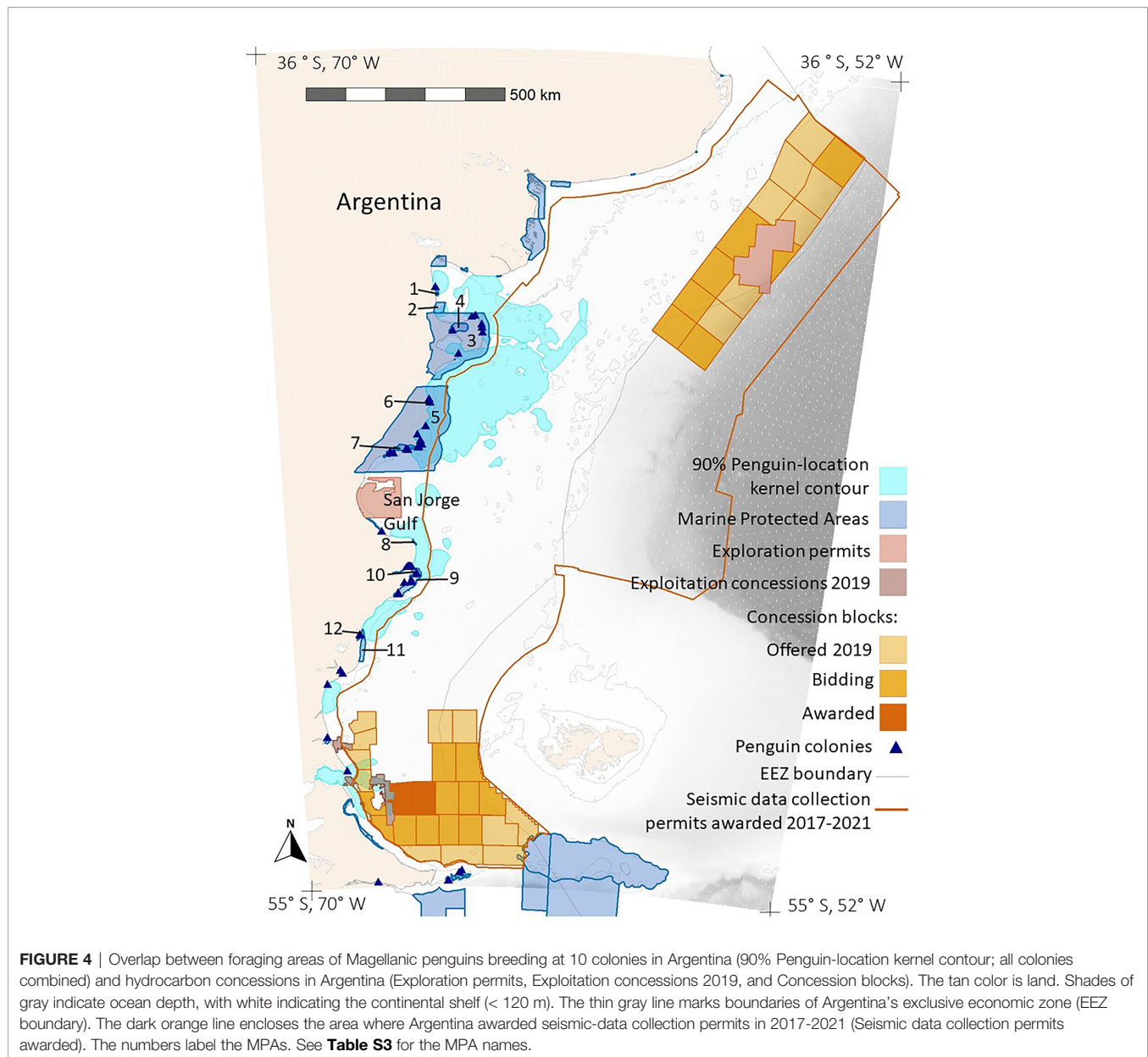
In addition to competing with individuals from their own and nearby colonies, seabirds may compete for prey with other species (Ainley et al., 2006) and with fisheries (Gandini et al., 1999; Bertrand et al., 2012). This competition could lead to depletion of prey beyond that caused by one species, and complicate the relationship between colony size and foraging distance. For example, Magellanic penguins breeding in northern Patagonia likely compete with other seabirds, marine mammals, and fish such as hake for anchovy (Koen-Alonso and Yodzis, 2005).

The relationship we found between colony size and foraging distance indicates that there may be a threshold effect between small (< 5000 pairs) and large (> 10,000 pairs) colonies, but we would need more small colonies to test this. We used back-transformed confidence intervals to account for

uncertainty. Measured mean foraging distance for four of the ten colonies fell outside the 95% confidence intervals of the predicted distances. Furthermore, interannual variation in colony size was not related to interannual variation in foraging distance.

There is a relationship between colony size and foraging distance for populations of some species (Lewis et al., 2001), but it is not universal. The foraging-radius approach has been used to design effective protection for a species (Ludynia et al., 2012). Whenever foraging behavior varies among colonies or years, however, the effectiveness of the foraging-radius approach will depend on the representativeness of the available data.

The interannual variation in foraging distance within a colony argues for caution in assuming tracking data from one year are representative of all years. Population size varies among years at colonies because Magellanic penguins that skip breeding frequently stay at sea (Boersma and Rebstock, 2010; Gownaris and Boersma, 2019). Egg and chick mortality vary among years (Boersma et al., 1990; Boersma and Rebstock, 2014). The number of chicks remaining by January varied, sometimes due to density-independent factors such as rainstorms (Boersma and Rebstock, 2014) or heat (Holt and Boersma, 2022), as well as starvation and predation (Boersma et al., 1990; Boersma and Rebstock, 2014). In addition, marine productivity and strength of the fronts that concentrate penguin prey (Hansen et al., 2001; Alemany et al., 2009) vary over time scales of tidal cycles to years (Hansen et al., 2001; Marrari et al., 2013; Pisoni et al., 2015), affecting the



foraging locations of penguins within and among years (Rebstock et al., 2022).

Assumption of Uniform Distributions

Marine central-place foragers have often been assumed to spread out uniformly around colonies to minimize competition with other individuals from the colony (Cairns, 1989), but our data did not support this assumption. The assumption was not supported by several other studies as well (Grecian et al., 2012; Soanes et al., 2016). The expectation of uniform distribution is based on the assumption of uniform, or at least unpredictable, prey or prey patches (Cairns, 1989; Bolton et al., 2018). This assumption of prey distribution is seldom tested and not always even stated. When prey is concentrated at oceanographic

features (Hansen et al., 2001), those features attract individuals from multiple colonies (Weimerskirch, 2007; Bolton et al., 2018), as we found (Boersma et al., 2009; this study, **Figure 1**).

The uniform distribution is expected to be modified when a colony's foraging area overlaps with that of a larger colony, as individuals from the smaller colony should avoid the larger colony's foraging area (Bolton et al., 2018). In our study, penguins from two smaller colonies (Cabo Dos Bahías and Isla Leones) south of Punta Tombo swam north to overlap with penguins from the larger colony (**Figure 1**), because productive fronts are closer to Punta Tombo than to Cabo Dos Bahías and Isla Leones. The negative relationship we found between colony size and the percentage of available area used may result from penguins at a few colonies concentrating effort at productive

fronts, and hence using a smaller range of directions than penguins at some smaller colonies. The distances penguins swim depend on the relative locations of the colonies and fronts.

Shorter foraging distances and more spread-out distributions at the two smallest colonies may indicate that unconcentrated prey is sufficient for penguins from small colonies, whereas penguins from larger colonies do deplete prey unless it is concentrated at oceanographic features. Complejo Isote Lobos and El Pedral, the two smallest and newest colonies, are also the only colonies in our study where penguins forage within the northern Patagonian gulfs, which may have foraging habitats unlike those of the open shelf.

Assuming that central-place foragers spread out to reduce competition ignores the benefits of group foraging. Penguins are sometimes more successful when foraging in groups (McInnes et al., 2017). Multispecies foraging aggregations are common at sea, including both seabirds and marine mammals (Veit and Harrison, 2017). Seabird flocks often serve as attractors to individuals looking for prey (Silverman et al., 2004). Groups of penguins from a large colony may need to spread out if other foraging groups deplete prey, but the assumption that seabirds forage independently and individuals spread out uniformly is too simplistic.

Nonuniform space use is not restricted to mainland colonies. Magellanic penguins tracked on New Island, in the western Falkland/Malvinas Islands did not use space uniformly in spite of having potential foraging areas available 360° around the island (Boersma et al., 2002; Masello et al., 2010). Gentoo and southern rockhopper *Eudyptes chrysocome* penguins tracked from the same location also showed nonuniform space use (Boersma et al., 2002; Masello et al., 2010). African penguins *Spheniscus demersus* breeding on islands in Namibia foraged exclusively northwest of their colonies (Ludynia et al., 2012), again suggesting the importance of prey distribution in determining penguins' foraging distances and distributions at sea.

Overlap With MPAs

Overlap with MPAs depended on the locations of the MPAs, how far offshore penguins foraged, and what direction they tended to go from the colony. We did not attempt here to delineate priority areas for protection of Magellanic penguins. We intended to show how variation among foraging areas among colonies affects planning for marine protection.

Data from colonies with few tracks are unlikely to be highly representative of the population of that colony (Soanes et al., 2013). We have sufficient data to show that penguins from Punta Tombo and Cabo Dos Bahías often forage far beyond provincial jurisdictions and cannot be protected by coastal MPAs. The mean foraging distance from El Pedral (16 km), however, is within provincial jurisdiction (12 nm = 22.2 km).

Penguins from Isla Chaffers and San Julián foraged north of the colonies, but protected areas are south of the colonies. Our sample sizes at those colonies are low. We would underestimate foraging area of the colony if individual penguins are faithful to foraging sites (Carroll et al., 2018) and directions to foraging sites vary by penguin. However, we show that Magellanic penguins do not spread out evenly from the colony. Furthermore, penguins

tracked with GPS tags at Puerto Deseado (near Isla Chaffers) in 2006, and San Julián in 2007 (Sala et al., 2012) generally foraged in similar areas to penguins we tracked in our study.

Marine protected areas in Argentina include provincial protected areas, national parks, interjurisdictional areas (joint national and provincial management), and UNESCO Biosphere Reserves. Most MPAs in Argentina are coastal (Gil et al., 2019) and provincial reserves cannot protect waters beyond 12 nm. The reasons for establishing the protected areas vary. In a few cases, MPAs were designed to protect penguins and other seabirds or pinnipeds (especially on land), but in general, protecting penguin foraging areas was not a focus.

Overlap With Hydrocarbon Concessions

Argentina currently has limited offshore hydrocarbon production (Nievas El Makte et al., 2021), overlapping the foraging area of only one of the colonies where we tracked penguins. Given the current leasing plans and seismic surveys, however, foraging areas of other colonies are likely to overlap with hydrocarbon extraction activities in the near future. Increasing offshore production increases the risk of pollution at sea (García Borboroglu et al., 2006; Etkin and Nedwed, 2021; Nievas El Makte et al., 2021). In addition, the northward flowing currents on and off the continental shelf of Argentina (Palma et al., 2008) make spatial connectivity high (Afán et al., 2018; Gil et al., 2019) and pollution in one region likely to affect penguins in other regions. In spite of limited offshore production, Argentina experienced large spills and chronic oil pollution that have affected penguins (Jenkins, 1978; Gandini et al., 1994; García Borboroglu et al., 2006; Boersma, 2008; Boersma, 2012; Nievas El Makte et al., 2021).

Most of the continental shelf of Argentina offshore of provincial waters (12 nautical miles) is now open for seismic exploration, potentially affecting foraging areas of Magellanic penguins at all colonies. Penguins that forage in gulfs or within provincial waters that do not overlap with the seismic permit area can still be affected by seismic surveys because attenuation of low-frequency sounds in water is low (Hildebrand, 2009). Seismic surveys produce loud sounds that affect many species of marine animals, from invertebrates to whales (Gordon et al., 2003; Hildebrand, 2009; Carroll et al., 2017). Penguins avoid seismic survey activities (Pichegru et al., 2017; Seco Pon et al., 2019) and loud experimental sounds in the water (Sørensen et al., 2020). African penguins avoided their usual foraging areas and increased their foraging effort up to 100 km from seismic activities (Pichegru et al., 2017).

Recommendations for Protecting Penguins and Other Seabirds at Sea When Colony-Specific Data Are Lacking

1) Do not wait for more data to take action; implement conservation measures that can be modified in light of new information.

We should use the best information we have even if it is incomplete. Penguins and other seabirds need protection now from a variety of human-caused problems, including fisheries,

pollution, climate change, introduced predators, and harvest (Croxall et al., 2012; García Borboroglu and Boersma, 2013; Trathan et al., 2014). Information and threats will change. Protection measures need to be flexible enough to be adapted to new information and situations (Boersma et al., 2002).

2) Secure minimum protection in nearshore waters around colonies. Penguins have to swim through nearshore waters around the colony twice on each foraging trip, regardless of how far away they forage. Seabirds, including penguins, often form rafts in the water near their colonies (Weimerskirch et al., 2010; Berlincourt and Arnould, 2014). Nearshore waters have high conservation value for Magellanic penguins, other seabirds, and pinnipeds (Pichegru et al., 2010; Boersma et al., 2015; Sherley et al., 2015; Sherley et al., 2018; Baylis et al., 2021). Keeping nearshore waters free of pollution and fishing pressure is essential (Boersma et al., 2002), and can be done without addition data, but protection of offshore foraging areas is also critical.

3) Manage economic activities to reduce threats in all regions of the ocean.

All fisheries should be managed so that prey is not depleted and bycatch is minimized (Trathan et al., 2014; Handley et al., 2020). Hydrocarbon activities should be drastically reduced as hydrocarbons are replaced by clean energy sources. In the meanwhile, hydrocarbon activities should be managed to minimize marine pollution (Trathan et al., 2014; Handley et al., 2020). Argentina's development of offshore hydrocarbon reserves will increase greenhouse-gas emissions and pollution risks, and is insupportable in light of climate change. Climate change threatens penguins and biodiversity directly and indirectly (Boersma and Rebstock, 2014; Trathan et al., 2014; Orgeret et al., 2021; Holt and Boersma, 2022). One of the most effective ways to slow climate change is to leave fossil fuels in the ground (Johnsson et al., 2019).

4) Collect data needed to identify critical foraging areas and timing.

The creation of a protected area is a political challenge that involves sociopolitical, economic, and cultural variables (Gronrud-Colvert et al., 2021). Science is fundamental to inform, help justify, and design protected areas. Research can inform protection while reducing unnecessary restrictions that may prevent any protection. The time has passed where penguins should be paying for pollution, climate change, and resource extraction that harms not only penguins, but other wildlife and people.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by University of Washington Institutional Animal Care and Use Committee.

AUTHOR CONTRIBUTIONS

PDB conceived and initiated the tracking project; all authors conducted fieldwork to track penguins. All authors contributed to the conceptual framing of the study. GR analyzed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.815706/full#supplementary-material>

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Data Quality Influences the Predicted Distribution and Habitat of Four Southern-Hemisphere Albatross Species

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Few studies have assessed the influence of data quality on the predicted probability of occurrence and preferred habitat of marine predators. We compared results from four species distribution models (SDMs) for four southern-hemisphere albatross species, Buller's (*Thalassarche bulleri*), Campbell (*T. impavida*), grey-headed (*T. chrysostoma*), and white-capped (*T. steadyi*), based on datasets of differing quality, ranging from no location data to twice-daily locations of individual birds collected by geolocation devices. Two relative environmental suitability (RES) models were fit using minimum and maximum preferred and absolute values for each environmental variable based on (1) monthly 50% kernel density contours and background environmental data, and (2) primary literature or expert opinion. Additionally, two boosted regression tree (BRT) models were fit using (1) opportunistic sightings data, and (2) geolocation data from bird-borne electronic tags. Using model-specific threshold values, habitat was quantified for each species and model. Model variables included distance from land, bathymetry, sea surface temperature, and chlorophyll-*a* concentration. Results from both RES models and the BRT model fit with opportunistic sightings were compared to those from the BRT model fit using geolocation data to assess the influence of data quality on predicted occupancy and habitat. For all species, BRT models outperformed RES models. BRT models offer a predictive advantage over RES models by being able to identify relevant variables, incorporate environmental interactions, and provide spatially explicit estimates of model uncertainty.

RES models resulted in larger, less refined areas of predicted habitat for all species. Our study highlights the importance of data quality in predicting the distribution and habitat of albatrosses and emphasises the need to consider the pros and cons associated with different levels of data quality when using SDMs to inform management decisions. Furthermore, we examine the overlap in preferred habitat predicted by each SDM with fishing effort. We discuss the influence of data quality on predicting the wide-scale distributions of pelagic seabirds and how these impacts could result in different protection measures.

Keywords: albatross, species distribution models, relative environmental suitability, boosted regression tree, habitat suitability, geolocation, biologging, seabird conservation

1 INTRODUCTION

Continuing declines in biodiversity have prompted local and international agencies to advocate for much-improved spatial protection measures in both terrestrial and marine environments (Tancell et al., 2016; Dias et al., 2017; Augé et al., 2018; Hays et al., 2019; Hindell et al., 2020). This goal, in conjunction with the increased availability of high resolution location data for flora and fauna, have led to the wider application of species distribution models (SDMs) for conservation (Johnson and Gillingham, 2005; Rodríguez et al., 2007; Franklin, 2010; Porfirio et al., 2014). The power of SDMs lies in converting point locations into predicted (spatially explicit) probability of occurrence and preferred habitat. SDMs have become widely used for understanding geographic range (Torres et al., 2008; Goetz et al., 2012), estimating extinction rates (Benito et al., 2009; Plischoff et al., 2014; Stephenson et al., 2020), understanding impacts of climate change (Laidre et al., 2008; Kaschner et al., 2011), prioritizing biodiversity conservation (Moilanen et al., 2005; Oliveira et al., 2017; Fuentes-Castillo et al., 2019), and planning the size and location of protected areas (Hooker et al., 1999; Gerrodette and Eguchi, 2011). Ideally, reliable records of presence/absence data collected during systematic surveys (in space and time) which encompass the full potential range of a species would be used in SDMs to examine the relationship between occurrence and the environment. However, high-quality location data are not available for most mobile species and the field studies required to obtain such information over large spatial-temporal scales are prohibitively expensive or logistically unfeasible. Consequently, SDMs are often informed with the best available data, which is likely to be limited in space and time and may necessitate collation of data from different sources, including opportunistic sightings (Derville et al., 2018). Alternatively, when little or no data are available, relative environmental suitability (RES) models have been used to predict species occurrence using qualitative descriptions from the literature or expert opinion (Kaschner et al., 2006; Watson et al., 2013; Stephenson et al., 2020).

For management purposes, predictions from SDMs are frequently extrapolated to areas well beyond the spatial-temporal range of the underlying data. This approach may be acceptable when the ecology of a species is well understood, the

drivers of distribution change little from one area to another, or when long-term, high-quality data are used to predict species occurrence (Elith and Leathwick, 2009; Torres et al., 2015). However, when coverage of the data is insufficient, predictions may grossly over- or under-estimate occurrence and habitat use (Stockwell and Peterson, 2002; Elith et al., 2010), potentially resulting in protection measures that are inappropriate or ineffective (Rowden et al., 2019).

Technological advancements in bio-logging technology have led to an increased understanding of movement, foraging behaviour, and habitat use for some species (Block, 2005; Cooke, 2008; Evans et al., 2013; Wilmers et al., 2015). While bio-logging data is often considered the gold standard for understanding species distribution, in reality, high-quality data are often not available. Given resource limitations, management decisions for protected or threatened species, are frequently made on the basis of species distribution data that are far from complete. Under this paradigm, it is important to understand how results from SDMs informed with different types and quality of location data compare. In this study, we quantified and compared the predicted probability of occurrence and preferred habitat generated from SDMs informed by datasets of varying quality for Buller's (*Thalassarche bulleri*), Campbell (*T. impavida*), grey-headed (*T. chrysostoma*), and white-capped (*T. steadi*) albatrosses (hereafter referred to as BUAL, CAAL, GHAL, and WCAL, respectively), both globally and within New Zealand's (NZ) Exclusive Economic Zone (EEZ). Although two sub-species of BUAL are recognised in NZ (e.g. Robertson et al., 2017), in this study we refer exclusively to the southern sub-species *T. bulleri bulleri*.

Albatrosses are a highly threatened group of seabirds with distributions spanning entire ocean basins. Mortality from fisheries bycatch is a leading threat globally, and is a concern for the majority albatrosses breeding in NZ (Lewison and Crowder, 2003; Waugh et al., 2008; Anderson et al., 2011; Żydelis et al., 2011; Croxall et al., 2012; Jiménez et al., 2014). The International Union for the Conservation of Nature (IUCN) defines albatross (Family *Diomedidae*) as the most threatened family of seabirds in the world with 17 of the 22 species currently listed as 'Vulnerable', 'Endangered', or 'Critically Endangered' (Tuck et al., 2011). BUAL and WCAL are currently classified as 'Near Threatened', CAAL as 'Vulnerable', and GHAL as

‘Endangered’ on the IUCN Red List of Threatened Species (IUCN, 2021). Under the NZ threat classification system (Robertson et al., 2017), GHAL and CAAL are classified as ‘Threatened – nationally vulnerable’, WCAL as ‘At risk – declining’ and BUAL as ‘At risk – naturally uncommon’. All four species breed in New Zealand and are included in the ‘Assessment of Risk of Commercial Fisheries to NZ Seabirds’ (Richard et al., 2020).

In this study, we quantify the differences in preferred habitat predicted by SDMs fit with data of varying quality for four species of southern hemisphere albatross. Additionally, we quantify the monthly spatial overlap of preferred habitat predicted by four SDMs with fishing effort both globally and within NZ’s EEZ as well as the overlap in total preferred habitat predicted by the top two performing models with global fishing effort for each species. We hypothesized that SDMs fit with geolocation data would perform better than those fit using opportunistic sightings or qualitative descriptions of habitat use extracted from the literature. We also hypothesized that overlap in preferred habitat predicted by SDMs not fit with empirical data would result in greater overlap in fishing effort than models fit with high quality location data. We discuss the validity and caveats of predicting wide-scale distributions of pelagic seabirds from models fit with data of varying quality. Additionally, we compare the best performing SDMs to those currently used by managers to assess the risk of commercial fisheries to NZ seabirds (Sharp, 2017; Richard et al., 2020).

2 MATERIALS AND METHODS

2.1 Study Area

Due to the wide-ranging distributions of albatrosses, the study area extended around the world from ~30–80°S. Additionally, because BUAL, CAAL, GHAL, and WCAL breed at colonies within the NZ’s EEZ, results are also summarized within this boundary (Figure 1).

2.2 Species Location Data

Opportunistic sightings contributed by citizen scientists through eBird were available for BUAL, CAAL, GHAL, and WCAL. eBird is an online, publicly accessible database (eBird Basic Dataset, 2018) that is quality controlled; regional experts validate sightings and remove anomalous records (accessed August 2018). A total of 22,296 sightings records were available over a 46-year period (Supplementary Table 1).

Data from light-level loggers (or Global Location Sensing - GLS) were also available for each species. GLS tags (British Antarctic Survey (BAS), Cambridge, UK) were deployed on albatrosses during the breeding season at the following colonies: BUAL on North East Island, Snares Islands (48.03°S, 166.50°E), CAAL and GHAL on Campbell Island (52.48°S, 169.23°E), and WCAL on Auckland Island (50.83°S, 165.90°E) (Figure 1 and Supplementary Table 2). Breeding birds were caught by hand at the nest and the logger (< 3g), attached to a plastic band with cable ties, was fit to the tarsus. Each deployment took approximately two minutes to complete.

In most cases, GLS tags were recovered the following year from annually breeding species (BUAL and CAAL) and after two years for biennially breeding species (GHAL and WCAL).

Once recovered, light data were downloaded from the tags using ‘Decompressor’ software (BAS, Cambridge, UK). To process GLS data, we used the ‘twilight-free’ package (Bindoff et al., 2018) in R (version 3.6.1) which is capable of estimating locations without the need for users to estimate time of twilights. Similarly, the method is robust to light pollution from other light sources, such as ships and lighthouses. This was especially useful for species such as WCAL which frequently visit vessels at night. See **Supplementary Material** for additional details.

2.3 Environmental Data

To examine the relationship between species’ occurrence and environmental features, we calculated or obtained spatial data for distance to land (DLAND), bathymetry (BATHY), sea surface temperature (SST), and chlorophyll-*a* (CHL) (Supplementary Table 3). These variables often show relationships with seabird distributions (Hyrenbach et al., 2002; Louzao et al., 2006; Ramírez et al., 2013; Clay et al., 2016) and are known to influence the distribution and abundance of prey species of marine megafauna (Tynan et al., 2005; Etnoyer et al., 2006; Bluhm et al., 2007).

2.4 Species Distribution Models

2.4.1 Relative Environmental Suitability Models

RES is a mechanistic model where the relationship between occurrence and the environment is described by an environmental envelope. In the absence of empirical data, RES models can be used to predict geographic ranges using values for environmental variables found in available literature or informed by expert opinion (Kaschner et al., 2006; Stephenson et al., 2020). Following methods presented in Kaschner et al. (2006), we developed RES models by estimating a trapezoidal response curve based on the absolute minimum and maximum (Min_A , Max_A) and preferred minimum and maximum (Min_P , Max_P) ranges for each of the environmental variables used in our study. Habitat suitability was assumed to be uniform and maximal (value = 1) between Min_P and Max_P with suitability trending towards zero when approaching Min_A and Max_A .

Two RES models were developed using different data sources for minimum and maximum absolute and preferred ranges: 1) presences within monthly 50% kernel density contours generated from GLS data (Min_P , Max_P) and monthly background environmental data (Min_A , Max_A) (RES_{KERN}), and 2) primary literature or expert opinion (RES_{LIT}) (see **Supplementary Table 4** for additional details and values for each RES model and species). Methods describing the kernel density estimation are presented in the following section for BRT models.

By multiplying the suitability of each environmental predictor variable, this method produced an index of RES values scaled from zero to one. Values for any single predictor variable that fell outside the absolute range were assigned a zero to avoid predicting species occurrence in unsuitable environments. For both RES models, we generated monthly predictions of habitat suitability as well as an overall prediction based on the mean of all monthly predictions.

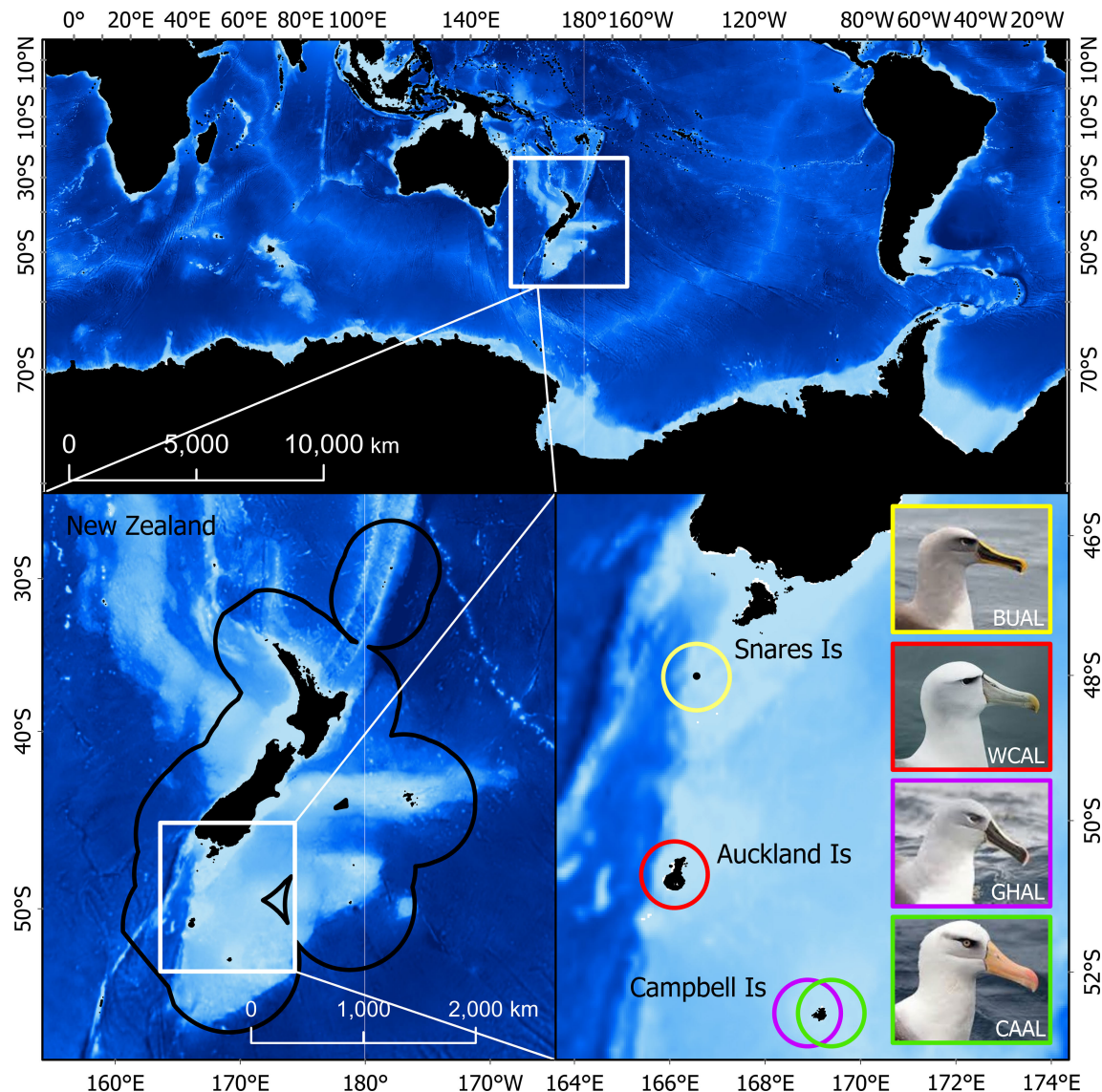


FIGURE 1 | The study region in which probability of occurrence and habitat were predicted (top). The bottom panels show the tagging locations (breeding colonies) within the New Zealand Exclusive Economic Zone for four albatross species: Buller's (BUAL), white-capped (WCAL), grey-headed (GHAL), and Campbell (CAAL).

2.4.2 Boosted Regression Tree Models

The relationship between species' presence/availability and environmental variables was investigated using BRT models within R statistical software (version 4.0.3) (R Core Team, 2020) that combines two algorithms (1) classifying to partition observations into groups with similar characteristics, and (2) boosting to combine a collection of models (Elith et al., 2008). Month, DLAND, BATHY, SST, and CHL were included in all models. BRT models were able to estimate non-linear relationships, and correlated, interacting variables (Guisan and Zimmermann, 2000; Elith and Leathwick, 2009). In this study, two BRT models were fit using (1) opportunistic sightings (BRT_{OS}), and (2) GLS data (BRT_{GL}).

For each albatross species, BRT_{OS} models were fit using presence data that remained after removing locations on land and aggregating into 5 km cells, while BRT_{GL} models were fit using a dataset created from previously established methods (Ramírez et al., 2013; Torres et al., 2015). Specifically, we generated monthly utilization distribution kernels with a 5 km grid size and a 186 km smoothing parameter (or bandwidth) to account for the mean error associated with GLS data (Phillips et al., 2004; Calenge, 2006). Then we calculated monthly 50% data contours that are commonly used to define core habitat (Hyrenbach et al., 2002; Ramírez et al., 2013; Torres et al., 2015) (**Supplementary Figures 1–4**). For each month, we used the midpoint for all 5 x 5 km cells within the 50% kernel density contour that encompassed at least one GLS location as

presence data in the species-specific BRT_{GL} model. For the purposes of model comparison, we assumed that opportunistic sightings and GLS data were representative of the distribution for each species.

True absences were not available for either the opportunistic sightings or the GLS datasets. As such, we generated background data for each BRT model by creating uniformly spaced points every 100 km within the global study area and then extracted those points within the minimum convex hull created from the presence data for each species. The ‘extract’ function (Hijmans, 2020) was used to sample the environmental layers at each presence and background location to match the resolution of the data. Values for environmental variables were extracted from the same month as the opportunistic sightings and GLS locations. Similarly, environmental variables were extracted for all background points for each month.

Each species-specific BRT model was fit using all presence/background data. Because the number of background points were much greater than the number of presences, background points were down-weighted so that the sum of their total was equal to the total number of presences (Table 1). For example, in the case of 80 presences and 1000 background points, presences would be assigned a weighting of 1 while background points would be assigned a weighting of $80/1000 = 0.08$. Although BRT models are generally robust to correlations between variables (Guisan and Zimmermann, 2000; Elith and Leathwick, 2009), the use of highly correlated variables complicates the interpretation of model results with only minimal improvement in predictive accuracy (Leathwick et al., 2006). Collinearity between environmental variables was assessed using Pearson’s correlation coefficient (Murdoch and Chow, 1996; Friendly, 2002).

The ‘gbm.step’ function in the ‘dismo’ package (Hijmans et al., 2020) and evaluation functions in the ‘gbm’ package (Greenwell et al., 2020) were used to fit and evaluate the BRT_{OS} and BRT_{GL} model for each species. Each BRT model was bootstrapped 200 times. For each iteration, a random training dataset consisting of 75% of the presence and background data was drawn and used to fit a BRT model with a Bernoulli error distribution. Following recommendation in Elith et al. (2008) and Leathwick et al. (2006), the learning rate was adjusted for each model type, species/data type, to ensure a minimum tree depth of 1000 was achieved for each bootstrap iteration (see **Supplementary Material** for additional details).

To assess the importance of each environmental response variable, we calculated the mean relative influence and standard deviation produced by the BRT model across bootstraps. Relative influence is calculated by summing the number of times each variable was chosen for splitting, weighted by the squared improvement of the model as a result of each split. Partial dependence plots were used to visualize model fit across a gradient of values for each environmental variable (Elith et al., 2008). Finally, for each BRT model, the mean monthly predicted probability of occurrence was generated across bootstraps and a final prediction was produced by taking the mean of all monthly predictions.

2.5 Model Evaluation and Predictions

Because RES models do not use presence/availability data to predict probability of occurrence, there are no internal model fit metrics.

Therefore, to assess model performance we generated a Receiver Operator Characteristic (ROC) curve by extracting RES model fit values for each presence/availability location used to train species-specific BRT_{GL} models. The threshold value and habitat were then calculated using methods described below for BRT models. The location and area of habitat was compared across models for each species, globally, and within the NZ EEZ.

For BRT models, we assessed model performance by calculating the mean and standard deviation of the deviance explained, the area under the receiver operator characteristic curve (AUC), and the true skill statistic (TSS) from each bootstrap. AUC values range from 0 to 1 with 0 indicating no discrimination, 0.5 no better than random chance, and 1 indicating perfect discrimination ability (Legendre and Legendre, 2012). Models with AUC values ≥ 0.70 are considered ‘useful’ and those with AUC values > 0.9 are considered ‘very good’ because sensitivity is high relative to the false positive rate (Swets, 1988; Pearce and Ferrier, 2000). The TSS scales from -1 to 1 (sensitivity + specificity - 1) and takes into account both omission and commission errors and success as a result of random guessing. Values of 1 are in perfect agreement while values ≤ 0 indicate performance no better than random or a systematically incorrect prediction (Allouche et al., 2006). TSS values > 0.6 are considered useful to excellent (Komac et al., 2016). The AUC is a highly effective measure of the performance and a threshold-independent measure of accuracy, whereas the TSS is a threshold-dependent measure of accuracy that is not sensitive to prevalence (Allouche et al., 2006; Komac et al., 2016).

The performance of BRT models was also assessed using an evaluation dataset consisting of the remaining 25% of the presence/background data not used in the training dataset for each iteration of the bootstrap. Additionally, BRT_{OS} models were further validated using an external dataset consisting of GLS presence/availability data. To create a spatially-explicit measure of uncertainty, we calculated the overall standard deviation for each grid cell by taking the mean of the monthly standard deviations derived from the bootstraps of each model.

To convert predicted probability of occurrence to habitat suitability for each month, we used a model-specific threshold value determined by maximizing the area under the ROC curve (Hijmans et al., 2020). This threshold is the point at which accuracy is the highest and where sensitivity equals specificity. Predicted habitat for each monthly mean probability of occurrence grid was created by classifying cells above the threshold value as 1, and all others as ‘NaN’. Monthly habitat grids were then summed and colour-scaled from 1 to 12, thus reflecting the importance of each cell based on the number of months in which it was classified as habitat. However, because chlorophyll-*a* data were biased towards the equator and data did not extend as far south in winter compared to summer months, the importance of areas further from the equator may be biased low.

2.6 Overlap With Fishing Effort

Using data downloaded from Global Fishing Watch (GFW) (2020), overlap between the preferred habitat of the four

TABLE 1 | Evaluation metrics for Boosted Regression Tree (BRT) models informed by opportunistic sightings data (BRT_{OS}) and geolocation data (BRT_{GL}) for each of the four study species: Buller's (BUAL), Campbell (CAAL), grey-headed (GHAL), and white-capped (WCAL) albatross.

SPP	Model	P/B (train)	lr	Dev Exp (train)	AUC (train)	TSS (train)	Threshold (train)	AUC (eval)	TSS (eval)	AUC (external)	TSS (external)
BUAL	BRT _{OS}	657/80,847	0.005	0.80 ± 0.01	0.99 ± 0.00	0.93 ± 0.00	0.45 ± 0.09	0.99 ± 0.00	0.92 ± 0.01	0.83 ± 0.01	0.53 ± 0.02
	BRT _{GL}	9,715/84,436	0.05	0.82 ± 0.00	0.99 ± 0.00	0.93 ± 0.00	0.60 ± 0.02	0.99 ± 0.00	0.92 ± 0.00	NA	NA
CAAL	BRT _{OS}	260/47,908	0.005	0.73 ± 0.01	0.98 ± 0.00	0.92 ± 0.01	0.42 ± 0.05	0.98 ± 0.00	0.88 ± 0.02	0.62 ± 0.01	0.18 ± 0.01
	BRT _{GL}	19,842/151,534	0.1	0.70 ± 0.00	0.97 ± 0.00	0.86 ± 0.00	0.56 ± 0.01	0.97 ± 0.00	0.85 ± 0.00	NA	NA
GHAL	BRT _{OS}	763/126,773	0.005	0.62 ± 0.01	0.96 ± 0.00	0.84 ± 0.01	0.50 ± 0.06	0.96 ± 0.00	0.81 ± 0.01	0.51 ± 0.01	0.05 ± 0.02
	BRT _{GL}	27,033/152,669	0.1	0.83 ± 0.00	0.99 ± 0.00	0.93 ± 0.00	0.56 ± 0.01	0.99 ± 0.00	0.92 ± 0.00	NA	NA
WCAL	BRT _{OS}	1,497/107,808	0.01	0.76 ± 0.00	0.98 ± 0.00	0.89 ± 0.00	0.55 ± 0.08	0.98 ± 0.00	0.89 ± 0.01	0.84 ± 0.00	0.57 ± 0.01
	BRT _{GL}	9,363/86,256	0.03	0.75 ± 0.00	0.98 ± 0.00	0.89 ± 0.00	0.54 ± 0.02	0.98 ± 0.00	0.88 ± 0.00	NA	NA

Model parameters include the number of presences (P)/Background (B) points used in the model, learning rate (lr), Model metrics included deviance explained (Dev Exp) the area under receiver operating characteristic curve (AUC) scaled 0 to 1, and the True Skill Statistic (TSS) scaled from -1 to 1 for the training (train), evaluation (eval) and external dataset as well as the threshold values used to determine habitat. NA, Not Applicable.

albatross species and fishing effort was examined. Daily global fishing effort data based on vessels fitted with automatic identification system (AIS) transceivers (Kroodsma et al., 2018), were available for five years (2012–2016) at 0.01° resolution. Fishing effort data were not restricted by fishing vessel or gear type. The number of fishing hours that were within the preferred habitat predicted for each species was summed for each month, both globally and within NZ's EEZ. Mean monthly fishing effort was calculated by averaging replicate months across years. Finally, we quantified the monthly spatial overlap between fishing effort and preferred habitat predicted by each SDM and species. For the top two performing SDMs, mean fishing effort for each month was averaged and bar plots generated using the 'ggplot2' package (Wickham, 2009) in R statistical software to show mean fishing effort for each of the four albatross species, both globally and within NZ's EEZ.

3 RESULTS

Collinearity between our chosen environmental variables was low (Pearson's correlation <0.5) and, as such, all variables were retained within our distribution modelling analyses (Supplementary Figures 5–8). Based on model fit measures generated from an evaluation dataset, all BRT models were considered 'very good' (AUC (eval) ≥ 0.96, Table 1). Model fit metrics produced from the training and evaluation datasets were similar suggesting limited overfitting to the data and increased transferability of the models to novel datasets. The standard deviations in AUC and TSS performance metrics for all BRT models was ≤0.01 indicating that models performed similarly across all 200 bootstraps. External validation of the BRT_{OS} models using GLS data resulted in lower performance when compared to validation using the evaluation dataset (AUC (external): 0.51–0.84; AUC (eval): 0.96–0.99; Table 1).

AUC values showed that BRT models performed better than RES models (Table 2). AUC values for RES models ranged from 0.57 to 0.88, whereas those for BRT models ranged from 0.96 to 0.99 (Table 2). While most RES models were 'useful' (> 0.70), both RES models for CAAL and GHAL were inadequate for distinguishing between presence and availability data and, therefore, not considered useful for predicting probability of occurrence (Table 2). These evaluation metrics showed that models for BUAL performed better than those for other albatross species; results for this species are used as a case study throughout the manuscript. Comparable figures for CAAL, GHAL, and WCAL can be found in the Supplementary Materials.

The environmental niche envelope (area under the trapezoidal response curve) produced from the absolute and preferred values for each variable used to fit RES_{KERN} models was larger than the envelope produced from values used to fit the RES_{LIT} model (Figures 2A–H for BUAL and Supplementary Figures 9A–H, 10A–H, 11A–H for CAAL, GHAL, and WCAL, respectively). The most notable differences between the two RES models were the substantially smaller maximum absolute CHL value used in the

TABLE 2 | The area under the receiver operator characteristic curve (AUC) produced from evaluation data, optimal threshold values for delineating habitat, and area of habitat within the overall study area and the New Zealand Exclusive Economic Zone (EEZ) for four models: two Relative Environmental Suitability models (one fit with values obtained from the monthly 50% kernel density contours from geolocation data (RES_{KERN}), and one fit with values from the literature and expert opinion (RES_{LIT})) and two Boosted Regression Tree models (one fit with opportunistic sightings data (BRT_{OS}), and one fit with geolocation data (BRT_{GL})) for four species of albatrosses: Buller's (BUAL), Campbell (CAAL), grey-headed (GHAL), and white-capped (WCAL).

SPP	Model	AUC (eval)	Threshold	Area (km ²)		NZ EEZ (%)
				Study Area	NZ EEZ	
BUAL	RES _{KERN}	0.85	0.75	110,653,708.0	4,016,394.3	97.8
	RES _{LIT}	0.88	0.01	45,328,932.7	3,921,504.8	95.5
	BRT _{OS}	0.99	0.45	30,433,177.3	2,035,380.2	49.6
	BRT _{GL}	0.99	0.60	27,416,286.5	2,954,014.9	72.0
CAAL	RES _{KERN}	0.57	0.58	143,359,281.4	4,030,595.9	98.2
	RES _{LIT}	0.66	0.18	94,261,337.9	3,537,254.4	86.2
	BRT _{OS}	0.98	0.42	41,010,812.1	2,377,047.7	57.9
	BRT _{GL}	0.97	0.56	47,375,661.6	3,409,506.6	83.1
GHAL	RES _{KERN}	0.59	0.67	109,318,536.9	3,763,640.3	91.7
	RES _{LIT}	0.69	0.12	61,674,978.4	1,368,070.0	33.3
	BRT _{OS}	0.96	0.50	32,307,978.2	1,614,390.1	39.3
	BRT _{GL}	0.99	0.56	25,137,023.8	906,738.8	22.1
WCAL	RES _{KERN}	0.70	0.79	111,270,532.0	3,967,647.3	96.7
	RES _{LIT}	0.88	0.28	34,595,760.8	3,669,605.0	89.4
	BRT _{OS}	0.98	0.55	25,152,717.5	2,496,569.3	60.8
	BRT _{GL}	0.98	0.54	26,584,783.0	3,205,970.2	78.1

RES_{LIT} than the RES_{KERN} model (Figures 2D, H and Supplementary Figures 9D, H, 10D, H, 11D, H).

Of the four environmental variables, DLAND made the highest or second highest relative contribution to BRT_{OS} models (Figures 2I, L; Supplementary Figures 9I–L, 10I–L, 11I–L). Additionally, BRT_{OS} model results showed that the probability of occurrence was highest closest to land, whereas results from BRT_{GL} models generally revealed more complex relationships (Figures 2I, M and Supplementary Figures 9I, M, 10I, M, 11I, M). With the exception of BUAL, SST had the greatest influence on the probability of occurrence in BRT_{GL} models (Figures 2M–P; Supplementary Figures 9M–P, 10M–P, 11M–P). However, the opposite was true for BRT_{OS} models in which the influence of SST on the probability of occurrence was <15% for all species (Figure 2K and Supplementary Figures 9K, 10K, 11K).

The predicted probability of albatross occurrence varied across the four models, with the RES_{KERN} model predicting the most widespread distribution (Figure 3A and Supplementary Figures 12A, 13A, 14A). Spatially explicit estimates of uncertainty (standard deviations) were higher and more widespread for BRT_{OS} than for BRT_{GL} models (Figure 4 and Supplementary Figures 15–17). In areas outside the minimum convex hull, BRT_{GL} models produced estimates with less uncertainty than BRT_{OS} models.

Threshold values used to indicate habitat ranged between 0.01 (BUAL RES_{LIT} model) to 0.79 (WCAL RES_{KERN} model) (Table 2). For all species, RES_{KERN} models predicted more habitat than RES_{LIT} models and both types of RES models predicted more habitat than BRT models (Figure 3 and Supplementary Figures 12–14). Compared to BRT_{GL} models, RES_{KERN} and RES_{LIT} models resulted in a 3.0–4.3 and 1.3–2.5 fold increase in global habitat, respectively (Table 2). Results from BRT_{GL} models showed that CAAL had the highest percentage (83%) of habitat within NZ's EEZ, followed by WCAL (78%),

BUAL (72%), and GHAL (22%) (Table 2, Figure 3 and Supplementary Figures 12–14). For BUAL and GHAL, the percentage of habitat within the overall study area predicted by the BRT_{OS} models was greater than from BRT_{GL} models, while the opposite applied to CAAL and WCAL. Higher probability of occurrence was predicted closer to the coast by BRT_{OS} than by BRT_{GL} models.

Overlap in fishing effort and predicted habitat varied by model, month, and species. For BUAL, CAAL, and GHAL, there was less overlap between fishing effort and preferred habitat predicated by BRT_{GL} models globally across all months than for the other three models (Figure 5 and Supplementary Figures 18–20). For WCAL, global overlap between preferred habitat predicted by the four models was more variable, with predictions from the BRT_{GL} model having higher overlap with fishing effort from March to May than some of the other models (Supplementary Figure 20). Within the EEZ, CAAL and WCAL experienced similar amounts of overlap between monthly fishing effort and preferred habitat across models, particularly from June to August (Supplementary Figures 18 and 20). For GHAL, overlap was the greatest between monthly fishing effort and preferred habitat predicted by RES_{KERN} models, both globally and within NZ's EEZ (Supplementary Figure 19).

Globally and within NZ's EEZ, BUAL and CAAL experienced the greatest amount of overlap between mean monthly fishing effort and preferred habitat, followed by WCAL (Figure 6). Across both locations and models, GHAL had the least amount of overlap between fishing effort and preferred habitat. The overlap in preferred habitat and fishing effort for WCAL was similar across models. However, for BUAL, CAAL, and GHAL, overlap between fishing effort and preferred habitat predicted by BRT_{OS} models was substantially higher than BRT_{GL} models both globally and within NZ's EEZ (Figure 6).

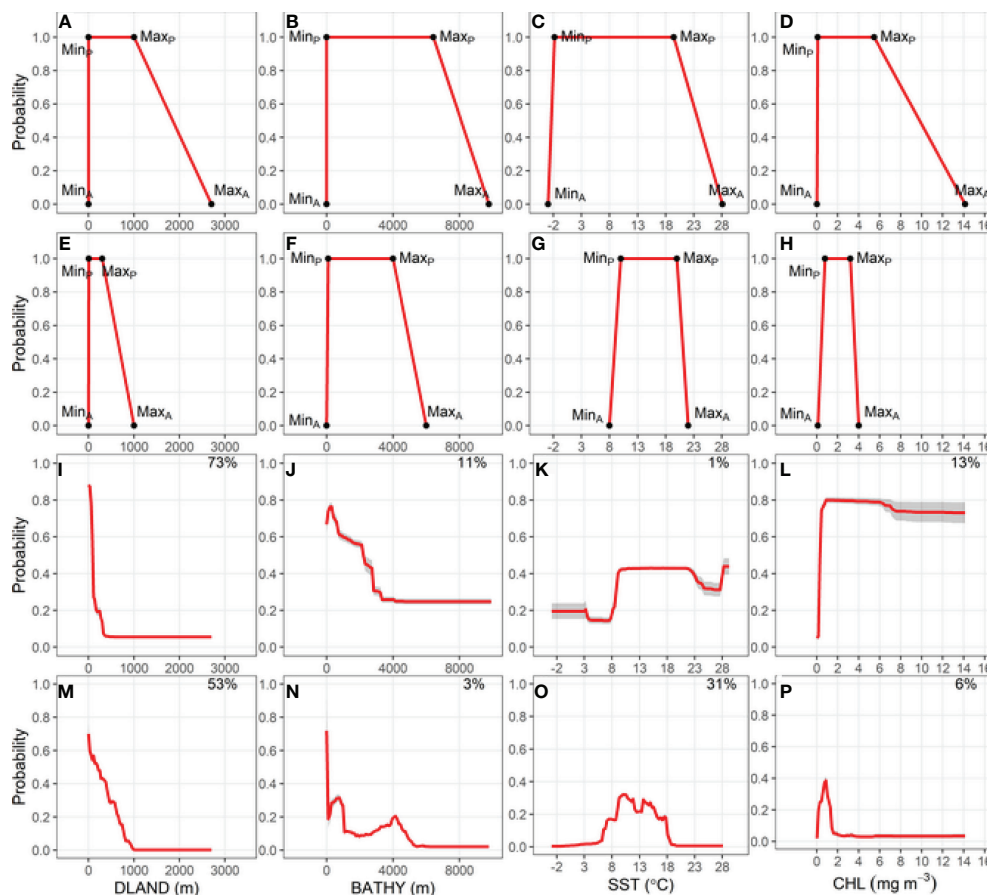


FIGURE 2 | Relationship between the probability of Buller's albatross occurrence and four environmental variables: Bathymetry (BATHY), distance from land (DLAND), sea surface temperature (SST) and chlorophyll-a (CHL). Top two rows show trapezoidal response curves for each environmental variable used in two Relative Environmental Suitability models (one fit with values obtained from the monthly 50% kernel density contours from geolocation data and background environmental data [RES_{KERN}, (A–D)], and one fit with values from the literature and expert opinion [RES_{LIT}, (E–H)]. Minimum and maximum absolute and preferred habitat values are denoted by Min_A, Max_A, Min_P, and Max_P. Bottom two rows show partial dependence plots for each environmental variable from two bootstrapped Boosted Regression Tree models (one fit with opportunistic sightings data [BRT_{OS}, (I–L)], and one fit with geolocation data [BRT_{GL}, (M–P)]). Red lines represent response curves with grey shading showing the standard deviation. Percentage contribution for each variable is shown on the top right corner.

DISCUSSION

This study is one of a growing body of work that compares results of different SDMs and/or assesses model sensitivity to differences in sample size or model parameters (Peterson and Cohoon, 1999; Stockwell and Peterson, 2002; Loisele et al., 2003; Johnson and Gillingham, 2005; Lütolf et al., 2006; Johnson and Gillingham, 2008; Mouton et al., 2010; Porfirio et al., 2014). Here we show that, while keeping environmental variables and modelling techniques as comparable as possible, incremental increases in data quality resulted in increased resolution of SDM predictions, adding value and confidence in derived species conservation efforts. In our study, BRT models for all four species of albatross outperformed RES models and predictions were in agreement with what is generally known about the species. BRT models offer a predictive advantage over RES models by being able to identify relevant variables and the

capability of incorporating environmental interactions. Additionally, BRT models provided explicit estimates of model uncertainty (as seen by the bootstrapping method employed in this study).

Evaluation metrics produced from the training and evaluation datasets showed that both BRT models performed well (AUC > 96; TSS > 0.81). However, evaluation metrics from an external dataset consisting of GLS data were greatly reduced (AUC: 51–84; TSS: 0.05–0.57; **Table 2**), suggesting that BRT_{OS} models are overly optimistic and may not be able to predict probability of occurrence and habitat suitability as accurately as BRT_{GL} models. While the partial dependency plots for BRT_{GL} models revealed a complex relationship between species occurrence and environmental variables, partial dependence plots for BRT_{OS} models for each species showed a distinct preference for shallow areas close to land which is likely the result of the sighting locations rather than a reflection of true

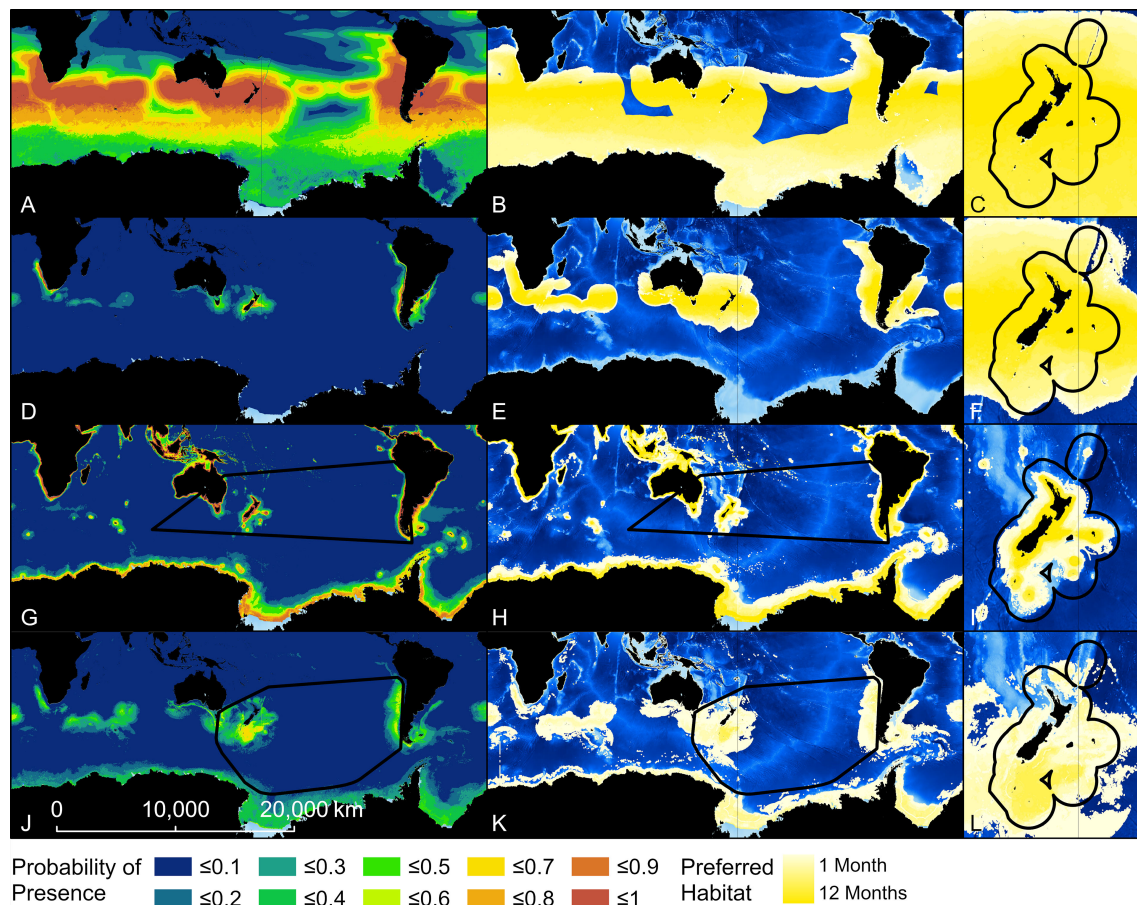


FIGURE 3 | Probability of presence and habitat of Buller's albatross predicted by four models. Top two rows show results from two Relative Environmental Suitability models [one fit with values obtained from the monthly 50% kernel density contours from geolocation data (RES_{KERN} , **A–C**)], and one fit with values from the literature and expert opinion (RES_{LIT} , **D–F**). Bottom two rows show results from two Boosted Regression Tree models (one fit with opportunistic sightings data [BRT_{OS} , **G–I**]), and one fit with geolocation data [BRT_{GL} , **J–L**]. Black boundaries indicate the minimum Convex Hull (**G, H, J, K**) or New Zealand's Exclusive Economic Zone (**C, F, I, L**) and habitat is colour-scaled from 1 to 12 indicating the number of months each cell was classified as habitat.

habitat preference. This finding is most certainly due to the notoriously biased nature of opportunistic sightings towards coastal areas with higher human populations which greatly under-represents the use of remote, at-sea areas important to albatrosses. Opportunistic sightings also lack a behavioural component, unlike GLS or other high resolution data from which it is often possible to differentiate between behaviors such as flying, resting, and feeding. For examples, the kernels produced in this study are greatly influenced by where animals spend the most time, most likely to be an indication of foraging as opposed to transiting.

However, in the absence of empirical data, RES models offer a standardized, quantitative approach for investigating the distribution of wide-ranging species (Kaschner et al., 2006; Watson et al., 2013) and offer more objectivity than hand drawn distribution maps (Kaschner et al., 2006). For all four albatross species, RES models resulted in at least double the area of habitat within the study region than BRT models fit with seabird GLS data. This finding is most likely due the

oversimplified trapezoidal response curve which is inadequate for capturing the complex relationship between species' occurrence and environmental conditions. Additionally, RES models assume that all variables are equally weighted in predicting species distribution, which is rarely true (e.g. as shown in the results of both BRT models presented here). Furthermore, due to information gaps that exist for many species, RES models are likely to underrepresent offshore areas that are less frequently observed. For these reasons, RES models should not be used as an alternative to empirical data which is able to more accurately predict species occurrence.

When comparing RES models, differences between RES_{KERN} and RES_{LIT} model predictions are due to the wider range of environmental values for used to fit RES_{KERN} models. These ranges were based on values from the year-round GLS data which may include a wider range of values than those found in the literature as studies are more likely to focus on a particular life stage (e.g. incubation or chick-rearing). RES models based on literature and expert opinion performed markedly better than

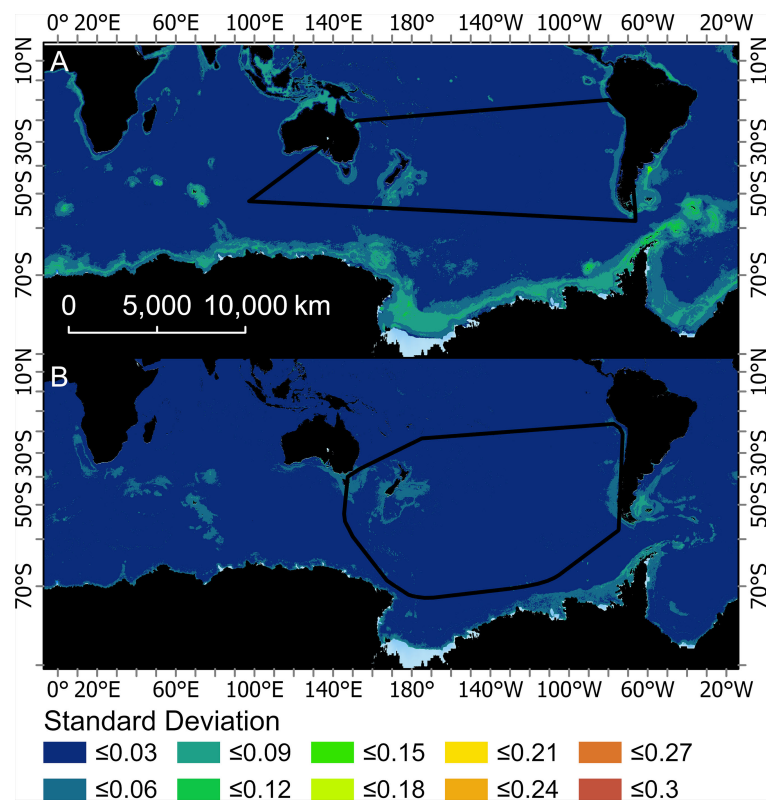


FIGURE 4 | Mean of the monthly standard deviations created from the 200 bootstraps for two boosted regression tree models used to predict the probability of occurrence for Buller's albatross (one fit with opportunistic sightings data [BRT_{OS}, (A)], and one fit with geolocation data [BRT_{GL}, (B)]. Black boundaries indicate the minimum convex hull around the data that were used to fit each respective BRT model.

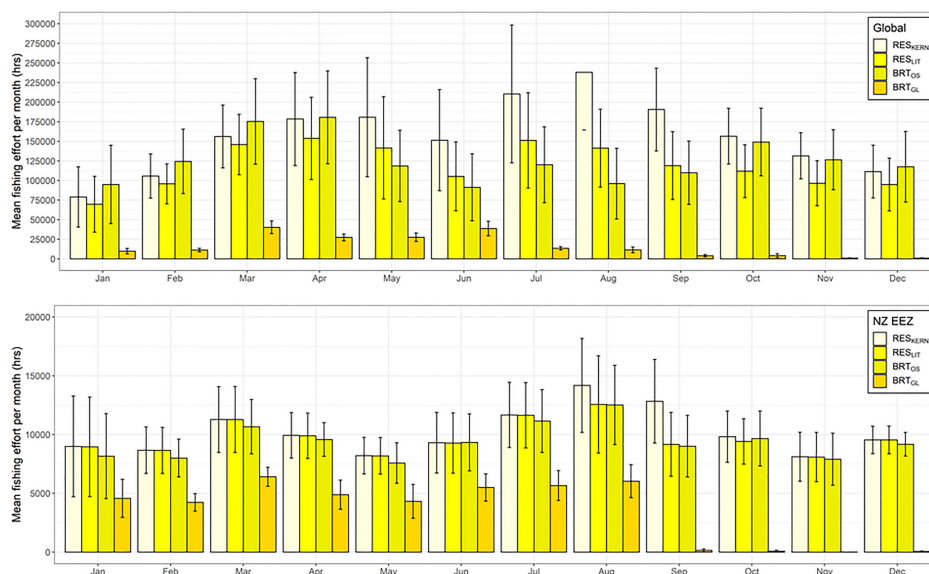


FIGURE 5 | Mean total fishing effort (hrs) (based on data from Global Fishing Watch) per month that occurs within the predicted preferred habitat of Buller's albatross both globally (top) and within New Zealand's Exclusive Economic Zone (bottom). Colour coding denotes different habitat suitability models and error bars indicate one standard deviation.

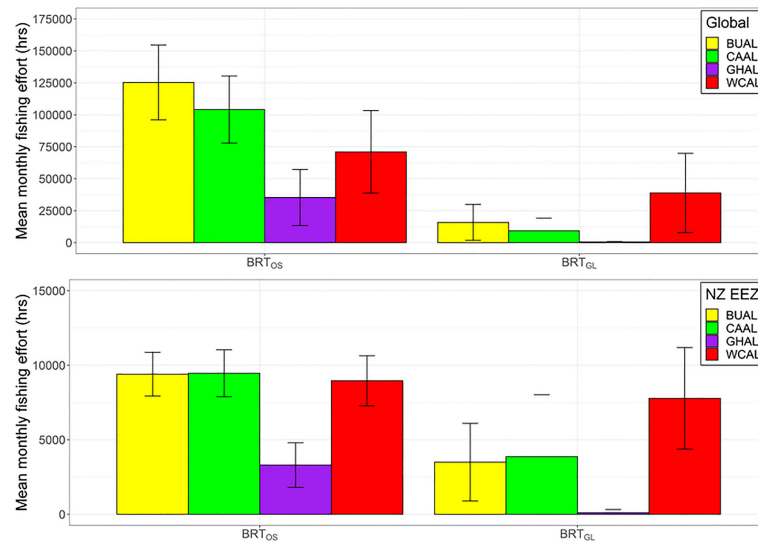


FIGURE 6 | Mean monthly fishing effort (hrs) (based on data from Global Fishing Watch) that occurs within the preferred habitat of four albatross species both globally (top) and within New Zealand's Exclusive Economic Zone (bottom) for two BRT models (one fit with opportunistic sightings data [BRT_{OS}, left], and one fit with geolocation data [BRT_{GL}, right]. Colour coding denotes different albatross species and error bars indicate one standard deviation.

the RES model with wider environmental ranges. The lower threshold for the RES_{LIT} models indicates a higher sensitivity or true positive rate. However, neither of the two RES models for CAAL and GHAL were able to adequately distinguish between presences and background data ($AUC \leq 0.7$), and, therefore, were not considered useful for predicting probability of occurrence or habitat. Thus, care must be taken when relying on less data-rich models.

Understanding potential biases in the data is important as it may lead to incorrect conclusions about species' habitat preference as well as the inability to identify population-level differences in habitat use patterns. Different populations of the same species can have different relationships to their environment (Torres et al., 2015). While this is not an issue for BUAL, CAAL, and WCAL that are endemic to an island group or small region within NZ waters, using sightings data for species that occupy multiple wide-spread colonies such as GHAL can result in incorrect relationships between species' occurrence and the environment. Further complicating the use of opportunistic sighting records is the difficulty in distinguishing between morphologically similar species such as CAAL/black-browed (*Thalassarche melanophris*) albatrosses, WCAL/shy (*Thalassarche cauta*) albatrosses and between sub-species such as southern and northern BUAL. For example, the southern sub-species of BUAL breeds only at the Snares and Solander Islands whereas the northern sub-species breeds three months earlier, mostly at the Chatham Islands (Stahl et al., 1998). The misidentification of species or sub-species is likely to result in inadequate or inaccurate predicted probability of occurrence and habitat over both space and time.

When developing SDMs to predict occurrence, care must be taken to collect data at the same spatial and temporal scale as its

intended conservation or management use. Species' movement and distribution may vary between breeding and non-breeding seasons (as is the case for many species of seabirds), thus distribution maps developed from data collected during the breeding season should not be used to extrapolate to the non-breeding season. SDMs built from data covering only a portion of a species' range may provide poor predictions on range-wide needs if data are extrapolated (Peterson and Cohoon, 1999). For comparison purposes, our study compared preferred habitat both globally and within NZ's EEZ for all species. However, preferred habitat predicted beyond the extent of the underlying data for both opportunistic sighting and GLS datasets should be interpreted with care. For example, BRT models frequently predicted preferred habitat in the Ross Sea, near Antarctica, where albatrosses are very unlikely to visit.

One example of how data quality can influence conservation and management is our ability to assess risk from fishing effort. Historically, in the absence of high-quality data on seabird movement and foraging behaviour, estimates of distribution ranges have consisted of hand-drawn maps outlining the proposed maximum extent of species' occurrence according to expert opinion (e.g. S. Ridgway and Harrison (1981), S. H. Ridgway (1985), and S. H. Ridgway and Harrison (1989)). Currently, tracking data are often used to estimate seabird-fisheries overlap (Suryan et al., 2007; Votier et al., 2010; Torres et al., 2011; Torres et al., 2013; Sztukowski et al., 2017; Clay et al., 2019). BTR models fit with relatively high-resolution GLS data offer greater refinement of predicted habitat than distribution maps included in NZ's National Aquatic Biodiversity Information System (NABIS, www.nabis.govt.nz) which, in the absence of other data, are sometimes hand-drawn and used to examine the overlap between seabird species occurrence and

commercial fisheries (Richard et al., 2017; Richard et al., 2020). Additionally, distribution maps used to calculate risk of seabird bycatch by NZ commercial fisheries are typically computed as annual averages and do not account for seasonal changes in distribution that would occur during migration or at different stages of the breeding cycle (Richard et al., 2017).

Our study showed that there are substantial differences in the overlap between fishing effort and preferred habitat across species. RES_{KERN} models based on little to no empirical data predicted the most preferred habitat which subsequently overlapped with the most fishing effort, globally, compared to the preferred habitat predicted by BRT models informed with opportunistic sighting or geolocation data. Even though BRT_{OS} models predicted either the smallest or next to the smallest area of preferred habitat, overlap with fishing effort was often higher than for the RES_{LIT} and BRT_{GL} models. This is likely due to bias from coastal sightings data that, in turn, biases model predictions towards coastal regions. This pattern tended to occur during from October to April for BUAL and WCAL, from September to March for CAAL, and nearly year-round for GHAL. For WCAL and CAAL, these times correspond to the breeding period where birds were constrained to regions near colonies where fishing occurs. While this timing does not correspond to the breeding period for BUAL, preferred habitat predicted by the BRT_{OS} model was located exclusively in coastal habitats or within NZ's EEZ where fishing is likely to be highest. For the two best performing models (BRT_{OS} and BRT_{GL}), the greatest overlap between predicted preferred habitat and fishing effort across all months occurred for BUAL and CAAL, both globally and within NZ's EEZ, while GHAL had the least amount of overlap, likely due to this species' preference for pelagic waters beyond NZ's EEZ where fishing effort is typically reduced. Additionally, overlap between mean monthly fishing effort and preferred habitat predicted by BRT_{OS} models was higher than for BRT_{GL} models for all species. Again, this finding is likely due to a coastal bias in opportunistic sighting data, resulting in SDMs that are unable to adequately predict to offshore areas where birds are known to occur. Although trends in overlap between fishing effort and preferred habitat between species and models may be accurate, it is important to keep in mind that the total number of fishing effort hours shown in this study are only an indication on minimum effort because GFW data represents only 50-75% of active vessels that are > 24 m in length that were fitted with AIS transceivers (Kroodsmma et al., 2018; Shepperson et al., 2018).

Currently, BUAL, CAAL, and WCAL are considered vulnerable to capture by NZ commercial fisheries, and across the different risk categories, albatross species comprise half of the 'very high' or 'high' risk categories (Richard et al., 2020). Both BRT models showed that WCAL, BUAL, and CAAL have the highest overlap with fishing effort. These species also have some of the highest number of capture by NZ commercial fisheries recorded by government observers (963, 681, and 46, respectively), between the fishing years 2006-07 and 2016-17 (Richard et al., 2020). These albatross species are categorized as 'high risk' (BUAL), 'medium risk' (WCAL), and 'low risk' (CAAL) of capture (GHAL is categorized as 'negligible risk'), which is largely driven by

calculated overlap with fishing effort (Richard et al., 2020). In our study, preferred habitat of CAAL within NZ's EEZ predicted by BRT_{OS} and BRT_{GL} models had the highest and second highest overlap with fishing effort, respectively, suggesting that commercial fisheries may pose a greater risk to CAAL than currently recognised. Additionally, the overlap of preferred habitat predicted by the best performing model (BRT_{GL}) with fishing effort was highest from June to August, further supporting the findings of Thompson et al. (2021) which determined that the risk of NZ fisheries to CAAL was greatest in the non-breeding season.

Because miscalculations in the overlap between seabird distribution and fishing effort can lead to ineffective mitigation measure to reduce seabird bycatch in commercial fisheries, resource managers will most certainly benefit in the collection of higher quality data. This study showed that higher quality data resulted in more refined areas of predicted habitat than NABIS maps used by NZ management agencies. Additionally, the predicted habitat from models that used higher quality data usually resulted in less overlap with fishing efforts. Therefore, investing in the collection of collecting high-quality seabird data may ultimately lead to cost savings and more targeted management solutions in the long run. One must carefully balance the trade-offs of (1) investing resources up front to collect robust long-term biologging data resulting in more accurate, targeted, areas of potential protection, and (2) using existing low-resolution or no data for relatively little cost resulting in larger, less-accurate, predicted habitat that will require substantial resources to protect and is less likely to provide conservation benefit. While using existing data saves money in the short-term, the collection of high-quality long-term data can provide distribution information at various spatial-temporal scales that are more likely to lead to effective future management decisions and the ability to better assess potential threats from commercial fisheries.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: BirdLife's Seabird Tracking Database (see <http://www.seabirdtracking.org/>).

ETHICS STATEMENT

Methods used to obtain tracking data from live animals were reviewed and approved by NIWA's Animal Ethics Committee.

AUTHOR CONTRIBUTIONS

DT and KG conceived the idea. RO, PS, LT, LS, CK, RP, SV, SB, GT, and DT collected the data. KG, RO, and DT collated the data. KG, FS, AH, and AB analysed the data. KG and DT led the writing. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.782923/full#supplementary-material>

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Movements and Diving Behavior of the Eastern North Pacific Offshore Killer Whale (*Orcinus orca*)

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The Pacific Offshore killer whale population is currently listed as data deficient on the IUCN Red List and Threatened in Canada. The population is estimated at 300 individuals with a range extending from Southern California to the Aleutian Islands in Alaska. Only 157 encounters with this ecotype have been photo-documented between 1988 and 2014; consequently, movement and behavioral data are limited and restricted to areas commonly surveyed. To better understand movements, habitat use, and diving behavior, we deployed seven dart-attached satellite tags during two encounters with Offshores off California and one encounter off Washington State in 2013. Group size estimates were 6, 9, and 30 whales, respectively. Transmission durations ranged from 6.3 to 147.4 days providing a combined 2,469 location estimates. Whales tagged in Southern California travelled from 30.7°N to 59.3°N degrees latitude, covering a larger latitudinal range in 75 days than all previous sightings (33.5°N to 60.0°N). Within most of the California Current (southern extent of locations up to 48.5°N), Offshores typically used waters deeper than the 200 m isobath. As they approached the northern extent of the California Current and travelled into British Columbia and Alaska, locations were more common near or inside the 200 m isobath. Individuals tagged in the same group disassociated and re-associated within the tracking duration, with animals tagged together separating by as much 1,339 km. Two of the tags also reported summarized diving behavior, and tags captured 1,110 total dives with median dive depths of 41 m and 100 m for each tagged whale; the maximum dive depth was 480 m. Dives were typically short (median = 3.9 and 4.1 min respectively, max = 12.3). A comparison of dive depths and bathymetry suggests that whales typically dove to or near the seafloor in continental shelf habitat. Despite the small number of tag deployments, these data provide new information on social structure, individual ranges, diving behavior, and habitat use of this seldom encountered killer whale ecotype.

Keywords: Argos (satellite location), dive behavior, habitat use, satellite tagging, LIMPET tag

INTRODUCTION

Three sympatric but socially isolated and distinct forms of killer whales (*Orcinus orca*) are found in the coastal waters of the Eastern North Pacific (Ford et al., 2000; Krahn et al., 2007; Dahlheim et al., 2008; Ford et al., 2014; Ford and Ellis, 2014). These three ecotypes are known as Resident, Transient, and Offshore killer whales. Of these ecotypes, the least known are the Offshores (Ford and Ellis, 2014).

The first photographic encounter with free-ranging Offshores did not occur until 1988 (Ford et al., 2014), though stranded individuals from the mid-20th century were later determined to be Offshore killer whales through the use of DNA (Morin et al., 2006). Since 1988, Offshores have been documented from Southern California (~33.5°N) to Prince William Sound, Alaska (~60.0°N) and as far west as the eastern Aleutian Islands (~160°W) (Dahlheim et al., 2008; Ford et al., 2014). Sightings of Offshores are rare relative to other ecotypes, with only 157 photographic encounters from 1988 through 2014, 103 of which occurred in the waters off British Columbia (Fisheries and Oceans Canada, 2018). Sightings have occurred primarily along the outer continental shelf and slope, though some sightings have occurred in shallow waters at the head of inlets (Ford and Ellis, 2014; Ford et al., 2014). Despite their name, the extent to which Offshores actually use habitat beyond the continental slope is unknown due to the paucity of field effort in those waters, though two individuals have been seen 389 km off the coast of Oregon in water depths >3,000 m (Dahlheim et al., 2008). Existing data suggests that in addition to the outer continental shelf waters, important habitats include the waters around Haida Gwaii and to the southwest and northeast of Vancouver Island (Ford et al., 2014). Clusters of encounters (visual and acoustic) have also occurred near submarine canyons such as Quinault Canyon, Washington, US, Monterey Bay, California, US, and Moresby Trough, British Columbia, Canada (Ford et al., 2014; Rice et al., 2017).

While Offshores have been found in deep water, Ford et al. (2014) assessed all sighting locations for distance from the 200, 500, and 1,000 m bathymetric contours. The frequency distribution of sightings in relation to the 200 m isobath show a peak of sightings just inshore of the 200 m mark, with the majority of other sightings occurring up to 100 km inshore of 200 m water depth (median depth = 122 m, range = 8 – 2,170). This distribution suggests Offshores are primarily associated with the top of the continental shelf area and inshore, though sighting locations are likely biased by effort.

Early studies suggest there may be a seasonal pattern in Offshore distribution, with sightings most frequent in California during late fall and winter months (Dahlheim et al., 2008), and in Alaska during summer and early fall (Zerbini et al., 2007; Dahlheim et al., 2008; Dahlheim et al., 2009). Sightings and acoustic detections indicate that Offshores are present year-round off of British Columbia and Washington, with some evidence of peaks in March, August, and December, but with no clear pattern of seasonality (Ford et al., 2014; Rice et al., 2017; Fisheries and Oceans Canada, 2018). Ford and Ellis (2014)

hypothesized that these seasonal movements may be associated with the distribution and availability of their prey.

Based on field observations, prey tissue samples, stomach contents of stranded whales, tooth wear in photographed and stranded whales, and stable isotope analyses of tissue, the Offshores are known to feed upon bony fish and elasmobranchs, with an apparent preference for sharks (Ford et al., 2000; Herman et al., 2005; Krahn et al., 2007; Ford et al., 2011; Ford and Ellis, 2014). Known prey species include the Pacific sleeper shark (*Somniosus pacificus*) spiny dogfish (*Squalus acanthias*), blue sharks (*Prionace glauca*) and possibly other carcharhinid sharks, Pacific salmon (*Oncorhynchus* sp.), Pacific halibut (*Hippoglossus stenolepis*), and opah (*Lampris guttatus*) (Heise et al., 2003; Jones, 2006; Morin et al., 2006; Dahlheim et al., 2008; Ford et al., 2011; Ford and Ellis, 2014). Of 40 prey items documented, 93% were sharks (68% of them sleeper sharks), and 7% were teleost fishes (Ford and Ellis, 2014). The relatively high trophic-level and long lifespan of these prey species may explain the high levels of PCB and DDT found in the tissues of Offshore killer whales (Krahn et al., 2007; Dahlheim et al., 2008). Such toxicity is one of the many potential anthropogenic threats that Offshores currently face, lending urgency to the ongoing efforts to increase our understanding of this population (Ford et al., 2014).

Offshore killer whales are thought to consist of a single population of approximately 300 individuals (Ford et al., 2014). The population size appears to be stable, but unable to sustain much human-caused mortality, if any, without risk of decline (Ford et al., 2014; Fisheries and Oceans Canada, 2018). The Offshore population is listed as Threatened in Canada, on the Provincial Red List in British Columbia, and as data deficient under the IUCN Red List (Ford et al., 2014). The apparently vast geographic range of Offshore killer whales coupled with their preference for the outer continental shelf make it challenging to collect unbiased habitat use and movement data from visual surveys alone. Here, we present insights into the movements and foraging ecology of individual Offshore killer whales using data collected from remotely deployed, externally attached, whale-borne tags.

METHODS

Data Collection

Surveys were undertaken in 6.5 m or 7.5 m rigid-hull inflatable vessels in a non-random, non-systematic format in both the outer waters of the Southern California Bight (SCB), and off the outer coast of Washington state (Figure 1A). Surveys in the SCB were conducted in conjunction with the Marine Mammal Monitoring on Navy Ranges (M3R) program at the Southern California Anti-submarine Warfare Range (SOAR) (Moretti et al., 2006; Jarvis et al., 2014). The M3R system at SOAR provides for near continuous monitoring of 153 broadband bottom-mounted hydrophones covering an area of approximately 1,000 sq. km to the west of San Clemente Island. The system performs fully automated detection, classification, and localization of select species (e.g. *Ziphius cavirostris*) who frequent the range area,

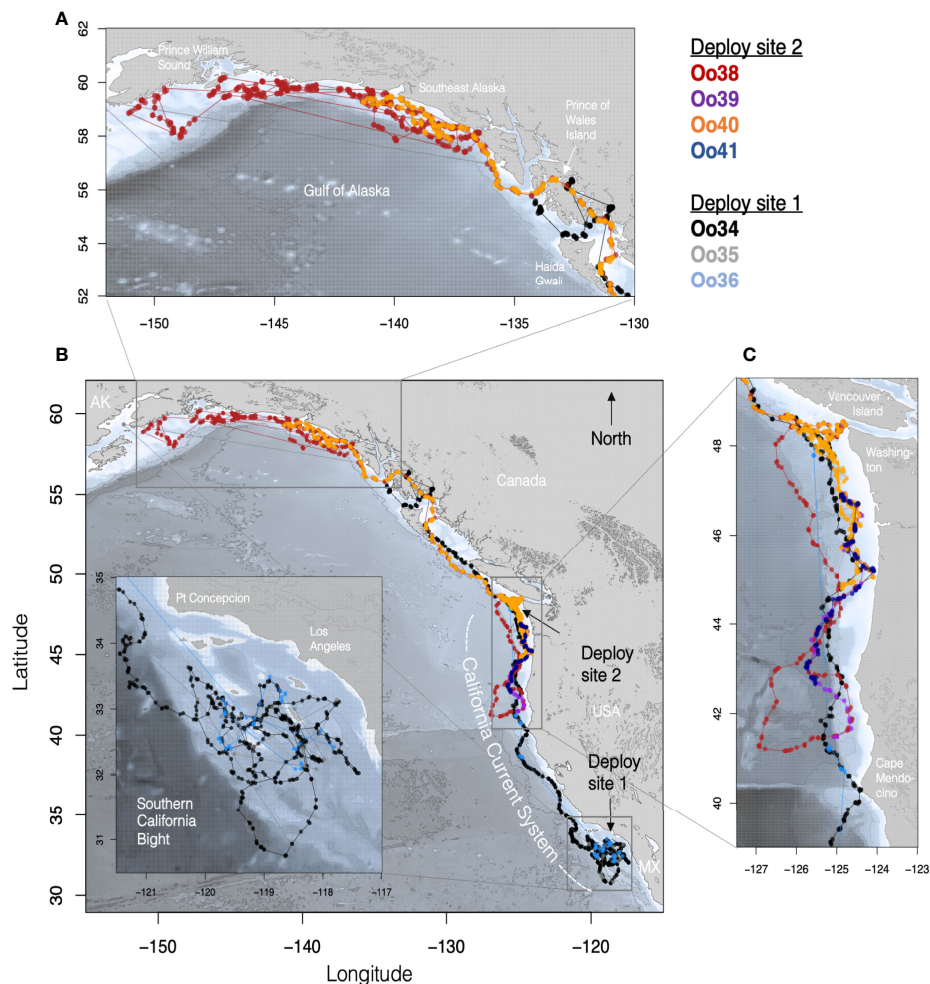


FIGURE 1 | Maps of tagged Offshore killer whale tracks with each Offshore killer whale assigned a different color. **(B)** shows the complete set of filtered Argos tracks for animals tagged in both California (Deploy site 1) and Washington (Deploy site 2). (Inset) details of movements within the Southern California Bight, with the deployment site being just west of the southernmost island (San Clemente). **(C)** Tracks of whales from southern British Columbia to northern Oregon with the deployment site off the coast of WA indicated by the black arrow. **(A)** Track details of the movements within the Gulf of Alaska.

and also provides interactive tools allowing operators to monitor the acoustic data, including spectrograms, from each of the hydrophones after which they can direct the visual survey team to locate the source of the acoustic signal. The survey off the coast of WA was conducted in association with a NOAA cruise focused on the Southern Resident killer whales.

Sighting data including the time, location, group size, and primary behavior, for each group of cetaceans encountered were recorded using a custom database (Access, Microsoft Corporation, Redmond, WA). Photographs were collected of as many individuals encountered as possible and provided to curators of existing Offshore killer whale photo-ID catalogs for ecotype verification and individual identification (e.g. Black et al., 1997).

Two versions of the remotely deployed Low Impact Minimally Percutaneous External-electronics Transmitting (LIMPET) tag were used, both manufactured by Wildlife

Computers, Inc. (Redmond, WA): the location-only SPOT5, and the location and dive reporting SPLASH10-A (Andrews et al., 2005; Schorr et al., 2014). Tag programming, including details on duty-cycling, are presented in **Table 1**. Tags were deployed using a Dan-Inject J.M. SP 25 pneumatic projector (Dan-Inject, ApS, Kolding, Denmark) at ranges of 4–16 m, and attached on or near the dorsal fin using two sterilized 6.7 cm long titanium darts with backwards facing ‘petals’ (Andrews et al., 2005). Reactions to tag deployments were recorded following Berrow et al. (2002), and information on the re-approachability of tagged whales was also documented to the best extent possible. Tag names were assigned according to a collaborative project naming scheme, including the Genus species code (Oo) followed by a sequential number code, regardless of ecotype. In this case, the first tag deployed on the group was the 34th LIMPET tag deployed on a killer whale, and thus the deployment was named Oo34.

TABLE 1 | Deployment details from Offshore killer whales tagged off California (Oo35 – Oo36) and Washington (Oo38 – Oo41), 2013.

TagID	Tag type	Deploy date	Tx duration (Days)	N locations (total/filtered)	Daily Tx	Duty cycle if relevant.
Oo34	Spot5	5-Jan-13	73.2	1004/833	60	Tx every 3rd day after 60.
Oo35	Mk10-A	5-Jan-13	147.4	56/26	20	Tx every 3rd day for 20 days, then every 9th day after.
Oo36	Mk10-A	8-Jan-13	66.2	180/75	20	Tx every 3rd day after.
Oo38	Spot5	8-Mar-13	98.8	1136/873	50	Tx every 2nd day for 2 wks, then every 3rd day after.
Oo39	Spot5	8-Mar-13	8.3	93/51	50	
Oo40	Spot5	8-Mar-13	40.3	685/507	50	
Oo41	Mk10-A	8-Mar-13	6.3	124/104	20	

Tx, Transmits.

Data Processing and Analysis

Argos location estimates were processed *via* the least-squared method (Argos User's Manual, 2011), and subsequently filtered using the Douglas Argos Filter (Douglas et al., 2012). Filtering parameters were set as follows: a maximum sustainable rate of movement of 20 km/hr, retention of all location estimates class 2 and above, a maximum redundant distance setting of 3 km, and the filter default ratecoef of 25. One tag, Oo35, suffered an apparent malfunction that resulted in infrequent location estimates during the deployment, with only 31 location estimates generated during the 147.4 days the tag transmitted. No dive data was reported by the tag. Therefore, locations from this tag were only used to describe large-scale movements and not used in any of the detailed movement or dive analyses.

All subsequent analyses were conducted using the filtered datasets from the remaining tags. These included assessing overall minimum distance travelled, daily average minimum distance covered, distance between tagged whales, and an assessment of time spent in geographic regions. Geographic regions were defined by State (within the US) and Canada, with an additional region included for the SCB, which was defined as south of Point Conception (32.45°N). The California Current was defined as all locations south of 48.5°N. Geographic region was analyzed to assess variables that might change within management areas (e.g. U.S. versus British Columbia). Each location estimate was assigned its corresponding solar elevation, using the R package “maptools” (Bivand and Lewin-Koh, 2020; R Core Team, 2020). Water depth and distance from the 200 m isobath were calculated for each location estimate using the ETOPO1 dataset (1 arc-minute resolution) in ArcGIS v10.7.1 (NAD 1983 UTM Zone 11N) (Environmental Systems Research Institute (ESRI), 2019). To assess group stability over days, filtered location estimates received within 2 hours of each other were used to calculate distance between each tagged whale. When multiple locations were received within 2 hours in a single day, the smallest distance between qualifying location pairs was selected as the daily individual distance (typically a function of better location quality). Animals were presumed to be associated on a given day when individual distance was less than 20 km to allow for Argos error and movements during that period.

A geographic comparison of minimum rates of horizontal displacement and habitat use was conducted using the Douglas filtered location data, though locations less than 1 hour and greater than 6 hours apart were removed from the rate of displacement analysis to control for spurious rates (e.g. Baird

et al., 2010). Locations were assigned to six latitudinal regions from Southern California to Alaska. The regions assessed were chosen to encompass management areas (U.S. versus Canada), then broken down either by other easily identifiable geographic boundaries such as State, or the SCB. Regions were, from South to North, SCB, Northern California, Oregon, Washington, British Columbia, and Alaska. The minimum rate of horizontal displacement and the distance to the 200 m bathymetric isobath were each modeled with generalized additive mixed models using the gamm4 package in R (Wood and Scheipl, 2020) as a function first of latitude (numeric) then of geographic region (categorical) with an additional categorical predictor for “TimeOfDay” (day or night as a function of solar elevation) and nested random effects for “GroupID” (TagID, with a single TagID used when two whales were considered associated as defined above), “Day” (yyyymmdd), and HrCutoff (location grouping within 4 hr time blocks). These random effects were used to account for the autocorrelation between locations from the same animal (or group) on the same day and within hours of each other. The program was allowed to initially apply model smoothing algorithmically, and then the smoothing term was fixed manually to reduce overfitting of the data.

SPLASH10-A tags, which collected summarized dive data in the form of a Behavior Log (BL) in addition to Argos location estimates (Wildlife Computers, 2015), were deployed on three whales. One of these tags was Oo35, which did not report any dive data in addition to providing sparse location data due to its malfunction and was therefore excluded from dive analysis. BL collection days followed transmission duty cycling (Table 1). The parameters to define and record a dive differed slightly between the two remaining tags, based on lessons learned from the first deployment. Both tags were set to record the start/end of a dive using the wet/dry sensor. Oo36 recorded all dives that were longer than 30 sec and deeper than 20 m, while Oo41 recorded dives that were longer than 60 sec and deeper than 20 m. The increase in dive duration was implemented to reduce the number of ‘qualifying dives’ recorded, and to thus generate fewer BL messages to transmit each day, ideally resulting in a more contiguous dive record. Solar elevation was assigned to the start of each BL dive and surfacing by estimating the location of each event on an interpolated trackline between filtered location estimates, with solar elevations above -12 degrees considered day and the remaining locations assigned to night. Bottom depth was also calculated using the above methods at dive positions along the interpolated trackline to generate a

rough assessment of dive depth compared to bottom depth. Given the limited sample size of individuals and somewhat lossy nature of telemetered data, it was neither feasible nor appropriate to quantify correlations among dive behavior and additional environmental factors, and only observational assessments were made.

RESULTS

Deployment Summary

Offshores were encountered during three small vessel surveys in 2013. The first and second encounters were in the outer waters of the SCB in January during marine mammal surveys at SOAR. The first encounter was with a group of six individuals on January 5th and was facilitated by acoustic direction from the M3R system (Moretti et al., 2010; Jarvis et al., 2014). Acoustic recordings were made of the hydrophones nearest the visually-verified encounter, and later comparison showed the structure of the calls to match published vocalizations of the ecotype (Filatova et al., 2012). Two tags were deployed during this encounter, one on an adult male (Oo34) and one on a subadult of unknown sex (Oo35). The second encounter occurred on January 8th and was facilitated by using locations from the two whales tagged during the first encounter. This group was estimated as nine individuals including both previously tagged whales, as well as at least two other individuals identified during the encounter on the 5th. An adult male, who was present during the encounter on the 5th, was tagged (Oo36). The third encounter with Offshores occurred near Grays Harbor Canyon off the outer coast of Washington on March 8th, during a joint survey with the Northwest Fisheries Science Center cruise for Southern Resident Killer whales, and was not associated with any of the previously tagged whales. This group was estimated at 30 individuals. Four tags were deployed during the encounter (Oo38–41), three on presumed adult females and one on an adult male based on morphology.

Tags transmitted data across an average of 62.9 days (median = 66.2, min = 6.3, max = 147.4, **Table 1**). The shortest transmission durations were associated with suboptimal tag placements: one tag was attached just below the dorsal fin and transmitted only 8.3 days, and one tag was attached at the trailing edge of the fin *via* a single dart and lasted 6.3 days. Reactions to tagging were classified as either “none” ($n = 1$) or “moderate” ($n = 6$), the latter of which consisted primarily of a tail flick with acceleration or a roll (Berrow et al., 2002). Four of the whales were reapproached to within 20 m within 45 min of tagging. None of the individuals demonstrated apparent avoidance behavior and two animals actively reapproached to within 4 m of the vessel after tagging, including swimming directly astern of the vessel while underway.

Movements and Habitat Use

Oo34 and Oo36 spent the first 34 days of their deployment associated together and circling broadly within the SCB, with coincident location estimates during this period an average of 10 km apart ($sd = 13.0$, $n = 25$), though after the first 20 days tag

Oo36 was duty cycled to transmit every 3rd day, reducing the number of coincident locations for the two whales during the latter part of the period. During this time, the whales spent most of their time in the outer waters of the SCB, never coming closer than 30 km of the mainland (**Figure 1B**). Thirty-four days after the first tag deployment, both whales moved out of the SCB, passing north of Point Conception with coincident Argos location estimates within 1 km of each other (**Figure 1A**). Oo35 transmitted infrequently, but the few locations received from the tag were near locations from the other two whales for the first 19 days of the deployment (range = 0.8 – 14.5 km, $n = 8$). The next location estimate from Oo35 was not received until 75 days later, when two locations were received in Prince William Sound, AK, more than 3,800 km from the tagging location (**Figures 1A, D**).

Oo34 and Oo36 appeared to travel together to the northern tip of Washington (48.1°N), and 52 days after tagging (February 26th), individual daily locations were within 3 km, more than 1,634 km away from where they were tagged. Oo36 then turned south, doubling back at least as far as southern Oregon (43.3°N) before the tag stopped transmitting. Meanwhile Oo34 continued travelling north, turning east into more inland waters upon reaching the south end of Haida Gwaii, British Columbia, then into the inner waters of Southeast Alaska (SEAK) (**Figure 1A**). By the 61st day (March 7th) after Oo34 was tagged, and the last day with concurrent locations, Oo34 and Oo36 were a straight-line distance of 1,339 km apart (**Figure 1B**). Ultimately, Oo34 travelled north through the inner waters of SEAK nearly to Wrangell, reaching a maximum of just over 2,800 km from the tagging location before heading west to the outer waters of SEAK, where the tag stopped transmitting.

When the next four tags were deployed on the other group of Offshores on March 8th, Oo34 was more than 1,000 km to the north and Oo36 was more than 400 km to the south of the location where these whales were tagged off the coast of Washington, based on locations received the previous day. The whales tagged off Washington remained associated for four days post-tagging while moving south, at which point Oo40 separated and turned back north. The maximum separation between Oo40 and the other three whales reached 730 km by the 6th day after tagging. The remaining three whales stayed together until Oo39 and Oo41 stopped transmitting (**Figure 1C**), travelling as far south as northern California. On March 16th, locations received from duty-cycled tag Oo36 indicate that the then northbound whales tagged in California likely passed the whales tagged off Washington somewhere off the coast of Oregon or Washington, with Oo36 now 100 km north of Oo40 and 550 km north of Oo38 and Oo39.

The grand mean of point-to-point horizontal movement rates ($n = 672$) averaged 3.5 km/hr (individual range 0.1 – 14.5 km/hr) (**Table 2**) throughout the deployment period. Model results of horizontal displacement rates as a function of latitude revealed no change in speed by latitude ($F = 0.0$, $df = 9$, $p = 1.0$).

Of the tags deployed in the SCB, Oo34 had the most complete location record, and was considered representative of regional habitat use by the whales that were tagged together in the region. The whale appeared to preferentially travel along the many

TABLE 2 | Movement details.

TagID	Min. distance traveled (km)	Avg. min. daily distance (km day ⁻¹)	Min. avg. rate of horizontal displacement (range) (km hr ⁻¹)
Oo34	7,539	103.06	3.56 (0.10 - 14.45)
Oo35	6,161	N/A	N/A
Oo36	1,974	29.81	N/A
Oo38	10,704	108.38	3.66 (0.04 - 10.63)
Oo39	779	93.41	N/A
Oo40	4,519	112.19	3.18 (0.19 - 8.38)
Oo41	571	91.07	N/A

Distances and rates are straight line distances between Argos location estimates and are therefore minimum estimates. Oo35 average minimum daily distance and horizontal rate of movement are not included in this table due to the infrequent number of transmissions received. N/A, Not Applicable.

submarine banks and ridges in the area, versus spending time in the center of the deep basins they surround. However, Oo34 used significantly deeper habitat in the SCB than he did in the northern extent of the California Current (median = 1,182 m versus 642 m, Kruskal-Wallis One-way ANOVA z-value = 6.97, $p < 0.0001$). As he, and the other tagged whales that were associated with him, moved up the coast through central and northern California, Oregon, and Washington, the whales spent nearly all their time along the continental slope, with most locations deeper than the 200 m isobath (**Figure 1**). Towards the northern end of the California Current, the whales shifted their distribution closer to the 200 m isobath, and within BC and Alaska the whales increasingly used waters shallower than 200 m (**Figure 2**).

By March 23rd, both Oo38 and Oo40 (now the only two tags deployed off Washington still transmitting) were using the waters off the coast of WA, but Oo38 was at the bottom of the continental slope while Oo40 was utilizing waters over the top of the continental shelf (**Figure 1**). Seventeen days after

deployment, and 13 days after separating, the two whales reunited at the shelf edge. In the next 24 days that both tags transmitted, the mean distance between assessed daily locations was 0.5 km (max = 5.9, $n=25$), as they traveled through BC, around Prince of Wales Island in SEAK, then west along the outer continental shelf, reaching as far as 1,720 km away from the tagging location before Oo40 stopped transmitting. Oo38 continued to move along the Pacific coast of Alaska, reaching as far north and west as the islands outside of Prince William Sound. While most of the time was spent along the shelf edge, the whale also spent time in deep water beyond the shelf break and in near-shore waters (**Figure 1**).

Latitude significantly predicted the distance to the 200 m isobath ($F = 0.9$, $df = 4$, $p = 0.0004$), with whales furthest from shore at latitudes around 30°N, generally approaching the 200 m isobath at latitudes near 50°N, then transitioning to habitat inside the 200 m isobath at latitudes further north (**Figure 2A**). Similarly, habitat use varied significantly by region, with locations off California and Oregon significantly

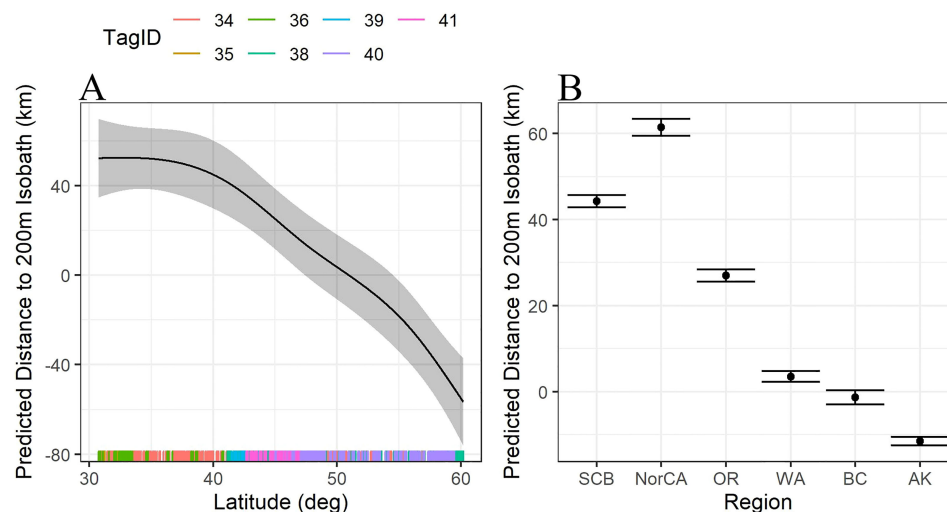


FIGURE 2 | (A) Trendline for the predicted distance to the 200m isobath (km) as a function of latitude. Distances below 0 are shallower than 200m, distances greater than 0 are deeper than 200m. **(B)** Predicted distance to the 200m isobath (km) as a function of region. Habitat use south of WA are much further offshore, habitat use north of WA is generally up on the shelf edge, inside the 200m isobath. SCB=Southern California Bight including all locations south of Pt Conception ($n=476$); NorCA = Northern California, including all latitudes north of Pt Conception to Oregon State boundary ($n=188$); OR, Oregon ($n=377$); WA, Washington ($n=447$); BC, British Columbia ($n=253$); AK, Alaska ($n=728$).

deeper than the 200 m isobath than those off Washington, British Columbia, and Alaska (**Figure 2B**).

Dive Behavior

Two deployments (Oo36 from California and Oo41 from Washington) were SPLASH10-A tags that recorded depth and duration of qualifying dives (**Figures 3A–E**) and duration of the surface intervals between them (**Table 3**). Oo36 transmitted 500 dives (qualifying dives are defined as submergences deeper than 20 m lasting at least 30 sec) and surface intervals over 66.2 days of transmission while it moved north along the California coast up into the northern end of Washington. Oo36's median dive depth was 41 m (max = 479.5), median dive duration was 3.9 min (Max = 10.1), and median surface interval was 3.7 minutes. The maximum time between qualifying dives during periods of continuous dive data collection was 618 minutes (10.3 hours). Oo41 transmitted 610 dives (submergences greater than 20 m lasting at least 60 sec) and corresponding surface intervals over 6.3 days of transmission while it moved south from Washington to northern California (**Figure 4**). Its median dive depth was 99.5 m (max = 479.5), median dive duration was 4.1 min (max = 12.3 min), and median surface interval was 2.5 minutes (max = 595). No dive data was recorded within B.C. or Alaska.

No strong diel patterns were evident in a visual exploration of the dive record, (**Figure 3E** and **5**); however more dives were recorded during daylight hours (59.0%), as were most of the deeper dives (>300m). Dive data from Oo41 revealed the following patterns of association with the seafloor depth: in regions where bottom depths were shallower than 450 m, this whale frequently appeared to dive to or near the seafloor (**Figure 4**). These dives to seafloor depth happened primarily during nighttime, though this may have been coincidental. In waters deeper than 450 m, dive depth did not appear correlated with seafloor depth and shallower dives were regularly executed to midwater depths (100 – 300 m), with the deepest dives occurring during the day.

DISCUSSION

Movements and Habitat Use

Offshores are known to travel more extensively than other ecotypes of the northeast Pacific based on photo-ID records (Dahlheim et al., 2008; Ford et al., 2014). The extent and rates of movements observed with these tags, which included individuals using nearly the entirety of the population's known range within the transmission period, generally corresponded with the photograph-based movements documented in previous studies (Dahlheim et al., 2008; Ford et al., 2014), though they expand the known range of this ecotype further south than has been previously documented through sightings and adds substantial detail on their movement patterns during the period of tag transmission. While movements across the entire range within a single year have been documented photographically (Dahlheim et al., 2008), the tag data demonstrates that whales move these distances in less than three months. Four whales were documented travelling at least 4,000 km and covering at least

100 km per day, increasing the previous best estimate of Offshore travel rates by two-to threefold (Dahlheim et al., 2008). The whale with one of the longest transmitting tags, Oo38, traveled at least 10,704 km in 99 days. These daily travel rates are comparable to those documented for killer whales elsewhere in the world, including the Southern Ocean (up to 223 km/day, $n = 6$; Durban and Pitman, 2012) and the North Atlantic (96.1–159.6 km/day, $n = 1$; Matthews et al., 2011). Both the broad-scale movement patterns and the finer-scale movement rates captured by these tags between January and June are consistent with the hypothesis that Offshores engage in a diffuse northward shift in habitat use in the first half of the year (Ford and Ellis, 2014; Ford et al., 2014), though animals were present in Alaskan waters earlier in the year than has been previously documented. All five individuals with transmission durations greater than one month traveled to higher latitudes during their deployments. Four of these whales tagged off the US West Coast in winter arrived in Alaskan waters and remained there for weeks before their tags ceased transmitting. For example, Oo38 remained in Alaskan waters from its arrival in early April until the end of tag transmission in mid-June. To date, Offshores have been encountered in Alaskan waters primarily during surveys in summer and early fall (Zerbini et al., 2007; Dahlheim et al., 2008; Dahlheim et al., 2009). Oo34 arrived in SEAK by early March, and Oo35 and 40 were both in SEAK by early April. All of these whales remained in the waters of Alaska and northern B.C. throughout the spring, including time within nearshore passages and inlets. These findings corroborate the suggestions that existing data, which are seasonally biased, underrepresent the importance of Alaskan waters during spring (e.g. Dahlheim et al., 2008; Ford et al., 2014). These data also suggest the importance of habitat along the US West Coast and northern Mexico in winter has been previously underrepresented by the limited sightings from the region.

As part of this seasonal shift in their range, these tagged Offshores also appear to alter their preferred habitat, gradually shifting into shallower water as they move north in the spring (**Figure 2**). Offshores generally preferred deeper habitat beyond the shelf break along the US West Coast, which has likely contributed to low detection rates in this part of their range. One notable deviation from this pattern in these data occurred off Cape Mendocino, CA (latitude ~40.35°N), where locations were received as close as 3.2 km from the coast. While this shift may have been habitat-associated, a deep canyon comes very near shore in this area, coincidentally, a concurrently tagged Southern Resident killer whale (SRKW, K25) was also present in the nearshore waters of Cape Mendocino at the same time (Hanson et al., unpublished data). Multiple Argos location estimates were received from both ecotypes within a 12-hour period, the closest of which was 2.0 km and 2 hours apart. By itself, this event may have been unremarkable. However, the larger group of Offshores that was encountered and tagged off WA in March was initially sighted by a NOAA survey vessel that had acoustically tracked a group of SRKW to the shelf break, an unusual movement away from the coastal waters that represent their typical range (Hanson et al., 2017; Rice et al., 2017).

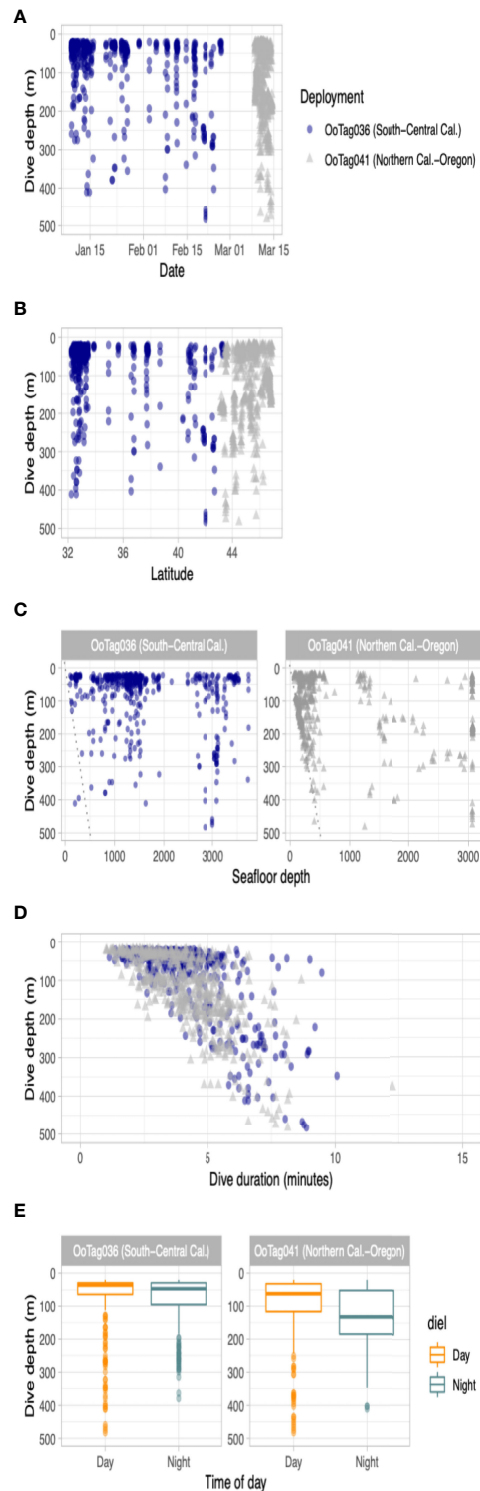


FIGURE 3 | Parameters of dive data recorded by the two whales tagged with SPLASH10-A dive reporting LIMPET tags. Dive activity is plotted by **(A)** dive depth versus date; **(B)** dive depth versus latitude; **(C)** dive depth versus seafloor depth; **(D)** dive depth versus dive duration and; **(E)** dive depth by time of day. In the scatter plots, blue circles are data from Oo36 and gray triangles are data from Oo41.

TABLE 3 | Dive and surfacing summary of the two SPLASH10-A tagged whales that reported data.

TagID	Dives						Surface		
	n	Depth (m)		Duration (min)			Duration (min)		
		Median	Max.	Median	Min.	Max.	Median	Min.	Max.
Oo36	500	41	479.5	3.9	1.1	10.1	3.7	0.03	618
Oo41	610	99.5	479.5	4.1	1	12.3	2.5	0.03	595

These two anecdotal events taken together suggest that these two ecotypes may occasionally leave preferred habitat to spatially associate, at least briefly. Though there is no evidence of recent gene flow among sampled Offshore and Resident ecotypes, the two are more closely related to each other than they are to sympatric Transient killer whales (Morin et al., 2006).

Using photo-identified individuals from different encounters of Offshore killer whales, Ford et al. (2014) assessed social organization within the ecotype using a pair-wise association approach. While the results suggested some possible stable groupings of individuals, the results were clear that the social structure of Offshores is not as strong as that of sympatric Resident and Transient ecotypes, with only some individuals showing recurrent associations over multiple encounters. Persistent bonds lasting more than a decade have been observed between Offshore adult females and males, but not between reproductive females, as are seen in the multi-generational matriline of Residents (Ford and Ellis, 2014).

Though some whales tagged in the same group remained associated for as long as 52 days, all individuals whose tags transmitted more than nine days ultimately separated from each other. This was true even for the whales tagged together in a relatively small group of nine. While apart, some whales tagged together moved along similar routes, just with the timing offset from one another (Figure 1). For example, O34 and Oo36 appeared to travel up the west coast of the US, before parting ways. Oo35 began with this same group but was present in Prince

William Sound at the same time as whales tagged in WA were travelling south into CA. Oo38 and Oo40 traveled north along similar routes with their paths only crossing periodically, such as when they passed off the southern tip of Haida Gwaii on the same day. Taken together, the movements we observed support prior observations that the social structure of Offshores is more fluid than that of other ecotypes (Ford et al., 2014), and includes some persistent and recurrent associations that may occur over long distances as whales use similar seasonal travel routes.

Dive Behavior

Though the sample size is small, this is the first study to report dive data from Offshore killer whales. The dive patterns of these tagged whales indicate that Offshores may use the water column broadly while foraging, including the seafloor in certain locations (Figure 3C and Figure 5). Several known prey species of Offshores are associated with the seafloor; these include the Pacific sleeper shark (Ford et al., 2014), spiny dogfish, and Pacific halibut (Fisheries and Oceans Canada, 2018). Sleeper sharks are also known to occupy both demersal and pelagic habitats at a wide range of depths (Hulbert et al., 2006), and this broad availability may explain the apparent importance of this prey species to Offshores (Ford et al., 2014). The remaining species of known prey, including blue sharks, Pacific salmon, and opah, are also wide-ranging inhabitants of epipelagic to mesopelagic waters (e.g. Polovina et al., 2008; Markaida and Sosa-Nishizaki, 2010; Wright et al., 2017). The wide range of

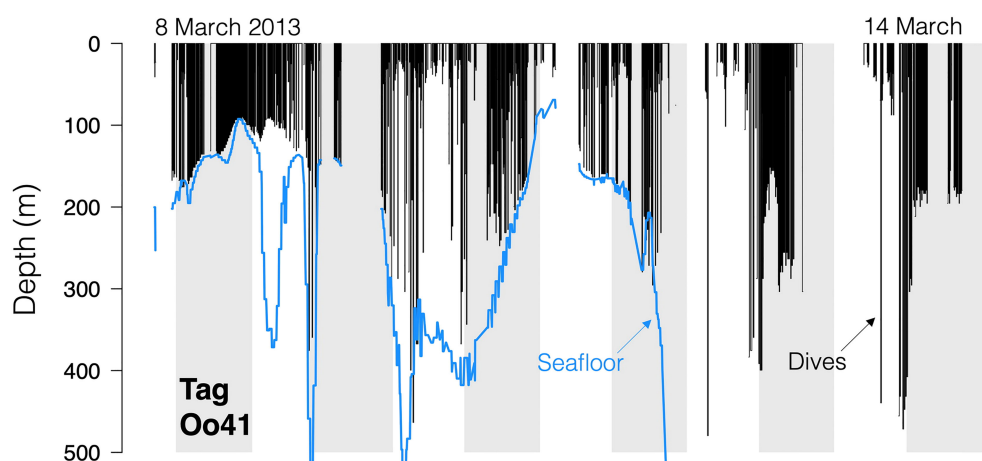


FIGURE 4 | Dive traces for Tag Oo41 (March 2013, off northern California and Oregon and Washington, USA). Black bars are the dives, with line discontinuities representing periods where no dive data was received. Blue line is the local seafloor depth.

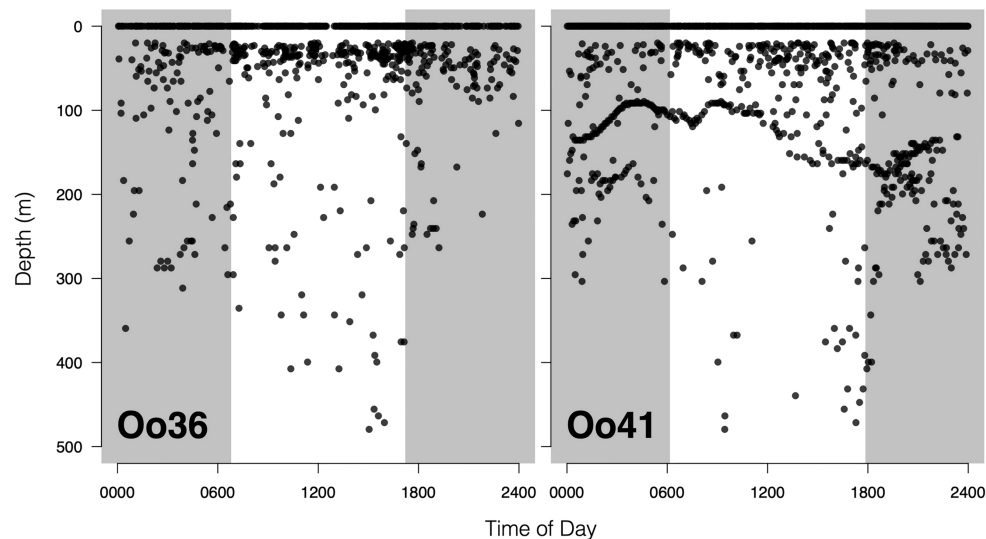


FIGURE 5 | Offshore killer whale dive activity plotted as function of time of day. Shaded areas are periods of dark, defined by the mean sunrise time and mean sunset time during the deployment. The lack of activity between 1 and 20 meters is a function of tag programming, which considers all dives shallower than 20m as 'surface' time. The striking undulating pattern in dive depths for Tag Oo41 is likely a response to local seafloor depth.

vertical habitat used by these whales, coupled with their extensive movements, supports the hypothesis that Offshores can respond flexibly to prey availabilities that vary by region, season, and seafloor depth.

Many dives in this dataset were deep relative to those described from other sympatric ecotypes in the northeast Pacific. Previous dive records from this region include a maximum of 254 m for Transient killer whales (Miller et al., 2010), 379 m for Northern Resident killer whales (Wright et al., 2017), and a maximum of 300 m for whales in the SRKW population (Tennessen et al., 2019). Dive depths recorded here were more similar to those seen in killer whales of the Southern Ocean, which regularly dive deeper than 350 m (maximum = 767.5 m), presumably to forage upon vertically migrating cephalopods and the demersal Patagonian toothfish (*Dissostichus eleginoides*) (Reisinger et al., 2015).

CONCLUSIONS

Here we present the first telemetry data on the movements, habitat use, and dive behavior of Offshore killer whales in the northeast Pacific. Many of our findings are consistent with inferences from photograph-based research over the last three decades (e.g. Ford et al., 2014), including that Offshores undertake seasonal latitudinal shifts. These data provide valuable insights into how individual Offshore killer whales move throughout their expansive range, covering remarkable distances in periods of less than three months, and suggest they are relative ecological generalists among the other, more specialized, northeast Pacific killer whale ecotypes thus

described. This detailed and relatively unbiased look at habitat use can inform management decisions in US waters and beyond.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

All methods and protocols were reviewed by the NMFS permit office, and all work was conducted under NOAA Research Permits, No.'s 16111 and 16163. Tagging conducted under Cascadia Research Collective IACUC protocol number CRC-2011-AUP-01-03.

AUTHOR CONTRIBUTIONS

GS, EF, and SJ conducted the field work in CA. GS, EF, MH, and CE led the field work in WA. GS and EK conducted the data analysis. RA led the development of the LIMPET tags. All authors contributed to the generation of the manuscript. All authors contributed to the article and approved the submitted version.

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Residency and Use of an Important Nursery Habitat, Raja Ampat's Wayag Lagoon, by Juvenile Reef Manta Rays (*Mobula alfredi*)

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The behaviour and spatial use patterns of juvenile manta rays within their critical nursery habitats remain largely undocumented. Here, we report on the horizontal movements and residency of juvenile reef manta rays (*Mobula alfredi*) at a recently discovered nursery site in the Wayag lagoon, Raja Ampat, Indonesia. Using a multi-disciplinary approach, we provide further corroborative evidence that the lagoon serves as an important *M. alfredi* nursery. A total of 34 juvenile rays were photo-identified from 47 sightings in the sheltered nursery between 2013–2021. Five (14.7%) of these individuals were resighted for at least 486 days (~1.3 years), including two juveniles resighted after 641 and 649 days (~1.7 years), still using the nursery. Visually estimated ($n=34$) disc widths (DW) of juveniles using the nursery site ranged from 150–240 cm (mean \pm SD: 199 ± 19), and the DW of two juveniles measured using drones were 218 and 219 cm. Five juveniles were tracked using GPS-enabled satellite transmitters for 12–69 days (mean \pm SD: 37 ± 22) in 2015 and 2017, and nine juveniles were tracked using passive acoustic transmitters for 69–439 days (mean \pm SD: 182 ± 109) from May 2019–September 2021. Satellite-tracked individuals exhibited restricted movements within Wayag lagoon. The minimum core activity space (50% Utilisation Distribution-UD) estimated for these five individuals ranged from 1.1–181.8 km² and the extent of activity space (95% UD) between 5.3–1,195.4 km² in area. All acoustically tagged individuals displayed high residency within the nursery area, with no acoustic detections recorded outside the lagoon in the broader Raja Ampat region. These juveniles were detected by receivers in the lagoon throughout the 24 h diel cycle, with more detections recorded at night and different patterns of spatial use of the lagoon between day and night. The observed long-term residency of juvenile *M. alfredi* provides further compelling evidence that the Wayag lagoon is an important nursery area for this globally vulnerable species. These important findings have been used to underpin the formulation of management strategies to

specifically protect the Wayag lagoon, which will be instrumental for the survival and recovery of *M. alfredi* populations in Raja Ampat region.

Keywords: movements, coral reefs, marine megafauna, home range, satellite telemetry, passive acoustic telemetry, photo-identification, spatial ecology

1 INTRODUCTION

Although nursery areas have been identified for a variety of elasmobranch species (Heupel et al., 2019), few studies have specifically examined the benefits of nursery areas for newborn and juvenile elasmobranchs, such as improved fitness and increased survival. Many elasmobranch species, including manta rays and other mobulid rays (*Mobula* spp.), use shallow and sheltered habitats like lagoons as nursery areas for newborns (Heupel et al., 2007; Stewart et al., 2018b). Reef lagoons provide several benefits for juvenile elasmobranchs, such as calm sea conditions, protection from large predators, reliable food availability, and opportunities for social interaction with conspecifics (Guttridge et al., 2011; Jacoby et al., 2012; McCauley et al., 2014; Rojas et al., 2014; Heupel et al., 2019). Occupying sheltered nursery areas may also contribute to higher chances of newborn survival by enabling individuals to grow in a safe environment and become better equipped to later escape predators and find diffuse prey (Branstetter, 1990).

In the last five decades, global populations of oceanic sharks and rays, including the reef manta ray *Mobula alfredi*, have declined significantly (Pacoureau et al., 2021). To promote the recovery and persistence of manta ray populations, Stewart et al. (2018a) highlighted the importance of identifying critical habitats, including pupping and nursery areas, as an urgent priority to support conservation management efforts. While the majority of literature on the spatial ecology of *M. alfredi* has focused primarily on large or sexually mature individuals, with juveniles included opportunistically (Jaime et al., 2014; Braun et al., 2015; Kessel et al., 2017; Couturier et al., 2018; Peel et al., 2019; Lassauce et al., 2020; Peel et al., 2020; Venables et al., 2020), the ecology and ontogeny of juvenile *M. alfredi* remain understudied. Information on juvenile movements, residency, and habitat use in nursery areas is urgently required to inform the planning and management of existing marine protected areas (MPAs), specifically to develop the most appropriate strategies and regulations to safeguard this vulnerable species (Stewart et al., 2018a).

Several locations around the globe have been proposed as manta ray nurseries. The Flower Garden Banks National Marine Sanctuary in the northwestern Gulf of Mexico has been suggested as a nursery habitat for Caribbean manta rays *M. cf. birostris* (Childs, 2001; Stewart et al., 2018b). Similarly, Pate and Marshall (2020) suggested a coastal region of southeastern Florida may also function as a nursery for that species. Additionally, several potential nursery areas for *M. alfredi* have been suggested in the Maldives (Kitchen-Wheeler et al., 2011; Stevens, 2016), Palmyra Atoll (McCauley et al., 2014) and Nusa Penida in southern Indonesia (Germanov et al., 2019).

In the Raja Ampat archipelago of West Papua, Indonesia, four areas have also been identified as potential *M. alfredi* nurseries (Setyawan et al., 2020), based upon the three criteria proposed by

Heupel et al. (2007) to define elasmobranch nurseries. These criteria, as applied to *M. alfredi*, include (1) Young-of-the-Year (YoY) and juvenile animals are more commonly encountered in the nursery area than in other areas; (2) YoY and juveniles remain in the nursery area for extended periods; and (3) the nursery area is used repeatedly by YoY and juveniles across years.

Of the four proposed *M. alfredi* nursery areas in Raja Ampat, the Wayag Lagoon has been the focus of the most intense research efforts. Based upon surveys in the Wayag lagoon between 2013–2019, Setyawan et al. (2020) provided evidence that the area fulfills Criteria (1) and (3) of Heupel et al. (2007) in functioning as a *M. alfredi* nursery. Specifically, those authors showed that YoY and juvenile animals [defined as individuals ≤ 2.0 m DW and ≤ 2.4 m DW (Peel et al., 2019), respectively] are more commonly observed within the Wayag lagoon than in the general population. YoY and juvenile *M. alfredi* comprise 47.6% and 95.2% of individuals recorded from Wayag lagoon, compared to only 4.7% and 11.1% of the 4,052 sightings recorded for the entire Raja Ampat population. Moreover, they reported that YoY and juvenile *M. alfredi* were observed on all 26 surveys conducted over the seven-year period, confirming Criterion (3) that the nursery is used repeatedly across years.

As noted by Heupel et al. (2019), assessing Criterion (2) of their elasmobranch nursery definition (residency within the nursery for extended periods) is best conducted using acoustic or satellite telemetry. Preliminary results of a pilot study using a Wildlife Computers SPOT5 satellite tag showed a YoY *M. alfredi* remained in and near the Wayag lagoon continuously for 6.5 months (Setyawan, Unpubl. Data). Here, we expand upon that study to assess Criterion (2) of the elasmobranch nursery definition using a combination of photo-identification (photo-ID), satellite telemetry, and passive acoustic telemetry to further describe the movement patterns and residency of juvenile *M. alfredi* in and around the Wayag lagoon. For the purposes of this study, we use the definition proposed by Chapman et al. (2015) that residency represents a nearly continuous occupancy by an individual in a restricted area for an extended period of time. Finally, we describe the home-range and habitat use patterns of the tracked juvenile *M. alfredi* in relation to the Wayag lagoon nursery area.

2 MATERIALS AND METHODS

2.1 Study Area

The Raja Ampat archipelago in West Papua, Indonesia, is home to large populations of both *M. alfredi* and oceanic manta ray (*M. birostris*) that appear to be in a healthy state with high survival rates and reproductive periodicity (Beale et al., 2019; Setyawan et al., 2020). Both species have been fully protected in this region

since the Raja Ampat government designated the entire archipelago as Southeast Asia's first shark and ray sanctuary in 2012 (Dharmadi and Satria, 2015; Setyawan et al., 2022a). Wayag (S 0.172995°, E 130.035316°), located in the northwest of the Raja Ampat archipelago (**Figure 1**), is an island comprised of mountainous limestone karst. It is part of the SAP (*Suaka Alam Perairan* – marine reserve) Waigeo Barat MPA, established in 2011 and covering an area of 1,550 km² (Mangubhai et al., 2012). The Wayag lagoon covers an area of ca. 14 km² and has been identified as a potential *M. alfredi* nursery area (Erdmann, 2014; Setyawan et al., 2020).

2.2 Data Collection

2.2.1 Photo-Identification

Between January 2013 and May 2021, surveys were undertaken every three to six months in Wayag. In all these surveys, we collected photo-ID images of *M. alfredi* in the Wayag lagoon via 1) underwater surveys by free diving and deploying GoPro camera traps at cleaning stations, and 2) starting in 2019, opportunistic aerial surveys of somersault-feeding manta rays using drones (Setyawan et al., 2020; Setyawan et al., 2022b). Individuals were identified using the unique spot patterns on their ventral side (Marshall and Pierce, 2012; Stevens et al., 2018) and visually matched to catalogued individuals in the “Bird’s Head Seascape *M. alfredi* Photo-ID Database” (Setyawan et al., 2020) to determine whether each juvenile was a newly-sighted individual or a resighting. For each photo-ID, we recorded date, time, location, sex, colour morph, and estimated disc width (DW) to the nearest 10 cm (Setyawan

et al., 2020). The DW of juvenile *M. alfredi* was also measured opportunistically to the nearest 1 cm using a novel photogrammetry method using drones (Setyawan et al., 2022b). The sex of each individual was determined through observation of claspers on males and lack thereof for females (Marshall and Bennett, 2010; Stevens, 2016).

2.2.2 Transmitter Deployments

We equipped five juvenile *M. alfredi* with SPLASH10-F-321A satellite transmitters (Wildlife Computers, Redmond, USA) in the Wayag lagoon in 2015 (n = 3) and 2017 (n = 2) (**Table 1**; **Figure 1**). Additionally, nine juvenile *M. alfredi* were tagged using V16-5H acoustic transmitters (Innovasea, Halifax, CA) operating at 69 kHz frequency and transmitting pings randomly every 60–130 s. The transmitters were deployed in Wayag lagoon (**Figure 1**) over four different periods: May 2019 (n = 2), October 2019 (n = 2), January 2020 (n = 2), and May 2021 (n = 3) (**Table 2**), following Setyawan et al. (2018). Briefly, each transmitter was attached to a titanium dart via a 25 cm (satellite tags) or 12 cm (acoustic tags) stainless steel tether coated with heat shrink tubing. Both satellite and acoustic transmitters were coated with non-toxic silicone based PropSpeed™ ablative coating to prevent fouling of the transmitters and antennae. Transmitters were deployed while free diving using a pole spear to insert the titanium dart tip into the dorsum of the ray in the muscle band between the right pectoral fin and the body cavity. Prior to tagging, we also collected identification photographs of each juvenile and sexed them, whenever possible.

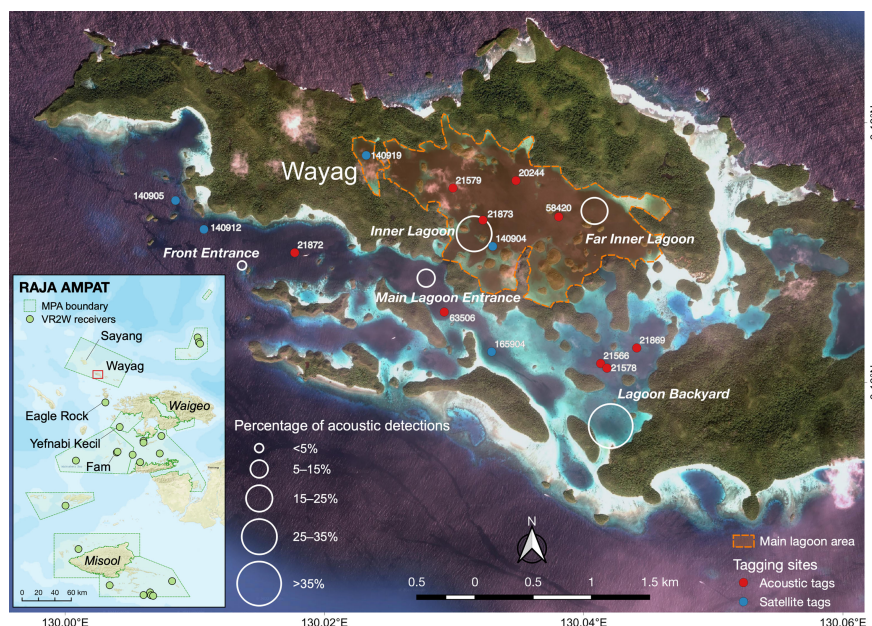


FIGURE 1 | The Raja Ampat, West Papua, Indonesia region (inset) and Wayag lagoon denoted in the red box. Green points on the inset map depict the location of acoustic receivers deployed throughout the Raja Ampat archipelago. White circles on the main map indicate the location of the passive acoustic telemetry array deployed in the study area to monitor juvenile *M. alfredi* residency and habitat use. The size of circles indicates the proportion of tagged *M. alfredi* acoustic detections recorded by each receiver throughout the study period. Red and blue points on the main map indicated the deployment locations of all transmitters.

TABLE 1 | Summary details for juvenile *M. alfredi* satellite tracked in Wayag lagoon in 2015 and 2017.

PTT ID	ID #140905	ID #140912	ID #140919	ID #140904	ID #165904
Sex	F	U	U	F	F
Est. DW (cm)	230	190	200	220	210
Tagging date	28 Jan 2015	28 Jan 2015	24 Feb 2015	22 Feb 2017	22 Feb 2017
Release date	11 Feb 2015	09 Apr 2015	13 Apr 2015	03 Apr 2017	18 Mar 2017
Tracking period (days)	12	69	45	38	22
Min. dist. travelled (km)	185.6	630.9	164.3	135.6	115
Daily mean min. dist. (km)	15.5	9.1	3.7	3.6	5.2
50% UD (km ²)	181.8	2.0	18.3	43.5	1.1
95% UD (km ²)	1,195.4	12.8	120.7	311.9	5.3

Sex = M (male), F (female) and U (unknown) Est. DW = estimated disc width. The tracking period represents the number of days between the transmitter deployment and release date. Min. dist. travelled = minimum distance travelled (straight line including over land) by the tagged juveniles during the deployment period (km). Daily mean min. dist = mean minimum distance travelled per day (km). Core activity space (50% UD) and the extent of activity space (95% UD) calculations for each tagged juveniles are based on Continuous Time Movement Modelling. All UD are expressed in km².

The SPLASH10-F-321A satellite transmitters were programmed to remain attached for 180 days to collect Fastloc GPS locations every hour with a maximum of 24 locations per day. Upon surfacing, the SPLASH10-F-321A satellite tags transmitted location data, including both ARGOS and Fastloc GPS locations. For subsequent analyses, we only report on GPS positions based on their higher accuracy for estimating home range and fine-scale habitat use patterns (Dujon et al., 2014; Thomson et al., 2017). Additionally, the satellite transmitters were programmed to record and archive dive-depth, light levels, and ambient sea temperature. In this study, however, we only focused on horizontal movements and therefore don't report on these other data.

2.2.3 Acoustic Receiver Deployments

To record detections transmitted by the V16-5H acoustic transmitters, we deployed Innovasea VR2W-69 kHz acoustic receivers at five sites, approximately 550–1900 m apart, inside the Wayag lagoon (Figure 1). The receivers were deployed at depths ranging from 8–26 m, and they were securely cable-tied to

buoyed moorings that were directly attached to the substrate using galvanised chain anchors and ropes, with each receiver approximately 1.5 m above the surrounding substrate (Setyawan et al., 2018). Four of the receivers were deployed in areas where juvenile *M. alfredi* had been previously observed feeding or cleaning (Setyawan, Unpubl. Data), while the “Front Entrance” (Figure 1) receiver was strategically placed to record any manta rays leaving the lagoon through the main channel connecting the lagoon to the deeper waters outside of Wayag. One receiver (“Main Lagoon Entrance”) was deployed in May 2019, while the other four were deployed in January 2020, for a period of 325–460 days (Table 3). At the same time, a larger array of 23 VR2W-69 kHz acoustic receivers were deployed throughout the Raja Ampat archipelago. These receivers were part of a broader study on manta rays and were located 35 (Eagle Rock) to 280 km (Misool) away from the Wayag lagoon receivers (Figure 1).

Importantly, the detection range of each acoustic receiver can vary dramatically depending upon ambient noise levels, receiver biofouling, and environmental conditions, and has been

TABLE 2 | Summary details for the nine juvenile *M. alfredi* tracked within the Wayag lagoon using passive acoustic telemetry.

Transmitter ID	ID #21873	ID #21872	ID #21566	ID #21578	ID #20244	ID #21869	ID #21579	ID #58420	ID #63506
Sex	U	F	F	U	F	U	U	U	M
Est. DW (cm)	180	190	200	170	180	180	190	200	190
Tagging date	17 May 2019	18 May 2019	18 Oct 2019	18 Oct 2019	12 Jan 2020	12 Jan 2020	11 May 2021	12 May 2021	25 May 2021
Last date detected	13 Sep 2019	30 Jul 2020	25 Mar 2020	09 Jun 2020	07 Aug 2020	04 Jul 2020	16 Sep 2021	20 Jul 2021	12 Sep 2021
No. receivers	1 (1)	5 (5)	5 (5)	5 (5)	5 (5)	5 (5)	5 (5)	5 (5)	5 (5)
Total detections	2,066	20,357	8,661	12,249	23,722	4,772	13,872	5,527	6,257
Days detected	52	327	106	185	126	91	125	64	108
Tracking duration (days)	119	439	159	235	208	174	128	69	110
Residency Index (%)	43.7	74.5	66.7	78.7	60.6	52.3	97.7	92.8	98.2
Mean visitation duration (min)	56.1	46.9	72.5	50	96.9	46.4	90.7	56.6	48.9
No. visitations	119	1,694	418	994	669	452	603	395	430
No. movements	-	976	183	568	375	280	333	233	186
Max. consecutive detection days	25	118	82	112	79	75	119	69	107

Residency index, visitations and movements as defined in section 2.3.2 on acoustic telemetry data analysis. Further explanations of metrics in the first column as follows: Est. DW: estimated disc width; No. receivers: total number of receivers at which each individual registered detections. Number in bracket represents the number of receivers deployed in the array; Total detections: total number of acoustic detections recorded for each individual; Days detected: total number of detection days; Tracking duration: total number of days between transmitter deployment and last date of detection; No. visitations: total number of visitations recorded for each individual; Mean visitation duration: mean time spent within detection range of a receiver; No. movements: total number of movements recorded between receivers; Max. consecutive days: maximum number consecutive days a tagged individual was detected by receivers.

estimated to vary between ~0–800 m (Heupel et al., 2008; Kessel et al., 2014; Huveneers et al., 2016). Receivers were serviced and downloaded every 3–6 months when our team was on site, and thus biofouling did not impact receiver performance. In order to quantify the detection range of the receivers in our array, a basic range test was conducted at the “Lagoon Backyard” receiver (**Figure 1**). Limited time and resources prevented us from undertaking a rigorous range test at all receiver sites. The range test was undertaken by deploying a fixed delay transmitter for one hour during the day at each of the following distances from the receiver: 0, 100, 150, 175, 200, 300, and 400 m. The tag was secured at 2 m depth by a rope attached to an anchor and buoy. The shallow (<8 m), sandy bottom location in the vicinity of that receiver was most likely to restrict detection range and hence this receiver was considered to be the “worst case scenario” and a conservative estimate for range detection for the five receivers in the array (Babin et al., 2019). No detections were recorded by this receiver from the fixed delay transmitter placed further than 150 m from the receiver. This test indicated reliable detection when a transmitter was within ~150 m of the receiver, which is similar to the detection range estimated in a study using the same types of receivers and transmitters in other areas of Raja Ampat (Setyawan et al., 2018).

One undeployed acoustic transmitter (#21839), that accidentally fell off and was not able to be recovered, was continuously detected by the receiver at MLE from 16–29 May 2021 (the receiver battery was exhausted and therefore the receiver stopped recording on 29 May 2021). We used the detection data from this lost ‘sentinel tag’ to assess the temporal variation of detections recorded by a receiver throughout the 24-hour cycle, as well as to examine receiver ability to detect a transmitter when the tagged juveniles were absent from areas where receivers had been deployed (Couturier et al., 2018).

2.3 Data Analyses

2.3.1 Satellite Telemetry Data Analysis

Each SPLASH10-F-321A satellite transmitter was equipped with a Fastloc GPS receiver that takes a “snapshot” of the radio signals produced by all GPS satellites orbiting above the transmitter at

any given time the manta ray is on the surface and the transmitter’s GPS antenna exposed to the air. Each snapshot was compressed onboard the transmitter and the data were transmitted to the Wildlife Computers Data Portal *via* the ARGOS satellite network. GPS location datasets were initially processed using the Wildlife Computers’ Fastloc GPS Processor as described in the “Location Processing (GPE3 & Fastloc GPS)” in the Wildlife Computers Data Portal User Guide (v.202007). GPS locations were further processed in Movebank (<https://www.movebank.org>) in order to allow us to manually remove outliers based on a maximum plausible swimming speed of 2 m/s. Furthermore, any GPS locations situated on land and further than 70 m inland from shore, based upon the accuracy of Fastloc GPS locations (Dujon et al., 2014), were also removed. These processed and filtered data (Setyawan et al., 2022c) were then used to track the patterns and scale of movements of juvenile *M. alfredi*.

Given the small scale and very fractioned landscape in Wayag, we did not restrict movement tracks to preclude movement over land masses. We calculated the minimum distance (including crossing land) travelled by the tagged juveniles using the ‘move’ package (Kranstauber et al., 2021) in R version 4.1.2 (R Core Team, 2021). To estimate core activity space (50% UD) and the extent of activity space (95% UD), we fitted an optimally weighted Autocorrelated Kernel Density Estimator (AKDE) (Fleming et al., 2018) on the filtered GPS locations using the ‘ctmm’ R package (Calabrese et al., 2016). The optimally weighted AKDE takes into account the autocorrelation of GPS locations obtained from satellite-tagged individuals and the highly irregular nature of location data collection in the marine environment (which, if ignored, typically leads to underestimation of home range size), and has been demonstrated to be applicable for *M. alfredi* satellite tag data (Fleming et al., 2018).

Despite the satellite transmitters being programmed to collect GPS locations every hour, the resulting GPS data were obtained irregularly, with time difference between subsequent GPS locations across tagged individuals ranging from 2.2–11.0 hours (mean \pm SD: 6.2 \pm 4.4 hours) due to the unpredictable nature of manta ray surfacing behaviour. Given the irregularity

TABLE 3 | Summary of acoustic receiver deployments within the Wayag lagoon, Raja Ampat. Further explanations of metrics in the first column as follows: No. transmitters detected: Total number of transmitters that were detected by the receiver.

Receiver ID	VR2W-123685	VR2W-135749	VR2W-128687	VR2W-123682	VR2W-123681
Receiver station	Main Lagoon Entrance	Front Entrance	Far Inner Lagoon	Inner Lagoon	Lagoon Backyard
Deployment date	16 May 2019	11 Jan 2020	11 Jan 2020	12 Jan 2020	12 Jan 2020
Recovery date	29 May 2021*	16 Sep 2021	16 Sep 2021	16 Sep 2021	16 Sep 2021
No. transmitters detected	9 (9)	8 (8)	8 (8)	8 (8)	8 (8)
Total detections	12,364	1,792	17,196	27,412	38,719
No. detection days	370	171	302	320	248
Tracking period (days)**	460	325	337	336	336
Detection Index (%)**	80.4	52.6	89.6	95.2	73.8
No. visitations	1,628	216	1,098	2,001	831
Mean visitation duration (min)	30.3	28.5	65.6	60.2	123

Number in bracket represents total number of active transmitters when the receiver was deployed; No. detection days: total number of detection days; No. visitations: total number of visitations recorded by each receiver from tagged juveniles. * The battery in the receiver at the Main Lagoon Entrance site was exhausted on 29 May 2021 and stopped recording on that day, despite being recovered on the same date as other receivers. ** Tracking period and Detection Index were calculated by excluding the period during which there were no active transmitters in the Wayag lagoon (275 days, from 8 August 2020 and 10 May 2021). Station locations reported in **Figure 1**.

of the available GPS location data, we fitted a state-space model on the GPS location data to estimate the most likely movement tracks for each individual using the 'foieGras' R package (Jonsen and Patterson, 2020). We applied correlated random walks with a six-hour time step to produce estimated locations every six hours. We used the move persistence index between estimated locations to characterise the likely behaviours of the tagged individuals during the tracking period (Jonsen et al., 2019). The move persistence index, which captures autocorrelation in both movement speed and direction, ranges between 0 and 1, with a low index suggestive of correlated random walks or Area Restricted Search (ARS) behaviour, and higher index values indicative of uncorrelated movement steps or likely transiting behaviour (Jonsen et al., 2019).

2.3.2 Acoustic Telemetry Data Analysis

Acoustic detection data (Setyawan et al., 2020c) were recorded as a timestamped log of transmitter IDs detected by each of the five receivers. We used a two-sample t-test to compare the hourly mean number of acoustic detections between daytime (06:00–18:00) and night-time (18:00–06:00). To examine residency of the tagged juveniles, we used the 'VTrack' R package and its Animal Tracking Toolbox (Campbell et al., 2012; Udyawer et al., 2018). A residency index (RI) (Couturier et al., 2018; Andrzejczek et al., 2020; Venables et al., 2020) was calculated for each tagged juvenile using the following formula:

$$RI = \frac{\text{No. of days a transmitter was detected by acoustic receiver array}}{\text{No. days between tagging date and last detection}} \times 100$$

We used a linear model to examine the correlation between tracking period and RI. In addition to RI for each tagged individual, we calculated a Detection Index (DI) for each acoustic receiver in the array using the following formula:

$$DI = \frac{\text{No. of days recording detections}}{\text{No. days between first deployment and last detection}} \times 100$$

We also examined the number and duration of visitations at receiver stations. A visitation represents a period when a tagged juvenile was detected continuously by a receiver. It begins when a transmitter is detected by a given receiver and terminates if either the transmitter is not detected again by that receiver within 60 mins or if the transmitter is detected by another receiver (Setyawan et al., 2018). In addition to visitations, we also calculated the number of movements of these juveniles between receivers. Overall, data were visualised using 'ggplot2' R package (Wickham, 2016), while the number of movements were visualised using the circular layout in the 'circlize' R package (Gu et al., 2014).

3 RESULTS

3.1 Juvenile Reef Manta Ray Sightings

Juvenile *M. alfredi* were observed at multiple sites within the Wayag lagoon. Most sightings occurred when individuals were somersault feeding near the surface, and some when they visited

cleaning stations. A total of 34 individuals were photo-identified from 47 sightings between May 2013–May 2021. Twelve of these (35.2%) were female, 11 (32.4%) were male, and 11 (32.4%) were of unknown sex. Nine of the 34 juveniles (26.5%) were resighted at least once within the Wayag lagoon (**Figure 2**); five were resighted once and the other four were resighted twice over periods ranging from 1–648 days (~1.7 years), with six of the nine individuals recording sighting spans in excess of 320 days (**Supplementary Table 1**). None of the remaining 24 photographically identified juveniles from the lagoon have been resighted to date as part of regular visits to the site every three to six months. The size of the 34 juveniles ranged between DW of 150–240 cm at first sighting (mean \pm SD: 199 \pm 19 cm), with 18 individuals with a DW \leq 200 cm at first sighting and thereby considered as YoY (*Setyawan et al., 2020*) (**Supplementary Table 2**). The DW of two unidentified juveniles measured using drones were 218 cm (95% CI: 216–220) and 219 cm (95% CI: 218–221). Several of the YoY *M. alfredi* recorded in the Wayag lagoon appeared to be true newborns, as evidenced by their small size (estimated 150–180 cm DW), unmistakably “clean” and unmarked appearance with no scratches evident (Marshall and Bennett, 2010), and obvious “creases” between pectoral fins and body cavity, presumably from the folding of the fins over the body while *in utero* (Marshall et al., 2008).

3.2 Movements and Regional Habitat Use as Revealed by Satellite Telemetry

3.2.1 Core and the Extent of Activity Space

The tracking duration across all five juvenile *M. alfredi*, three females and two of unknown sex (**Table 1**), ranged from 12–69 days (mean \pm SD: 37 \pm 22 days) between January and April 2017. The filtering procedure resulted in the removal of 15 (1.25%) out of 1,199 Fastloc GPS locations. The minimum straight-line distance travelled, including over land (a result of the complex geography of the lagoon), ranged from 115.0–630.9 km (mean \pm SE: 246 \pm 96.9 km), with mean daily distances travelled ranging from 3.6–15.5 km (mean \pm SE: 7.4 \pm 2.25 km).

Despite occasional excursions to areas outside the Wayag lagoon and the MPA boundary (**Figure 3**, **Supplementary Figure 3**), the majority of satellite-tracked juveniles demonstrated narrow and restricted core activity space (50% UD) located within the Wayag lagoon or near Wayag Island (**Figure 4**). The 50% UD core activity space ranged from 1.1–181.8 km², while the extent of activity space (95% UD) was 5.3–1,195.4 km². The size of the 95% UD varied between individuals, from just outside Wayag lagoon to areas up to ~45 km away from the lagoon. The smallest 50% and 95% UD were registered by ID #165904 (1.1 km² and 5.3 km²), while ID #140905 exhibited the largest (181.8 km² and 1,195.4 km²) (**Table 1**) with 50% UD (mean \pm SD: 49.3 \pm 76.0 km²) and 95% UD (mean \pm SD: 329.2 \pm 499.8 km²) across all tracked individuals.

3.2.2 Regional Movements and Residency Within the Wayag Lagoon

The estimated movement tracks derived from the state-space model suggested that all of the tagged *M. alfredi* spent the majority of their

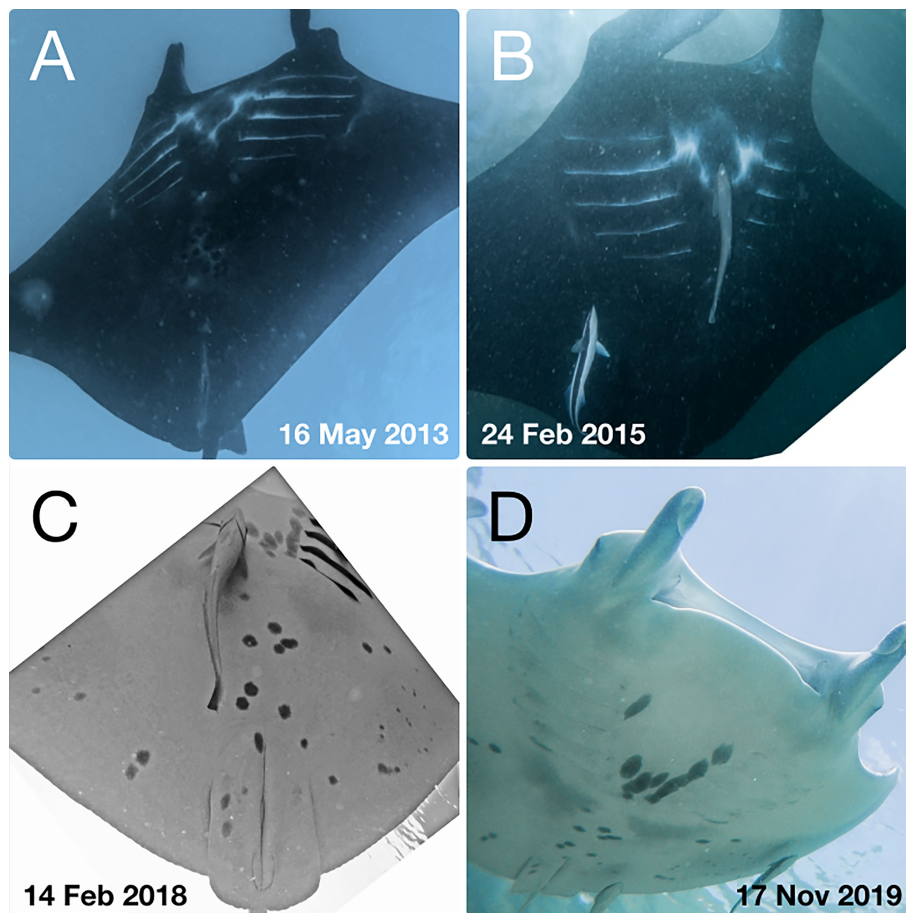


FIGURE 2 | Example of resighted juvenile *M. alfredi* RA-MA-1322 (**A, B**) and RA-MA-0525 (**C, D**) within the Wayag lagoon, Raja Ampat.

time within the Wayag lagoon, where they were tagged, or in waters adjacent to Wayag (**Figure 5A**). When in or around the Wayag lagoon, all tagged individuals displayed less persistent and directed movements in their localised tracks, suggesting affinity to this area (**Figure 5B**). Individuals occasionally made excursions to other areas around the small islands to the east and just outside of the Wayag lagoon. Three juveniles (ID #140904, #140905, and 140919) exhibited movements likely indicative of transiting behaviour, with more directed and faster movements as shown by higher move persistence index values for estimated locations outside of the Wayag lagoon (**Figure 5B**). Two individuals (ID #140905 and #140919) also travelled to areas outside the MPA boundary. While traveling outside of Wayag, ID #140905 also displayed low move persistence values in Wayag. ID #140912 spent all of its time within 5 km of the Wayag lagoon and showed low move persistence values during the 69-day tracking period.

3.3 Residency and Fine-Scale Habitat Use Within the Wayag Lagoon as Revealed by Acoustic Telemetry

Between May 2019–September 2021, nine juvenile *M. alfredi* (size-range = 170–200 DW) were tracked *via* passive acoustic telemetry

(**Table 2**). Individuals were tracked for periods of 69–439 days (mean \pm SD: 182 ± 109 days), with a total of 97,483 detections recorded across the five monitored receiver sites within the Wayag lagoon. Nearly a quarter (23,722 detections; 24.3%) of these detections were registered from ID #20244. The maximum number of consecutive detection days ranged between 25 (ID #21873) and 119 days (ID #21579) (mean \pm SD: 87 ± 30 days). Excluding ID #21873 that was only detected by one receiver, the maximum number of consecutive days ranged from 69–119 days (mean \pm SD: 95 ± 21 days). In addition, a total of 11,728 detections were recorded from the ‘sentinel tag’ by the ‘Main Lagoon Entrance’ receiver from 16–29 May 2021. Across 24-hour periods, the hourly mean number of detections of the sentinel tag was relatively constant (**Supplementary Figure 1**). During that period, the mean detection rate at night-time (35.6 detections/hour) was slightly higher than that at daytime (35.3 detections/hour), and the difference (0.38 detections/hour) was not significant (two-sample t-test, $p = 0.285$).

3.3.1 Detection Patterns and Residency

Detection patterns for the nine tagged *M. alfredi* varied between sites. The receiver deployed at Lagoon Backyard (**Figure 1**)

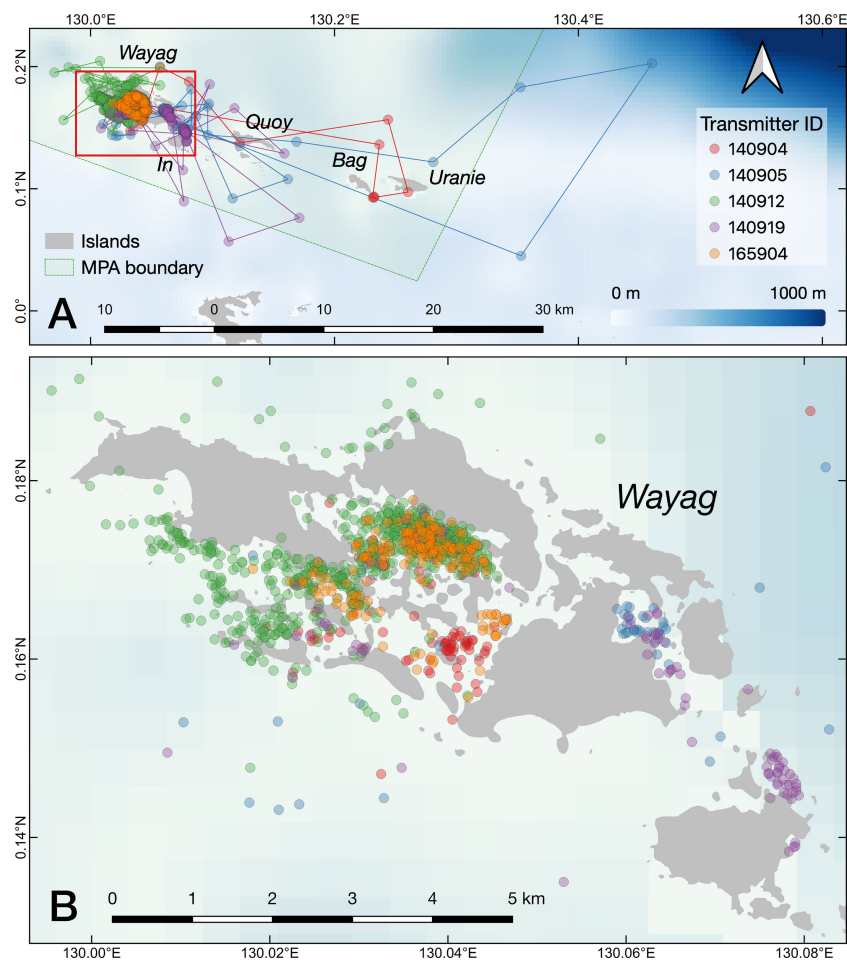


FIGURE 3 | The raw movement tracks (lines) derived from GPS locations (dots) recorded by the satellite transmitters on the five tagged juvenile *M. alfredi*. **(A)** the SAP Waigeo Barat MPA with names of the islands; **(B)** a close up of the Wayag lagoon.

recorded the most detections (38,719; 39.7% of all detections) with Front Entrance recording the fewest detections (1,792; 1.8%) (**Table 3**). The receiver at Main Lagoon Entrance, deployed in May 2019, detected all nine tagged individuals while the other receivers, deployed in January 2020, detected all eight available transmitters (as the first transmitter deployed, ID #21873, was no longer active in the lagoon at the time these four receivers were deployed). Importantly, none of the acoustically tagged *M. alfredi* were recorded by an extensive array of 23 receivers deployed within the broader Raja Ampat region (**Figure 1**).

The Detection Index (DI) calculated for acoustic receivers deployed in Wayag lagoon similarly varied between receiver sites. The Front Entrance receiver accounted for the lowest DI of all receivers (56.2%) (**Table 3**). DIs at receivers inside the main lagoon of Wayag (i.e., the Inner Lagoon and Far Inner Lagoon receivers) were higher than 89% for both receivers, and overall larger than those outside the main lagoon. This suggests that the tagged juveniles were more detectable within the main lagoon, especially around the two receivers, than outside of the main lagoon on a daily basis.

Residency behaviour varied slightly among the nine tagged individuals yet indicated high residency of the tagged rays to the Wayag lagoon. The RI of each tagged juvenile, particularly the eight individuals detected by all five receivers, ranged between 52.3–98.2% (mean \pm SD: $77.7 \pm 17.4\%$). The single individual detected by only one receiver accounted for a smaller RI of 43.7%. A linear model showed that even though the tracking period was negatively correlated ($R^2 = 0.13$) with the RI of eight individuals, this correlation was not significant ($p = 0.38$). On average, juvenile *M. alfredi* spent between 46.4–96.9 mins around a given acoustic receiver for each recorded visitation (**Table 2**). Detectability of individuals varied between sites, with the Inner Lagoon receiver recording the highest number of visitations (2,001), and the Front Entrance receiver recording the lowest (216; **Table 3**). Despite recording the second highest number of visitations, the mean duration of these visitations at the Main Lagoon Entrance receiver was relatively low (30 mins) compared to other sites further into the Wayag lagoon, where the mean duration was over one hour for the Inner Lagoon and Far Inner Lagoon receivers, and up to two hours at the Lagoon Backyard receiver.

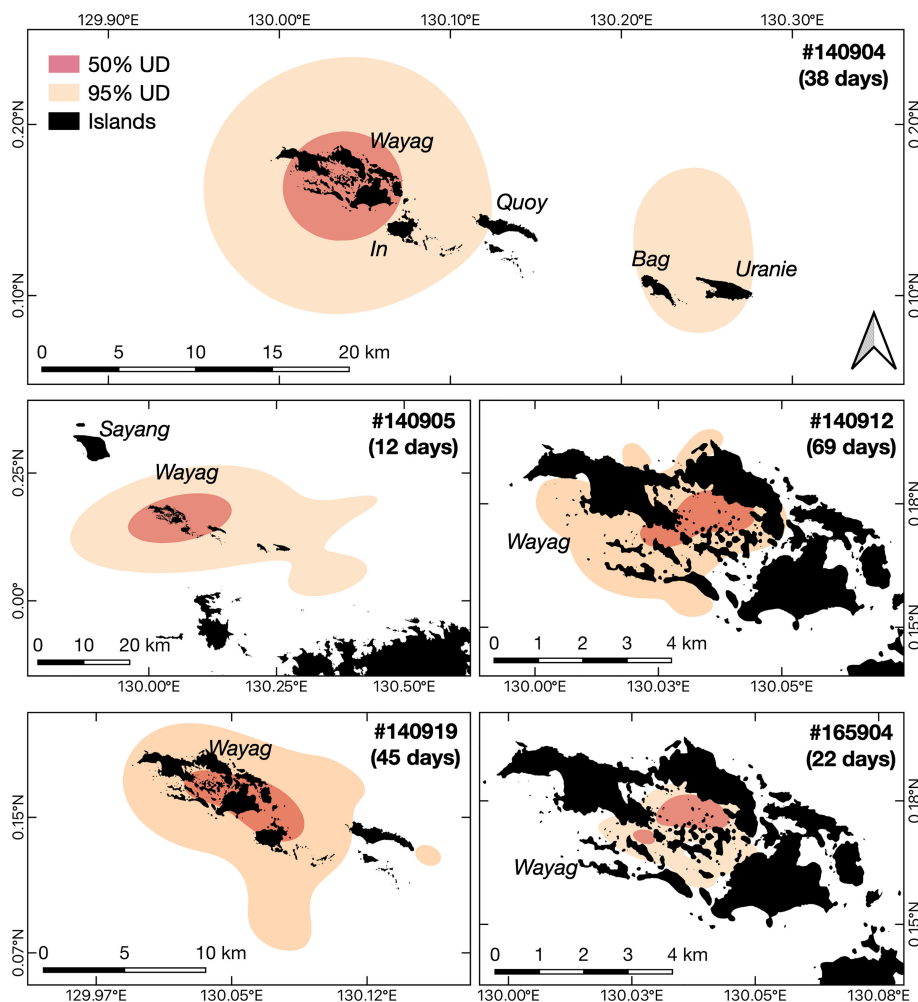


FIGURE 4 | Core activity space and the extent of activity space for each of the five juvenile *M. alfredi* satellite tracked around Wayag, Raja Ampat. The red polygons (50% UD) and the orange polygons (95% UD) denote the smallest estimated core activity space and the extent of activity space, respectively, where the tagged juveniles were expected to spend their time during the tracking period.

Overall, the longest continuous visitation was recorded at the Lagoon Backyard receiver, where ID #20244 remained continuously for 16.6 h (**Figure 6**), followed by ID #21579 remaining within the detection range of the Inner Lagoon receiver for 10.6 h. At the other receiver sites, the maximum visitation durations were less than half of that in Lagoon Backyard, with Front Entrance receiver recording the same individual for 3.6 h, Main Lagoon Entrance receiver for 7.8 h, and Far Inner Lagoon receiver for 8.3 h.

Within the lagoon, the tagged juveniles moved numerous times between receivers, ranging from 183–976 movements per individual (mean \pm SD: 392 ± 267 movements), with a total of 3,134 movements recorded. No movement was recorded from ID #21873, as only a single receiver was deployed in Wayag during its period of detection (**Table 2**). Movements recorded between receivers were variable and were generally made between nearby receivers (**Figure 7**). For example, of the 357 movements starting from the Lagoon Backyard receiver, 41% ended at the Main Lagoon Entrance, 33% at the Inner Lagoon, and 21% at the Far Inner Lagoon receiver.

3.3.2 Seasonality and Periodicity in Visitations

The five acoustic receivers deployed within the Wayag lagoon recorded transmitter detections more or less continuously after their initial deployment (**Figure 6B**). However, some of the juveniles were not detected by any receiver in the array in several instances, suggesting that they may have left the lagoon for brief periods, or at least remained in areas of the lagoon where they were not detectable (**Supplementary Figure 2**). For example, ID #21869 disappeared from the array in late March 2020 for 40 days before being detected again in early May 2020 (**Figure 6A**). During the same period, considerable gaps in detection of all tagged individuals were also observed at Lagoon Backyard (though detections were continuous through this time at the other four receivers). Importantly, the six transmitters deployed on juveniles in May and October 2019 and January 2020 all disappeared from the array by early August 2020 (**Figure 6**). Of these, two (ID #21873 & #21566) were detected for periods of four and six months, respectively, while the other four transmitters all disappeared

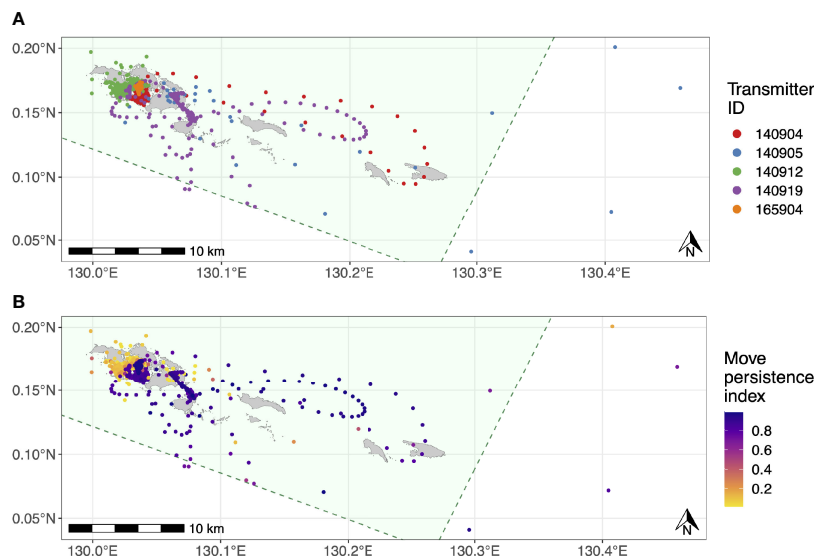


FIGURE 5 | Movement tracks for the five satellite-tracked juvenile *M. alfredi* estimated using state-space models with six-hour time steps. **(A)** Most likely track for each tagged individual; **(B)** Move persistence behavioural indices for all estimated *M. alfredi* positions. The green polygons in both panels denote SAP Waigeo Barat MPA boundary and the grey polygons represent islands.

from the array between early June 2020 and early August 2020 (**Figure 6B**). No detections occurred on the array between August 2020 and May 2021, until the final deployment of three transmitters in early May 2021. All receivers then continued to record detections until 16 September 2021, when they were downloaded for the final time for this study. Unfortunately, the Main Lagoon Entrance receiver's battery inexplicably ceased to function on 29 May 2021 (despite having been replaced with a new battery in early May at the time of transmitter deployment).

Overall, the mean hourly number of acoustic detections recorded by all receivers combined was significantly different (two-sample t-test, $p = 0.01$) between daytime (mean \pm SD: $3,817 \pm 343$ detections) and night-time (mean \pm SD: $4,307 \pm 494$ detections). The juveniles displayed a striking contrast in spatial use of the Wayag lagoon between day and night (**Figure 8A**). While the Inner Lagoon and Far Inner Lagoon receivers recorded the majority of their detections during daylight hours, the Lagoon Backyard and Main Lagoon Entrance receivers recorded most of their detections during night-time (detections at the Front Entrance receiver were too few to discern a pattern). Every tagged individual was detected by receivers throughout the 24 h diel cycle, with variations in daytime and night-time occupancy among individuals at each hour of the day (**Figure 8B**).

4 DISCUSSION

Using multiple investigative techniques, this study provides compelling evidence that fulfils Criterion (2) for elasmobranch nursery areas as proposed by Heupel et al. (2007); i.e., demonstrated residency by juveniles within the proposed nursery area for extended periods. We reveal juvenile *M. alfredi* tend to

remain within or briefly leave and return to the Wayag lagoon for extended periods, with only short excursions outside of the study area. Some of the photo-identified juveniles were resighted within the Wayag lagoon up to 1.7 years after their first observation, while satellite and passive acoustic telemetry data revealed restricted movements and near-continuous use of the lagoon for extended periods of up to ~14.5 months. Previously, Setyawan et al. (2020) showed conclusively that the Wayag lagoon fulfils Heupel et al. (2007)'s elasmobranch nursery Criteria (1) and (3); i.e., YoY and juvenile *M. alfredi* are more commonly encountered in the Wayag lagoon than in other areas and that the lagoon is used repeatedly by YoY and juveniles across years. Taken together, these studies present the most robust assessment to date of a *M. alfredi* nursery and show conclusively that juveniles use Wayag lagoon in northwestern Raja Ampat as a nursery.

The body size distribution of *M. alfredi* observed in the Wayag lagoon obtained from visual estimation and drone measurements suggests that the Wayag lagoon not only serves as a primary nursery area used by newborn or YoY individuals, but also serves as a secondary nursery area (Bass, 1978) based on the presence of juveniles sized ≤ 2.4 m DW (Setyawan et al., 2020). Primary and secondary nurseries occur in the same areas for a number of elasmobranch species (Simpfendorfer and Milward, 1993), and have been identified in several tropical marine regions (Yokota and Lessa, 2006; Palacios et al., 2021). We suggest that the Wayag lagoon may also act as a pupping ground. Despite the general dearth of adult manta ray sightings in the lagoon, since the start of our monitoring program in 2013, three near-term pregnant female *M. alfredi* have been observed in Wayag, in particular in the channel between the Front Entrance and Main Lagoon Entrance receivers (Setyawan et al., 2020). A pregnant female acoustically tagged in the Dampier

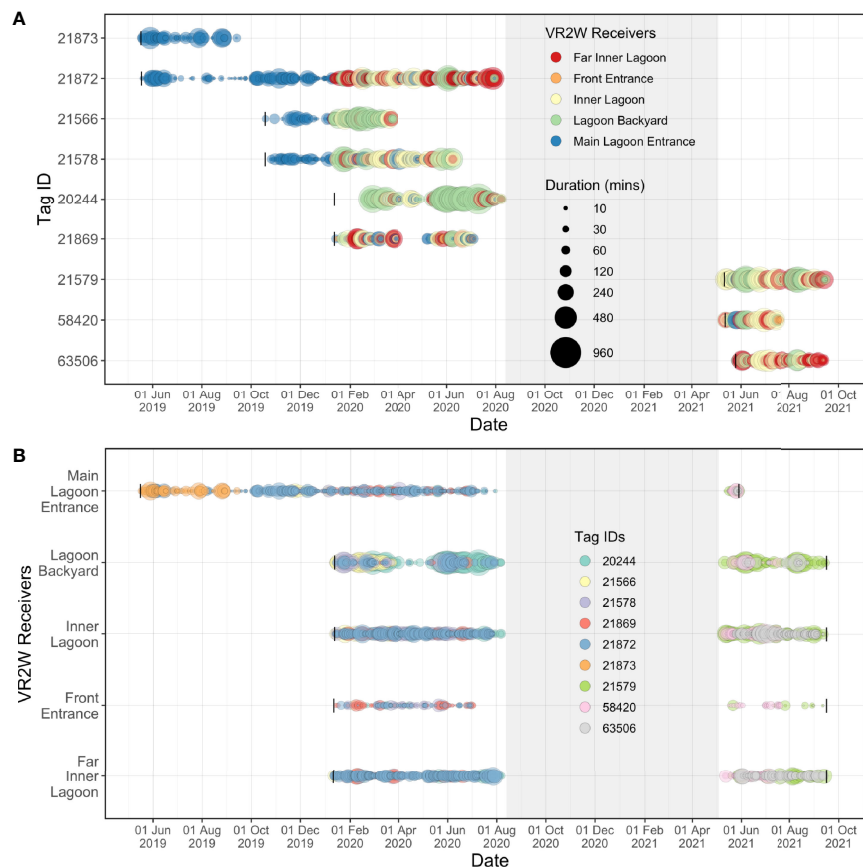


FIGURE 6 | Acoustic detections recorded over time for each tagged juvenile *M. alfredi* at each receiver deployed in the Wayag lagoon between May 2019–September 2021. The size of the bubbles indicates **(A)** the duration of visitations recorded by each receiver for each individual; and **(B)** the duration of visitations recorded for each individual at each receiver site. The grey shaded areas denote the period during which there were no active acoustic transmitters on manta rays in the lagoon, yet the receivers were still deployed in the lagoon. Black vertical lines in Panel A represent deployment dates of each transmitter, while black vertical lines in Panel B represent deployment and recovery dates of each receiver.

Strait region of Raja Ampat (**Figure 1**) was detected several months later (close to her estimated time of parturition) by a receiver in the Wayag lagoon (Setyawan et al., 2018). Additionally, the estimated sizes of several YoY *M. alfredi* that appeared to be newborns, are equal to the smallest reported birth size of *M. alfredi* by Murakumo et al. (2020). Furthermore, the obvious “creases” observed on these individuals, where their pectoral fins would have been dorsally folded over their body cavity within the mother’s uterus, were much like those shown by Marshall et al. (2008) for a late-term *M. alfredi* foetus in Mozambique.

Whilst all of the satellite-tracked juveniles exhibited sustained and restricted movements inside the Wayag lagoon area, occasional excursions to adjacent areas were also recorded. Individuals equipped with acoustic transmitters occasionally went undetected for a period of weeks by the acoustic receiver array inside Wayag lagoon, particularly from the end of March to early May. We hypothesise that these excursions outside of the nursery area were likely associated with maximising foraging activities in nearby highly productive waters to the east of Wayag

at the end of the northwest monsoon. A mature male *M. alfredi* satellite tagged in Eagle Rock (**Figure 1**) in Feb 2015 transmitted a substantial number of GPS locations from areas between Quoy and Uranie islands (**Figure 3**) in March–April 2015 (Setyawan, Unpubl. Data), which might indicate that these locations were associated with extensive surface foraging activities. Additionally, it is possible that the acoustically tagged juveniles that disappeared between the end of March and early May from the array in Wayag visited nearby Sayang and Piai islands, approximately 15 km to the northwest (**Figure 1**). Juvenile *M. alfredi* are frequently sighted foraging at the surface along the south coasts of Sayang and Piai islands around March–April (Ferdie Ballamu pers. comm.) during the transitional period between the northwest and southeast monsoon. These excursions may be evidence of the juvenile manta rays’ exploratory behaviours and developing their foraging behaviours including searching for prey in a more open ocean environment – a necessity for young elasmobranchs like basking sharks (*Cetorhinus maximus*), which have lower prey encounter success rates than adults (Sims et al., 2006). Such behaviour is

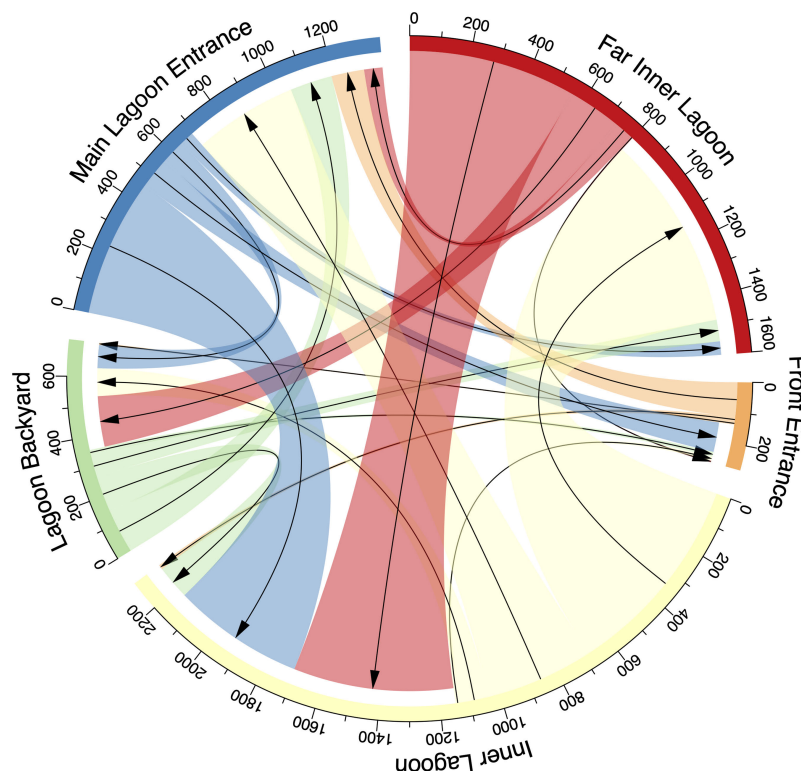


FIGURE 7 | Connectivity plot presenting the number of movements of acoustically tagged juvenile *M. alfredi* between receivers in the Wayag lagoon. The arrows show the direction of movement from one receiver to another, and the colour-coded receiver location names are outside the circle.

reported in a number of ocean-going taxa; for instance, Grecian et al. (2018) found differences in foraging proficiency between mature and immature gannets (*Morus bassanus*), while younger individuals of narwhals (*Monodon monoceros*) demonstrated different movement patterns from older individuals, likely associated with increased exploratory behaviours and less developed foraging proficiency (Laidre et al., 2004).

Though *M. alfredi* are capable of travelling up to several hundred kilometres to visit seasonally-productive sites (Anderson et al., 2011; Couturier et al., 2014; Jaine et al., 2014), the 14 satellite or acoustically-tagged individuals in this study showed high residency to the Wayag lagoon, with a maximum movement of 47 km to the east of the lagoon. None of the acoustically-tagged individuals were detected within the array of 23 acoustic receivers placed at all known *M. alfredi* aggregation sites in the Raja Ampat archipelago (Figure 1), including at the heavily-visited cleaning and feeding aggregation site Eagle Rock, just 36 km to the south of the Wayag lagoon (Setyawan et al., 2018).

Despite several movements to areas outside the Wayag lagoon, the tagged juveniles repeatedly returned to and showed a strong residency to the study site. Three of five satellite-tagged juveniles exhibited the extent of activity space (95% UD) that extended less than 10 km from the Wayag lagoon (Figure 4). Notably, the core activity space (50% UD) of all satellite-tagged juveniles mainly encompassed the Wayag lagoon and nearby

areas within a 5 km radius. The largest 50% and 95% UD identified in our study encompassed 182 and 1,195 km², respectively. These are much smaller than those of a juvenile male in the Red Sea, with 50% and 95% UD of 414 and 2,457 km² (Kessel et al., 2017). It is important to note that the activity space estimated in our study was restricted to short periods of satellite tracking (12–69 days), therefore it might realistically be larger than what is currently estimated. We also note that satellite tagged juveniles in our study were mostly females, therefore we were unable to explore sex-linked nuances in the spatial movements of juveniles, though maturity is a more relevant factor than sex when identifying nurseries.

The restricted activity space and low move persistence recorded for satellite-tracked individuals in the vicinity of the Wayag lagoon suggest strong residency within this site. This residency may be driven by the safe habitat for juveniles or could also reflect the reliable availability of prey in this area. For manta rays, which rely on finding large quantities of diffuse zooplankton prey in a dynamic pelagic ocean, sheltered coral reef lagoons may supply reliable and sustained quantities of prey to support the energetic needs of juveniles. Numerous studies have documented large *M. alfredi* foraging aggregations at isolated coral reefs where local tidal dynamics act to concentrate zooplankton prey (Jaine et al., 2012; Weeks et al., 2015; Armstrong et al., 2016), including inside the lagoons of coral reef atolls (Papastamatiou et al., 2012; Armstrong et al.,

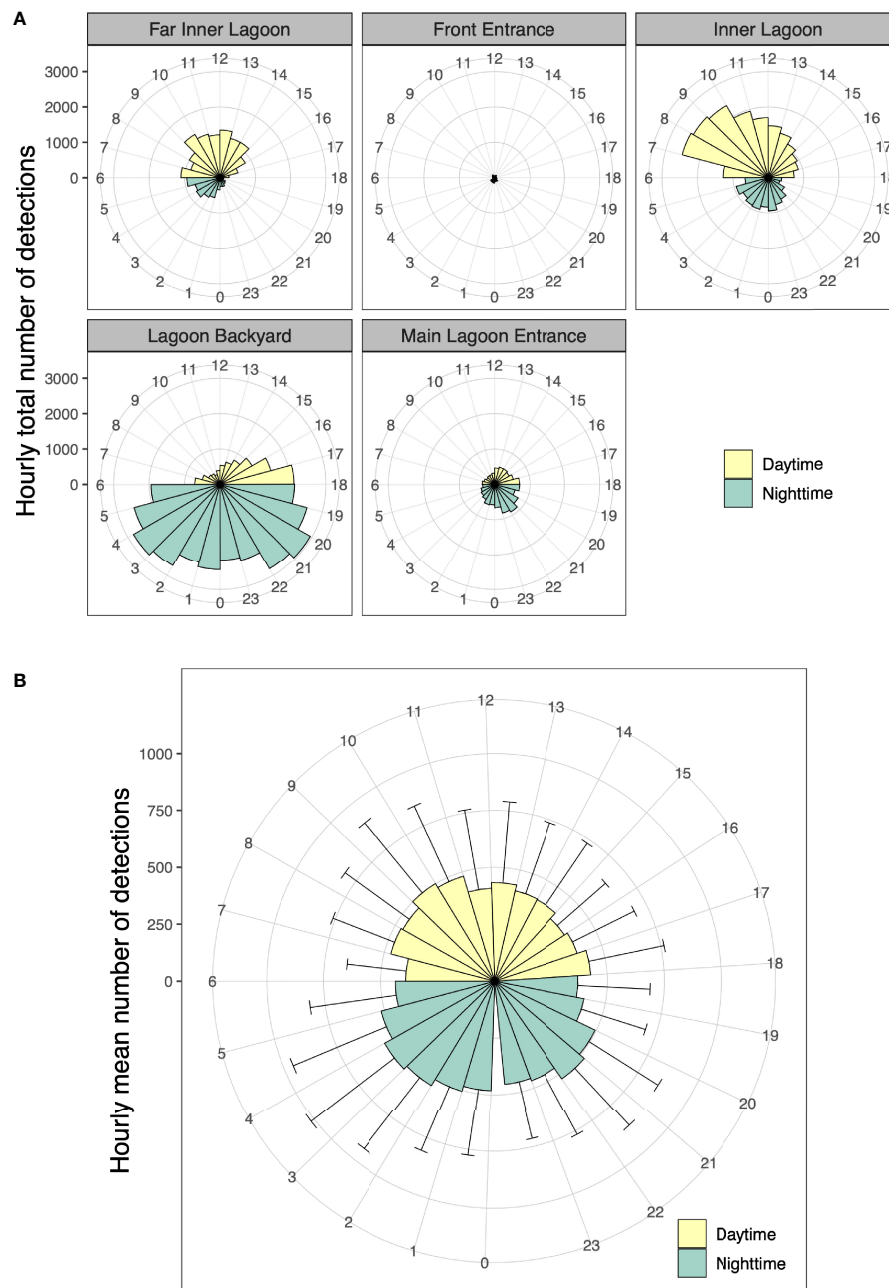


FIGURE 8 | (A) Hourly total number of acoustic detections for 24 h (0–23) in the Wayag lagoon between 17 May 2019 and 16 September 2021 recorded by each receiver, and **(B)** Hourly average number of detections for all tagged juveniles with error bars showing the variability across individuals. As Wayag is less than 20 km north of the equator, daylight hours are more or less constant throughout the year and denoted here as 06:00 to 18:00.

2021). Within the Wayag lagoon, juvenile *M. alfredi* are frequently observed using surface and somersault feeding strategies (Setyawan et al., 2020) similar to other lagoon habitats (McCauley et al., 2014; Stevens, 2016). We did not investigate the taxonomic composition or biomass of the planktonic prey targeted by feeding juvenile manta rays in the Wayag lagoon, though this certainly represents an important future field of study.

Acoustic telemetry detections of the tagged juvenile *M. alfredi*, in particular eight individuals that were detected by all receivers, indicated high residency indices (RI: 52–98%) at the monitored sites within the Wayag lagoon. Such residency levels are substantially higher than that of individuals (mostly adults) tagged during a previous acoustic tagging study in northern Raja Ampat (RI: 21%) (Setyawan et al., 2018). Similarly, acoustically-tagged juvenile *M. alfredi* in the Amirantes, Seychelles, also

showed a higher residency than adults around key habitats (Peel et al., 2019). In the Red Sea, the residency of small (<2.5 m DW, likely juvenile) *M. alfredi* was also relatively high at 65% (Braun et al., 2015). Lower residency levels (15–40%) of acoustically-tagged animals have been reported from other populations (Clark, 2010; Couturier et al., 2018; Andrzejczek et al., 2020; Venables et al., 2020), presumably because the studies tagged adult individuals. It is also possible that our RI may have been affected by the design of our acoustic tracking array. In addition to age-class (Chapman et al., 2015; Peel et al., 2019), the number of receivers, their position and the design of the acoustic array are important considerations (Espinoza et al., 2016; Peel et al., 2019). This artefact of array design is demonstrated by the fact that the lowest RI in our study (43.7%) was registered by ID #21873 when there was only one receiver deployed in the lagoon at the beginning of the study period.

Passive acoustic monitoring of tagged juvenile *M. alfredi* revealed individual and temporal variability in fine-scale (<4 km) space use and site occupancy within the Wayag lagoon. The nine acoustically tracked individuals exhibited strong site affinity, with high residency times around acoustic receivers and frequent, repeated visits to the sites. The maximum consecutive days of acoustic detections by tagged juveniles of up to 119 days (~4 months), with an average of 95 days (~3 months) of maximum consecutive detection days for tagged juveniles detected by five receivers, clearly indicate that these sites provide important habitat in Wayag lagoon. The long-term residency of juvenile *M. alfredi* in Wayag lagoon has been documented through individual photo-ID, with some juveniles resighted on several occasions over a 21-month period, as well as by passive acoustic telemetry revealing quasi-continuous occupancy in the nursery for over 14 months. Globally, it is still unclear how long juvenile reef manta rays use a nursery area, and at what age or size they decide to leave the nursery. In another proposed *M. alfredi* nursery area located in Fam, Raja Ampat (approximately 100 km to the south of Wayag), three juveniles were visually resighted after 26 months, and one resighted after 28 months, still present in the nursery (Setyawan et al., 2020); however, it is unknown whether these individuals had left the area during this time. We provide here the first documented continuous occupancy of juvenile manta rays in a nursery area. Coupled with multi-year presence of the juveniles, their continuous occupancy highlights the importance of this nursery area for their early-stage development. Further studies are required to better understand the ecological function of nursery areas in contributing to recruitment into adult populations of *M. alfredi*. Setyawan et al. (2020) documented one such recruitment; a juvenile *M. alfredi*, first sighted in Wayag lagoon as a 180 cm DW YoY male in November 2013, was resighted six years later as a 260 cm DW adult in the South East Misool MPA in southern Raja Ampat, 296 km to the south. Other valuable lines of future investigation include examining the social interactions and bonds created between newborns and juveniles within nurseries and their persistence over time, as well as investigating the “carrying capacity” of the area to serve as a nursery for newborn and juvenile *M. alfredi*, given the small size of the Wayag lagoon.

Passive acoustic tracking in Wayag lagoon yielded similar proportions of juvenile detections between day (47%) and night (53%), though the number of night-time detections was significantly higher than during the day. This is in sharp contrast with similar studies conducted in several other sites in Indonesia (Dewar et al., 2008; Setyawan et al., 2018) and other countries (Clark, 2010; Couturier et al., 2018; Peel et al., 2019; Andrzejczek et al., 2020; Venables et al., 2020), in which the numbers of acoustic detections of adult or subadult *M. alfredi* were significantly lower during the night than during the daytime. Most of these studies reported that manta rays would visit and occupy receiver sites mainly during the day for foraging and cleaning, but at night, tagged individuals would disappear from the tracking arrays, presumably moving to offshore or deeper waters to feed on vertically migrating deep scattering layers or emerging benthic zooplankton (Clark, 2010; Couturier et al., 2013; Braun et al., 2014). This doesn't appear to be the case in Wayag, where the juveniles were detected in the lagoon throughout both day and night. Furthermore, the distinct variations in the daytime and night-time detections between those receivers inside main lagoon area, that are surrounded by deep water, and Lagoon Backyard, located in shallow water, highlight a potentially interesting distinction in habitat use by juveniles in nursery areas. McCauley et al. (2014) observed that *M. alfredi* in a sheltered lagoon in Palmyra Atoll continuously used large areas of the lagoon and spent more time at greater depth during the day than at night. Further research into the vertical movements of *M. alfredi* in and outside of the Wayag lagoon using satellite telemetry will help understand the diel diving behaviour of juveniles.

In contrast to the main lagoon area (**Figure 1**) that was used extensively by juvenile *M. alfredi* during the day, the shallow Lagoon Backyard site was primarily visited around dusk and at night, often for extensive periods up to 16 hours. In most other acoustic telemetry studies conducted in reef environments and published in the literature, it is indeed possible that biological noise emanating from the reef at night may have prevented some detections to be recorded by the receivers (Kessel et al., 2014). However, data from the sentinel tag detected at the Main Lagoon Entrance receiver showed no obvious reduction in tag detectability based on time of day, suggesting continuous ability of the receiver to detect transmitters in the absence of tagged juveniles. Therefore, the distinctive diel pattern in visitation at the receivers in Wayag lagoon was likely due to actual juvenile visitations rather than being an artefact of detection range. Sheltered, shallower sites can act as ideal night-time habitats by providing safety from potential predators (Wetherbee et al., 2007; Guttridge et al., 2012) and a potential suitable supply of demersal zooplankton emerging from the shallow seabed (Alldredge and King, 1977; Ohlhorst, 1982). In southern Mozambique, acoustically tagged *M. alfredi* visited a feeding site mostly at night (Venables et al., 2020), though it is unclear whether they were foraging around the receiver at this site. At Palmyra Atoll in the Line Islands, Papastamatiou et al. (2012) recorded high nocturnal area-

restricted search behaviour associated with high zooplankton prey patches at specific sites inside a coral reef lagoon. It is possible that juvenile *M. alfredi* in Wayag use the Lagoon Backyard site for the same reason. Further research into the night-time behaviour of *M. alfredi* at this site, potentially using active acoustic tracking, may help ascertain the drivers of the observed high nocturnal residency times in this shallow area of the Wayag lagoon.

Importantly, the findings of this study have been shared with the Raja Ampat MPA Management Authority and have already been used to redesign and improve conservation and management measures for manta ray protection in the SAP Waigeo Barat MPA. Our findings have contributed to the designation of manta rays as one of the primary conservation targets for this MPA due to the importance of the Wayag lagoon as a manta ray nursery. Given the status of manta rays as a conservation target, stricter protection must now be implemented in Wayag; therefore, some areas within the main lagoon of Wayag have recently been designated as a “core conservation zone” with strictly restricted access. The areas outside of this core zone remain designated as tourism zones, where visitors, but no fishing, is allowed. The MPA Management Authority is currently working on finalising the legislation for both the revised zonation system and the management plan for SAP Waigeo Barat MPA, which will include important regulations (e.g., boat speed limits of less than 5 knots inside the main lagoon and the areas around Lagoon Backyard, as well as stipulated mooring areas for liveaboards far from known manta sites) to ensure the nursery function of the Wayag lagoon is not compromised.

5 CONCLUSIONS

This study shows conclusively that the Wayag lagoon in Raja Ampat archipelago serves as a nursery for newborn and juvenile *M. alfredi* and provides the most robust assessments to date of a *M. alfredi* nursery. It also provides key information on the residency and fine-scale habitat use of *M. alfredi* in this nursery area. These important findings have been used to underpin the formulation of management strategies to specifically protect the Wayag lagoon and its function as a manta ray nursery. Safeguarding this nursery could ultimately be instrumental for the survival and recovery of *M. alfredi* populations in the region.

DATA AVAILABILITY STATEMENT

The datasets generated during and/or analysed during the current study are available in the Movebank Data Repository, which can be found here: <https://doi.org/10.5441/001/1.n95c7182> ([Setyawan et al., 2022c]).

ETHICS STATEMENT

The animal study was reviewed and approved by The University of Auckland Animal Ethics Committee and was conducted following protocol 002228. Permission to conduct the research was granted by the Raja Ampat Marine Protected Area (MPA) Management Authorities (Balai Kawasan Konservasi Perairan Nasional (BKKPN) Kupang and BLUD UPTD Pengelolaan KKP Kepulauan Raja Ampat).

AUTHOR CONTRIBUTIONS

ES, ME, RM, AH, and AS collected the data. ES performed the statistical analysis and created figures, tables, and maps with guidance from FJ and BS. ES drafted the manuscript. FJ, ME, RC, and BS provided guidance and supervision, reviewed, and edited drafts of the manuscript. All authors discussed the results, contributed to and approved the final manuscript.

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Assessing Important Conservation Areas for Colonial Species From Individual Tracking Data: An Evaluation of the Effects of Colony Structure and Temporal Heterogeneity in Movement Patterns

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Sensitivity of marine ecosystems to human disturbance leads to an increasing need to devise effective conservation initiatives. One key conservation leverage tool is the establishment of marine protected areas, which can be derived by inspecting where marine sentinel species forage in their most sensitive life cycle phase (reproduction). Depending on their biological and legislative framework, important conservation areas (hereafter, ICAs) can correspond to Important Bird and biodiversity Areas, Key Biodiversity Areas, Marine Protected Areas, etc. Statistical methods allow for standardized assessment of ICAs based on GPS tracking data. However, several biological processes should be accounted for to provide reliable ICAs. In colonial seabirds and sea mammals, individuals breeding in different parts of a colony often spatially segregate while foraging at sea. Besides, environmental conditions may affect the location of foraging areas across years. To what extent relying on data collected in only one part of a colony or in a single breeding season may affect the location and size of ICAs remains unexplored. Here we aimed at 1) highlighting intra-colony and inter-annual heterogeneity of exploited marine areas during reproduction in a colonial seabird, the Scopoli's shearwaters *Calonectris diomedea*; and 2) providing guidelines on how to methodologically best account for such spatio-temporal heterogeneity when deriving ICAs. We relied on 397 foraging trips performed by 73 individuals breeding in two distinct areas within the same colony (hereafter, sub-colonies) over 3 years. We showed that areas exploited by shearwaters breeding in two nearby sub-colonies were clearly segregated and differed between years. Relying on only one sub-colony or a single breeding season led to drastically smaller ICAs, biased either east- or west-ward depending on the sub-colony considered. We proposed to account for such heterogeneity by merging the different ICAs

obtained for each sub-colony and year, instead of pooling tracking data and deriving a single ICA. Our method led to much larger ICAs, which were less affected by differences in sample sizes across sub-colonies or years, than when ignoring the spatio-temporal heterogeneity. Recently developed standardized statistical procedures and a careful consideration of population spatial structure and temporal heterogeneity will foster robust conservation actions for colonial marine species.

Keywords: colonial breeders, foraging, GPS tracking, key biodiversity areas (KBAs), marine conservation, scopoli's shearwater (*Calonectris diomedea*), spatial segregation, Important Bird and Biodiversity Areas (IBAs)

INTRODUCTION

Current environmental changes pose dramatic threats to biodiversity and wildlife (Acevedo-Whitehouse and Duffus, 2009; Hautier et al., 2015). Based on the IUCN Red List, 28% of the species are globally threatened (currently assessed species, IUCN, 2021), a percentage that will likely increase greatly in the near future due to climatic changes (Thomas et al., 2004). In response, the establishment of conservation areas proved to be an effective tool to locally protect species and ecosystems (Pimm et al., 2001; Eken et al., 2004). Various types of important conservation areas exist, each with their own specific applications (ecosystem or taxa) and regulations (see Eken et al., 2004). There is a particular and long-lasting interest in marine ecosystems conservation due to the multi-scale threats marine communities are facing: overfishing and bycatch (Jackson et al., 2001; Davies et al., 2009), water acidification (Doney et al., 2009), increased temperature (Johansen and Jones, 2011), and pollution (Cole et al., 2011; Wilcox et al., 2015). Since the 1970's, Marine Protected Areas have been implemented worldwide in marine ecosystems (Caveen et al., 2013). The following decade, more quantitative and criteria-driven approaches for conservation areas emerged, with Important Bird and biodiversity Areas (IBAs) used since then by BirdLife International (Eken et al., 2004; Lascelles et al., 2016). This standardized approach was then taken to a more taxonomic-general framework with the definition of Key Biodiversity Areas (KBAs, Eken et al., 2004). For simplicity and generalism, we refer hereafter to important conservation areas (ICAs), as simply any area of importance for the conservation of a target species, without referring to any specific regulatory or legislative framework as implied in MPAs, IBAs or KBAs.

Given their key functional role in marine ecosystems, marine megafauna species are often considered as sentinels of marine environmental conditions. Hence, their at-sea distribution, especially during the reproductive period, was used to reliably identify local ICAs (Karpouzi et al., 2007; Nelms et al., 2021). In the last 50 years, we witnessed a great improvement in tracking technologies allowing to record the movement of marine megafauna, especially seabirds (Wilmers et al., 2015). In parallel, statistical tools were proposed for a standardized identification of ICAs: Lascelles et al. (2016) introduced a standard methodological approach further developed and improved with the recent R package track2KBA (Beal et al., 2021b). While this statistical procedure offers exciting

possibilities for data-driven conservation planning, it still awaits to be thoroughly tested in real-world settings considering different aspects of species' ecology and the characteristics of available tracking data.

Some inherent biological processes affecting at-sea distribution of marine megafauna may limit the efficacy of ICAs if not appropriately accounted for. In particular, most seabird species breed in colonies (over 95% of species, Schreiber and Burger, 2001), and competition for food resources often leads to colony-specific segregated foraging areas (Cairns, 1989; in 79% of studied seabird populations, Bolton et al., 2019). Relying on a non-random sample of individuals (e.g. only one part of a colony) could lead to giving more weight to certain phenotypes in the final assessment of the population foraging areas (Aarts et al., 2008). A common practise when implementing large-scale conservation actions consists in relying on at-sea distribution of different colonies (e.g. Fort et al., 2013). However, colonies (i.e., assemblage of individuals breeding at close sites and having physically access to the same foraging areas) rarely form continuous spatial arrangements of breeders and are instead often divided in more or less discrete and isolated sub-groups (hereafter sub-colonies), which may also forage in distinct areas around the colony despite having access to the same areas (e.g., Waggitt et al., 2014; Pereira et al., 2022). Similarly to what has been observed between colonies, there is now a growing body of literature showing between-sub-colony spatial segregation of foraging grounds (in seabirds: Hipfner et al., 2007; Bogdanova et al., 2014; Ceia et al., 2015; Sánchez et al., 2018; Ito et al., 2020; Pereira et al., 2022; sea mammals: Kuhn et al., 2014; and a terrestrial colonial bird, Morinay et al., 2022), suggesting that such within-colony segregation could be widespread, and thus impact a population-wide representative definition of ICAs if overlooked. How to best account for such small-scale spatial segregation when deriving ICAs still remains an open question that we aimed to answer here with our methodological and empirical approach.

Another important aspect to consider for the establishment of efficient ICAs is the temporal change in habitat use. Indeed, locations of visited areas within a specific time-window (e.g. few days, a week, a year) may not be representative of the population habitat use over longer term, for instance if the resource itself moved or if individuals decided to visit other patches (e.g. nearer to the colony or further away). Sampling over short term may not be meaningful for deriving efficient long-term conservation actions. Challenges due to short term changes in habitat use

(within hours, days) can be overcome by collecting several independent foraging trips, ideally over different reproductive stages, or, if not possible, when individuals are most constrained and likely less plastic in their foraging activity, defining then the area exploited during the most critical period (usually during the nestling provisioning stage; Cecere et al., 2013). Dealing with longer term changes in habitat use require collecting data over enough breeding seasons (Bogdanova et al., 2014), which can be also technically and financially challenging. Some studies already documented among-year differences in some seabirds (Bogdanova et al., 2014; Cecere et al., 2014; Courbin et al., 2018) and their prey distributions (Saraux et al., 2014). It is thus crucial, when aiming at deriving ICA, to detect temporal heterogeneity in movement patterns, and ensure that data collected over different years cover the population extent of foraging range (see Bogdanova et al., 2014 for a worked example based on 15 years of data). Yet, when only few years are available, as it may be the case for many conservation plans, ignoring yearly-variation in habitat use and weighting equally data from the different years (with possibly different sample sizes and representativeness level) may strongly affect the inferences on habitat use (Schooley, 1994). Appropriately accounting for such temporal heterogeneity in spatial data remains a practical challenge.

To what extent spatial segregation of exploited areas among individuals from different sub-colonies and among-year differences in exploited areas may affect the location and size of ICAs remains to be assessed. To address this issue, we first analysed how the spatial extent of ICAs was affected by ignoring such spatial (among sub-colonies) and temporal (among years) heterogeneity in the data. Secondly, we provide guidelines on how to account for these sources of heterogeneity with the statistical tools already in place in order to identify the most ecologically appropriate ICAs. To achieve these goals, we used spatial data of Scopoli's shearwaters *Calonectris diomedea* breeding in Mediterranean Sea colonies. Through its apex role in the marine ecosystem and its sensitivity to environmental changes (Jenouvrier et al., 2009) and anthropogenic threats (Codina-García et al., 2013), this marine top predator is a good candidate as a sentinel species for marine ecosystems (Hazen et al., 2019), making it especially appropriate to study for the establishment of ICAs. Besides, even though Scopoli's shearwaters are considered as 'least concern' by the IUCN, they are of conservation concern in Europe (listed in Annex I of Bird Directive 2009/147/EC) as they are subject to multiple threats like predation by invasive species (Ozella et al., 2016), light pollution (Rodríguez et al., 2015), but also deadly interactions with fisheries (Afán et al., 2019) and plastic ingestion (Codina-García et al., 2013), which call for protected areas not only on land but also at sea for this species. We focused on the chick-rearing period, which is the most constraining period for breeding central place foragers as they must combine self-maintenance and offspring provisioning. Using the track2KBA package (Beal et al., 2021b) and relying on 397 foraging trips performed by chick-rearing Scopoli's shearwaters from two separated islands of a same archipelago (i.e. two sub-

colonies) across three breeding seasons, we aimed to detect the effect of spatial segregation between sub-colonies and year differences in habitat use in the delineation of ICAs. To achieve this goal, we compared ICAs derived when considering or ignoring such spatial and temporal heterogeneity and propose a method to derive a single and reliable ICA using tracking data from several sub-colonies and years.

MATERIAL AND METHODS

Studies Species and Site

The study was conducted between July and August in 2013, 2018 and 2019, in the Parco Nazionale dell'Arcipelago di La Maddalena (Italy) located between Sardinia and Corsica, and hosting 200-500 breeding pairs of Scopoli's shearwaters (from our surveys) distributed in about 12 islands. This archipelago is at minimum 7 km far from Lavezzi islands (France), hosting 350-400 pairs (Péron et al., 2018). We sampled individuals breeding on two small islets of this archipelago and located only 7 km apart, a very close distance for such a wide-ranging species (Figure 1). These two sub-colonies, Barretini (41°17'3.59"N, 9°24'5.96"E) and Spargiotto (41°14'59.93"N, 9°19'25.01"E), host the higher number of pairs of Scopoli's shearwaters per island in the archipelago, namely 40-50 and 60-80 pairs respectively. Barretini and Spargiotto are besides the most eastern and western sub-colonies in this archipelago, respectively (among the ones with more than 10 breeding pairs). There, shearwaters breed in relatively easily accessible burrows, enabling the capture and identification of many breeding individuals (between 24 and 37 each year on each islet), as well as the recapture of individuals equipped with GPS devices. Scopoli's shearwaters typically mate in late April, lay eggs in late May, and incubate them for about 55 days. They feed mostly on plankton and small pelagic fish (Grémillet et al., 2014) but they can also exploit discards from fishing vessels (Cecere et al., 2015; Cianchetti-Benedetti et al., 2018). During incubation, both partners undertake long lasting foraging trips (1-18 days, 7 days on average; Cecere et al., 2013), while upon chick-rearing (in July – October), they alternate few long trips lasting 6-20 days with shorter trips (1-4 days; Cecere et al., 2014).

GPS Deployment

During early chick-rearing period, the parent attending the nest was captured during night-time directly in its nest, ringed with a metal ring or identified if already ringed, and equipped with a GPS logger attached on the back feathers (see De Pascalis et al., 2020 for more details). The GPS loggers were set to record a position every 10 min. Similarly to De Pascalis et al. (2020), we removed positions within 5 km from the sub-colony. We relied on manual foraging trip identification for 2013 (from Cecere et al., 2014), considering a foraging trip as an at-sea excursion lasting more than five hours, starting and ending at the colony. For 2018 and 2019, we followed the same method as in De Pascalis et al. (2020), and automatically identified foraging trips following Lascelles et al. (2016) and its *tripSplit* function,

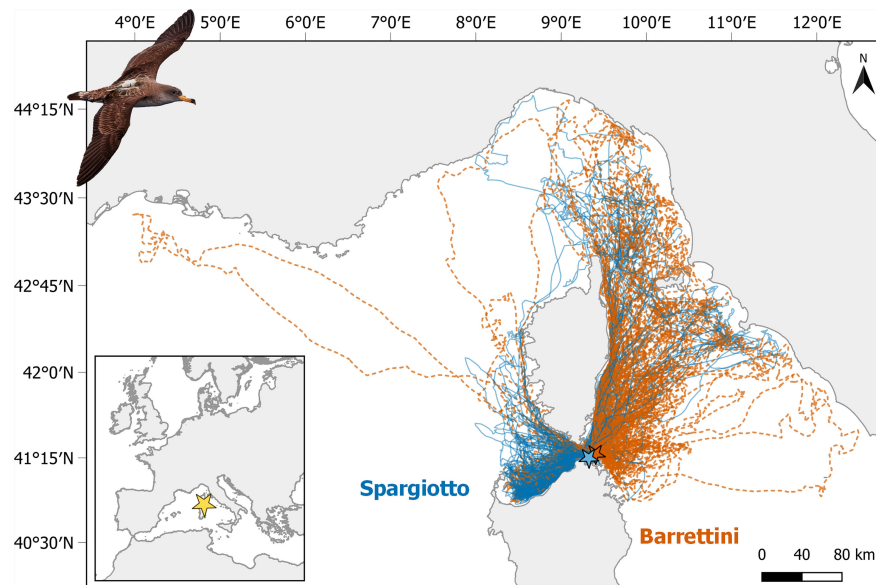


FIGURE 1 | Tracks of foraging trips performed by Scopoli's shearwaters breeding in Spargiotto (solid blue lines) and Barrettini (dashed orange lines) islets in La Maddalena archipelago (Sardinia) in 2013, 2018 and 2019. See **Figure S6** for the separation of trips by year. Picture of tagged Scopoli's shearwater courtesy by Mirko Ugo.

considering only trips lasting at least 5 hours, with inner-and outer buffers of 5 and 20 km respectively. We ensured the correct discrimination by visually inspecting each foraging trip in QGIS (v.3.16.10, QGIS.org, 2022). Overall, we relied on data from 32 individuals tagged in 2013, 44 in 2018, and 15 in 2019; 16 individuals were tracked in two years and one individual in three years. Sex-ratio (proportion of females) was well balanced in all years and sub-colonies (0.50 on average, range: 0.41–0.63). See **Table S1** for a detailed description of sample size per year, sex, and sub-colony.

Computation of Home Ranges and Selection of Foraging Trips

The entire statistical procedure is described in detail in **Figures S1, S2**. The first step consisted in deriving Kernel Density Estimates (KDEs), as this allowed then (1) to test whether individuals are site-faithful across trips and years and thus for us to retain only independent trips, (2) to test whether there is spatial and temporal heterogeneity in the spatial data, (3) to derive ICAs, i.e., delineate areas within the KDEs that most of the tracked population uses and so is deemed important for the whole population. All analyses were performed in R v4.1.0 (R Development Core Team, 2021), with functions from the R package *track2KBA* (Beal et al., 2021b).

For all subsequent analyses, we considered both 50% and 75% Kernel Density Estimates (KDEs). The choice of 50% KDEs (i.e., the smallest area on which the probability of finding an individual is 50%) was driven by the fact that this level best represents the core areas of activities for our population of Scopoli's shearwaters (see **Figure S3**, following BirdLife International, 2009) and is the usual level used when

proposing conservation areas (Beal et al., 2021b). However, we also used 75% KDE as this may lead to more unified (i.e., less divided) ICAs than 50% KDEs (see Discussion), and it might be advisable to focus not only on the core areas of activities (typically related to foraging areas) but also areas used for travelling back-and-forth from the colony and those used for rafting. All KDEs were derived at the trip level, with the smoothing factor *href* (determined using the *tripSummary* and *findScale* functions; see **Table S2** for the values *href* found for each sub-sample), and a resolution of 0.75 km. As already discussed in (Beal et al. 2021b), the choice of smoothing factor and resolution is crucial as these will affect the size and the precision of the KDEs and ICAs. It is thus important to select them based on the biology of the species and the aim of the conservation actions. Here, we chose *href* (instead of the *mag* value provided by the *findScale* function for instance) because our aim was to derive ICAs encompassing not solely foraging sites, but any important area used by shearwaters for foraging, resting, and travelling. This is also why we retained all sampled locations (and not only the ones corresponding to foraging behaviour; except locations within 5 km of the colony, to release some of the emphasis on the colony for this central place forager). We chose a resolution of 0.75 km based on preliminary analyses and graphical assessment (see **Figure S4**): this resolution precisely enough fit shearwaters' movements here, while limiting computational time.

We initially relied on 397 foraging trips performed by 73 individuals. We first tested if, for a given year and sub-colony, individuals were faithful to foraging sites as this would lead to autocorrelation among consecutive foraging trips of a same individual (function *indEffectTest*). In all but two combinations

of years and sub-colonies, individuals showed site fidelity across foraging trips ($p > 0.1$ for Barrettini in 2013 and 2019, with both 50% and 75% KDEs; $p < 0.003$ for all other cases). We thus down-sampled trips until site fidelity was no longer significant: we retained either all trips (Barrettini in 2013 and 2019), every second trip (Spargiotto in 2019), every third trip (Barrettini in 2018), every fourth trip (Spargiotto in 2018), or only one trip per individual (Spargiotto in 2013). Since some individuals were tracked in more than one breeding season, we ensured that individuals were not site faithful across years. To do so, we followed the same principle as the one proposed in the *indEffectTest* function. We estimated, separately for each individual sampled several years ($N=17$), the overlap between its KDEs derived at the trip level and differentiated between and within year overlaps. We then combined the overlap values of all 17 individuals and compared between and within year overlaps with a bootstrap Kolmogorov-Smirnov test (1000 iterations, $p > 0.07$). This allowed us to consider the foraging trips performed in different years as independent. In the end, we analysed 199 foraging trips, performed by 91 unique individual-year entities.

Detecting Spatial and Temporal Heterogeneity

To detect spatial heterogeneity, we tested whether individuals breeding in the two sub-colonies spatially segregated while foraging at sea, to assess the need of implementing the rest of the analyses at the sub-colony level. We used the function *indEffectTest* to test whether within- and between-sub-colony overlaps of individual KDEs were different. We expected here the within-sub-colony overlaps to be significantly greater than between-sub-colony ones, which would indicate that the area used by individuals (i.e., KDEs) from the same sub-colony were more similar than areas used by individuals from different sub-colonies. We performed this test for each year separately. To detect temporal heterogeneity, we used the same method and tested whether within- and between-year overlaps of individual KDEs were different. We performed this test for each sub-colony separately.

Deriving ICAs

We identified ICAs following the methodology initially developed by Lascelles et al. (2016), and recently improved by Beal et al. (2021b). This approach implied three steps (see **Figures S1, S2** for a graphical summary). First, based on this restricted dataset (i.e., with down-sampled independent trips) we aimed to identify KDEs at the foraging trip level (function *estSpaceUse*). Second, we ensured that sampled individuals were representative enough of their sub-colony by assessing the representativeness of the samples from each year and each sub-colony separately using the function *repAssess* and the KDEs (with 600 iterations, because the stability of estimates was reached from this number onwards for the smallest sample size, see **Figure S5**). Third, we identified ICAs with the *findSite* function, which delineates areas that are used by a certain percentage (at least 10%) of the tracked individuals given the location of the KDEs, and so are deemed important for the whole

population. This percentage is given by the argument 'thresh' in the *findSite* function. Here, we retained the default value for 'thresh', which adapts the percentage threshold depending on the representativeness of the sample (20% threshold for 70-80% representativeness, 12.5% threshold for 80-90% representativeness, and 10% for representativeness above 90%; see Appendix S1 in Lascelles et al., 2016; Beal et al., 2021b). We chose not to provide a total population size for the function *findSite*, as this parameter is only used for visualizing the number of individuals in the entire population predicted to use the identified ICA (instead of the default percentage of the tracked population). In other terms, the choice of population size does not affect in any way the contour of the ICA itself, which was the object of focus here. We could then extract the contour of the ICAs (**Figure S2**). This 3-step procedure – deriving KDEs, assessing representativeness, and deriving ICAs – was applied for each year and each sub-colony separately given the presence of spatial and temporal heterogeneity in foraging areas (see previous paragraph and results).

Comparing ICAs Across Sub-Colonies and Years

The function *indEffectTest* applied to individual KDEs (paragraph 2.5) allowed to test for the presence of spatial and temporal heterogeneity in foraging sites. Yet, whether these differences in overlaps of KDE within and between sub-colonies or years (see results) cascade to actual low overlap of ICAs (i.e., the parts of the KDEs supposedly used by the majority of the population), between sub-colonies or years, remained to be explored. Our first aim was then to quantify potential differences in ICAs resulting from accounting for a single sub-colony (spatial heterogeneity) or a single year (temporal heterogeneity). To quantify differences due to spatial heterogeneity, we estimated, for a given year, the overlaps between ICAs of both sub-colonies (e.g., Barrettini vs. Spargiotto in 2013). To quantify differences due to temporal heterogeneity, we estimated, for a given sub-colony, the overlap between ICAs obtained for different years (e.g. 2013 vs. 2018 for Barrettini). The proportion of overlap $Overlap_{i,j}$ between pairs of ICAs (i, j) was estimated as:

$$Overlap_{i,j} = \frac{A_{i \cap j}}{A_{i \cup j}} = \frac{A_{i \cap j}}{A_i + A_j - A_{i \cap j}}$$

A referring to the areas of the ICAs of i or j, their intersection ($i \cap j$), and their union ($i \cup j$).

Does Appropriately Accounting for Spatial and Temporal Heterogeneity Really Make a Difference?

Our second aim was to propose a method to derive a single and reliable ICA while accounting for the spatial and temporal heterogeneities in the data (method A) and show why this is better than ignoring these heterogeneities (method B). Once one has sampled several years and/or multiple sub-colonies, one can identify a global ICA by either (A) merging the areas found for each year and sub-colony separately, or (B) directly identifying

an ICA from the larger dataset comprising all years and sub-colonies (i.e., not accounting for possible temporal or spatial heterogeneity). We compared then the differences in total areas and the overlap between the ICAs obtained with these two (A, B) alternative approaches, 1) for each year, pooling both sub-colonies, 2) for each sub-colony, pooling the three years, and 3) for the three years and both sub-colonies pooled.

RESULTS

Spatial and Temporal Heterogeneity

Considering the tracks of each foraging trip (**Figures 1** and **S6**), there was a clear segregation of used areas between individuals breeding in the two sub-colonies: individuals from Spargiotto moved mostly south-west of the colony, while individuals from Barrettiini moved towards north-east. Accordingly, overlap of KDEs was greater within than among sub-colonies ($p < 0.001$ for each year and both for 50% and 75% KDEs). In other words, individuals breeding in the same sub-colony used more similar areas during foraging trips than individuals breeding in different sub-colonies. Overlap of KDEs was also greater within than among years for individuals breeding in Spargiotto (at least for core areas: $p < 0.001$ for 50% KDE, and marginally for larger areas: $p = 0.07$ for 75% KDE). Yet, this was not the case for individuals breeding in Barrettiini ($p > 0.5$ for both 50% and 75% KDEs). Given this spatial and (partially) temporal heterogeneity in the spatial data, we implemented the rest of the analyses for each sub-colony and year separately.

Samples' Representativeness for ICA Derivation

Representativeness was generally high (**Table S3**), and above 72% for all the year- and sub-colony specific sub-samples, except Spargiotto in 2019 when considering 50% KDEs. This latter sample, which was the smallest of all years and sub-colony combinations (**Table S1**), reached only 45.9% of representativeness and was thus discarded for the subsequent corresponding ICA estimations. Foraging trips from Spargiotto in 2019 were still considered for ICAs estimation based on 75% KDE (with a representativeness of 72.8%).

Comparing ICAs Across Sub-Colonies and Years

In accordance with the significant spatial and temporal heterogeneity found in section 3.1, the overlap between ICAs from different sub-colonies or years was rather low (below 0.5; **Figure 3**). In particular, the overlap between ICAs of the two sub-colonies was low each of the three years, whether considering ICAs based on 75% KDE (**Figures 2, 3**) or ICAs based on 50% KDE (**Figures S7** and **3**). ICAs' shape and location were rather different for each of the three years of the study, and this was particularly striking for 2019 compared to the other years (**Figures 2** and **S7**). Accordingly, the overlap between ICAs from different years were relatively low (**Figure 3**): from 0.16 to

0.49 for ICAs based on 75% KDE, and from 0.01 to 0.40 for ICAs based on 50% KDE.

Does Appropriately Accounting for Sub-Colony- and Year-Related Heterogeneity Really Make a Difference?

Combining data from different sub-colonies and/or years before deriving ICAs (method B) usually led to smaller ICAs than when merging the ICAs obtained for these years and/or sub-colonies (method A; **Table 1**; **Figures 2, 4, S7** and **S8**). These differences were particularly striking when ignoring both the spatial and temporal heterogeneity: pooling data from both sub-colonies and all years led to ICAs that were more than 70% smaller than when merging the ICAs from each of the sub-colonies each year (**Figures 4C, S8C** and **Table 1**). One exception was the comparison of ICAs based on 50% KDEs for both sub-colonies in 2013: the area obtained by merging the ICAs of Barrettiini and Spargiotto was 16% smaller than the ICA obtained by pooling initial data (**Table 1**). Yet, this peculiarity did not hold for ICAs based on 75% KDEs (**Table 1**). In 2019, the number of foraging trips from individuals of Spargiotto was so low compared to Barrettiini (10 versus 64 trips) that the potential ICA derived from data of Spargiotto only was almost not represented at all when combining both sub-colonies (**Figure 4C**).

DISCUSSION

The main challenge when deriving ICAs from tracking data is to obtain individual at-sea distributions that are representative, both in time and space, of the rest of the population. This implies to collect data over multiple time-steps (to account for temporal heterogeneity in at-sea distribution, here across years) and, for colonial breeders, which tend to spatially segregate in response to intraspecific competition, to collect data from individuals breeding in different parts of the colony. While spatial and temporal heterogeneity in at-sea distribution received recent attention, to what extent they may affect the location and size of ICAs and how to appropriately account for these effects remained to be explored. Here, we found that Scopoli's shearwaters breeding in two neighbouring islets spatially segregated while foraging at sea: those breeding in the western most islet foraged mostly south-west of it, while individuals breeding in the eastern islet foraged mostly towards north and east. This segregation of foraging grounds at a small spatial scale (few kilometres, while these birds forage hundreds of kilometres away from their nest) complements the growing body of literature showing similar patterns (Hipfner et al., 2007; Masello et al., 2010; Bogdanova et al., 2014; Kuhn et al., 2014; Waggitt et al., 2014; Ceia et al., 2015; Sánchez et al., 2018; Ito et al., 2020; Pereira et al., 2022). The areas used (as measured by KDEs) by members of one sub-colony differed across years. As a result, the overlaps between ICAs implemented per year and sub-colony were relatively low (from 0 to 0.49 overlap). We also highlighted that merging ICAs obtained for each year and sub-colonies (method A) resulted in larger ICAs than when ignoring

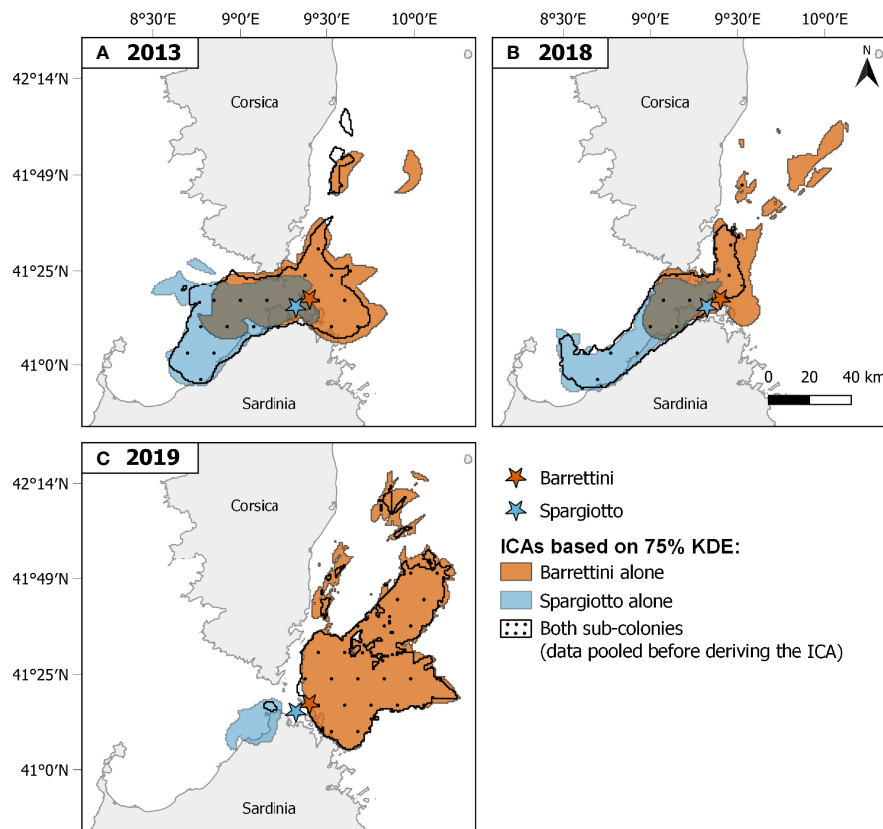


FIGURE 2 | Important Conservation Areas (ICAs) identified for both sub-colonies and years separately (**A**: 2013, **B**: 2018, **C**: 2019). ICAs correspond to areas, within the trip-level 75% Kernel Density Estimates, that are used by a certain percentage of the tracked population, and so are deemed important for the whole population (see main text). ICAs are represented by blue areas for Spargiotto, orange areas for Barretti, and black-dotted areas when ignoring within-colony spatial heterogeneity (i.e., combining data from both sub-colonies before deriving ICAs). Colored stars indicate locations of the corresponding sub-colonies. Sample size of foraging trips considered: Spargiotto: 17 in 2013, 48 in 2018, 10 in 2019; Barretti: 21 in 2013, 39 in 2018, 64 in 2019.

such spatial and temporal heterogeneities in the tracking dataset (method B). We discuss the importance to dynamically account for these and other sources of heterogeneity in tracking data when aiming at deriving sound conservation areas in a changing world.

Obtaining Robust ICAs

We showed that sampling only one year, only one sub-colony, or simply not accounting for spatial and temporal heterogeneity in large multi-scale datasets led to a very partial representation of ICAs, especially so when sample sizes greatly differed across groups. For example, in 2019, we obtained only 10 foraging trips for Spargiotto and 64 for Barretti after accounting for foraging site fidelity and removing correlated trips. These 10 and 64 foraging trips were representative enough of their sub-colony to derive ICAs (72.8% and 94.3% representativeness respectively when considering 75% KDE). When ignoring the spatial heterogeneity and deriving an ICA on the 2019 dataset (method B), we obtained an ICA (based on 75% KDE) encompassing nearly the entire ICA found for Barretti alone, and almost none of the ICA found for Spargiotto alone (Figure 2C). In 2013, when sample sizes were more balanced

across sub-colonies, we did not find this effect (Figure 2A). When sample sizes differ across groups (sub-colony and year here, but it could be sex for example), we advise to merge ICAs derived for the different groups, as it allows for usually more extended and representative ICAs. Indeed, up to 75% of the ICAs area was lost when not accounting for these sources of heterogeneity, biasing the location of ICAs toward those found in years or sub-colonies with the most foraging trips. In only one occasion, the ICA derived by pooling initial data was larger than the ICA obtained by merging group-specific ICAs (Table 1, Figure S7A). Surprisingly, this larger ICA also included an area just north of Barretti, which was not included in any of the sub-colony or year-specific ICAs (based on 50% KDE), and in that respect may not be that relevant conservation-wise if only a minority of the tracked breeders used it each year (less than 10%, the chosen minimum threshold for ICA definition here). The methodology we propose, by allowing the derivation of reliable ICAs from unbalanced sample sizes, should be of broad use for most conservation actors, which often do not have access to spatially and temporally balanced samples. Another possibility to account for spatial heterogeneity in the data is to use a predictive modelling approach, when individuals are known to select

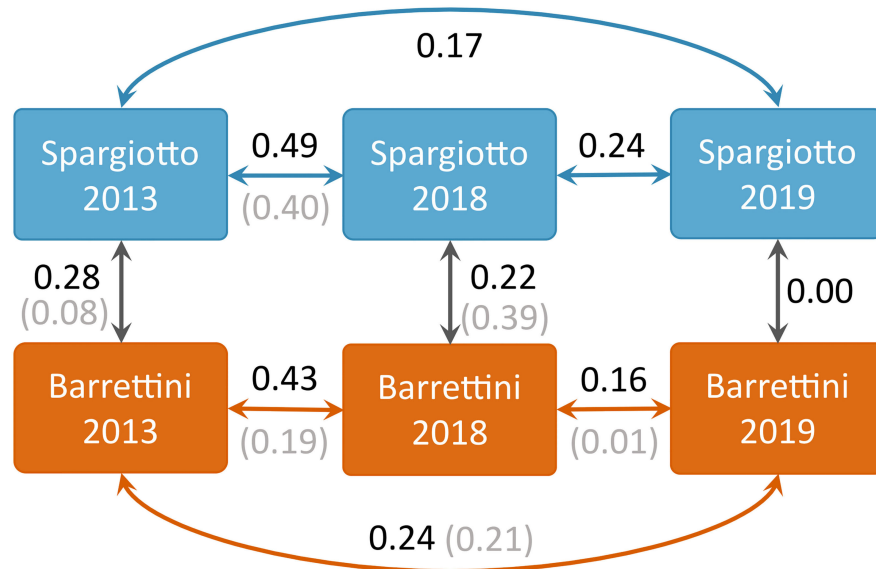


FIGURE 3 | Overlap values between ICAs derived for different sub-colonies and years. Values in black correspond to ICAs based on 75% KDEs, while values in grey (in parentheses) correspond to ICAs based on 50% KDEs.

similar physical habitat features when foraging (e.g., similar bathymetry, Ceia et al., 2015), an hypothesis that would remain to be tested across different sub-colonies.

Testing for within-colony spatial heterogeneity is a fundamental step before planning any conservation action, but this may be far from easy. The main obstacle for such investigation is practical: it can be highly challenging to

capture and tag wild animals at their natural breeding sites. For example, not all breeding sites, beaches, or cliffs might be accessible, and/or one might focus on individuals located at the edge of a colony to minimize disturbance to the rest of the group. In that respect, the Scopoli's shearwater colony studied here is ideal: pairs breed in well separated burrows between rocks on the ground, distant from each other by few meters, in

TABLE 1 | Comparison of ICAs when accounting or not for spatial and temporal heterogeneity in the dataset.

	ICA area (km ²) based on two methods		Difference in ICA area	Percentage of the largest ICA lost	Overlap between ICAs	Figure
	(A) ICAs merged	(B) Data pooled	(A) - (B)	1-(A)/(B)	$\frac{\cap (A)(B)}{\cup (A)(B)}$	
<i>ICAs based on 75% KDEs</i>						
2013 across both sub-colonies	4 160	3 175	985	23.7 %	0.72	2a
2018 across both sub-colonies	3 117	2 017	1 100	35.3 %	0.60	2b
2019 across both sub-colonies	4 766	3 494	1 272	26.7 %	0.72	2c
Spargiotto across the 3 years	2 667	1 962	705	26.4 %	0.66	4a
Barrettini across the 3 years	6 360	4 171	2 189	34.4 %	0.60	4b
Both sub-colonies across the 3 years	7 786	2 250	5 536	71.1 %	0.29	4c
<i>ICAs based on 50% KDEs</i>						
2013 across both sub-colonies	1 368	1 586	-218	-16.0 %	0.63	S7a
2018 across both sub-colonies	802	586	216	26.9 %	0.64	S7b
2019 across both sub-colonies	647	455	192	29.6 %	0.67	S7c
Spargiotto across the 3 years	1 273	974	299	23.5 %	0.68	S8a
Barrettini across the 3 years	1 154	406	748	64.8 %	0.34	S8b
Both sub-colonies across the 3 years	2 065	527	1 538	74.5 %	0.24	S8c

Method (A) "ICAs merged": we accounted for spatial and temporal heterogeneity by merging ICAs from different years and/or sub-colonies a posteriori. Method (B) "Data pooled": we discarded such heterogeneity by pooling data from different sub-colonies and/or years before deriving the corresponding ICA. Besides the three comparative metrics (difference, percentage of loss, and overlap), we provide references to the corresponding Figures illustrating these comparisons.

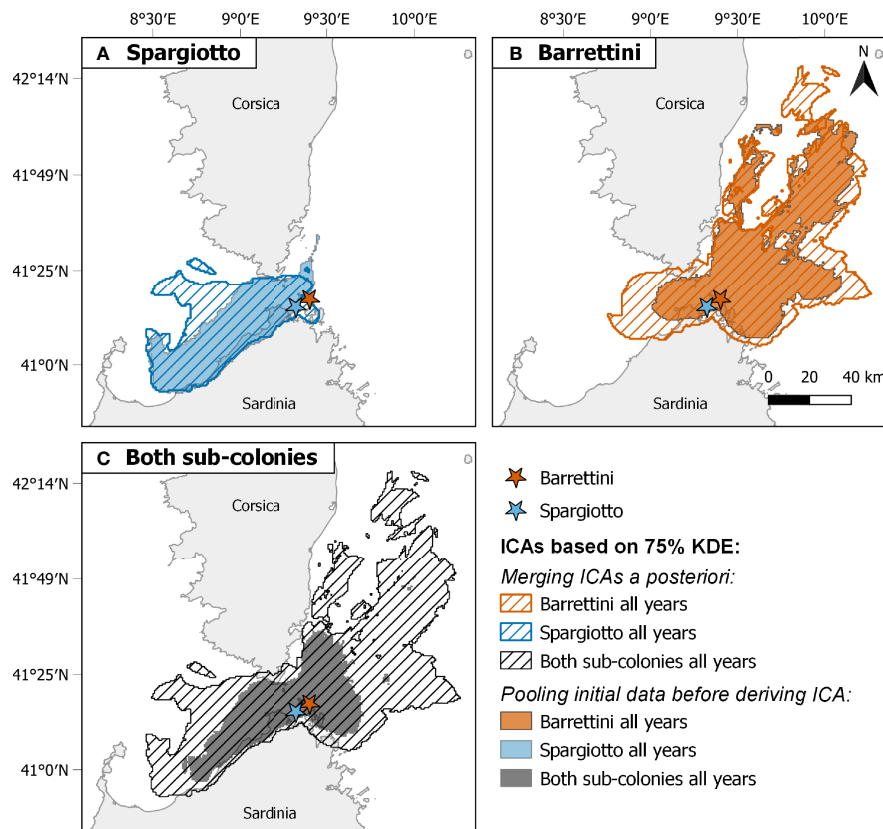


FIGURE 4 | Comparison of among-year and between-sub-colony Important Conservation Areas identified with two different methods: merging *a posteriori* ICAs derived from different years and/or sub-colonies (dashed areas) or pooling data before deriving a single corresponding ICA (filled areas). Comparisons are shown for **(A)** Spargiotto, **(B)** Barrettini, and **(C)** both sub-colonies. ICAs are based here on 75% Kernel Density Estimates. Sample size of trips considered: 75 for Spargiotto, 124 for Barrettini.

easily accessible islands. As in previous studies (Bogdanova et al., 2014), we advocate whenever possible to collect spatial data from various locations of the colony, to be able to generalize the detected exploited areas. Yet, if collecting spatial data from several parts of a colony is not feasible, we propose several other options. For example, if individuals tend to follow the route taken by conspecifics when departing from the colony or closely located rafts (Weimerskirch et al., 2010; Thiebault et al., 2014), observing the departure and returning angles of individuals from different sub-colonies might inform on the possibility that members of different sub-colonies segregate at sea. If one can only sample one part of a colony but knows its extent, it is possible to use a modelling approach to test for spatial segregation. Indeed, one can test whether the observed distribution corresponds to that of simulated tracks ignoring between-sub-colony competition for example (Ito et al., 2020), or, on the contrary, whether the observed distribution is biased towards one area, away from the rest of the colony (similar to colony-level simulations in Aarts et al., 2021). If spatial segregation of foraging grounds is then suspected, care should be taken when deriving ICAs. The combination of accurate resource availability maps and

modelling approaches accounting for competition between-but also within-colonies (e.g. Wakefield et al., 2011; Aarts et al., 2021), with a back-up verification on existing spatial data, may open exciting perspectives for accurately deriving ICAs from partial datasets.

Temporal Heterogeneity: Conservation in a Changing Environment

Our results highlight the importance of dynamic placement of ICAs given that environmental changes affect the distribution of the sentinel species and their prey (Perry et al., 2005; Poloczanska et al., 2016; and see Cashion et al., 2020 for a thorough discussion on the importance of dynamic ICAs in marine ecosystems). Indeed, we observed among-year differences in the areas exploited by Scopoli's shearwaters from La Maddalena Archipelago, which is not surprising given their foraging habits. Scopoli's shearwater feed mostly on plankton and small pelagic fishes (Grémillet et al., 2014), two resources whose distribution can vary between years (Marty et al., 2002; Saraux et al., 2014). Shearwaters also exploit discards from fishing vessels (Cecere et al., 2015; Cianchetti-Benedetti et al., 2018), whose locations are naturally dynamic and rather stochastic (changing within few minutes or hours) compared to the temporal

scale of shearwaters foraging trips (1–20 days, Cecere et al., 2014). Yet, Scopoli's shearwater breeding in the eastern sub-colony showed no significant difference in used areas (KDE) across the three studied years, unlike individuals breeding in the western sub-colony. One hypothesis could be that resources in the northern and eastern part of the colony were more stable across years than those located west, yet we unfortunately do not have any empirical evidence to formally test that. Other populations of the same species also showed both consistency (Grémillet et al., 2014) and differences (Courbin et al., 2018) in the areas exploited across years, which may suggest either a stochastic effect of the sampled year, or geographical differences in resources availability. Such discrepancies among populations also highlight the importance of testing for temporal and spatial heterogeneities when multi-year or sub-colony data are available, and not solely rely on findings from other populations or years. It is to be noted that we exclusively used data from the chick-rearing stage, and not from the incubation stage, because individuals are more spatially constrained when they must combine self-feeding with regular trip to the colony to provision offspring.

Among-year differences in exploited areas may arise from environmental stochasticity and longer-term environmental changes. Long-term investigation of variation in foraging behaviour in seabirds are still scarce, but one striking example, which also investigates sub-colony segregation, is the 15-year study of European shags in Scotland (Bogdanova et al., 2014). This study also provides a methodological framework enabling to test how many years are necessary to accurately represent the population-wide used areas. Our approach here that complements that previous study, shows how to best account for temporal heterogeneity when one does not have access to enough data to fully and certainly represent the population at-sea distribution (yet with representative enough within-year sub-sample). With three years of data and slightly contrasting sample sizes (Table S1), we cannot exclude that the observed temporal heterogeneity is the results of stochasticity. Yet, longer term datasets will certainly become more common in the coming years and will allow for a thorough assessment of longer-term temporal heterogeneity and account for that when deriving ICAs.

Other Sources of Heterogeneity

Our study focused on the effect of sub-colony and temporal heterogeneity in the implementation of ICAs. Yet, spatial segregation can also occur between sexes (Catry et al., 2006), age classes (Pelletier et al., 2014; Haug et al., 2015; Pettex et al., 2019), or personality types for example (Krüger et al., 2019). Here, the sex-ratio in our sample was well balanced (0.5 on average), and sampling was performed randomly regarding individuals' age and personality (random selection of individuals among the captured ones). Depending on the population or species, any source of heterogeneity can be accounted for with the same procedure as the one proposed here (see Figure S1 for a summary).

One aspect that should also be considered is the focus of the conservation actions: either on the foraging areas exclusively, or on any exploited areas, even the ones used for travelling between patches or rafting. Here, we chose to rely on any used areas (i.e., all GPS positions obtained, whether they corresponding to

foraging, travelling, or resting events), which led to a specific emphasis really close to the colony (Figures 2, 4, emphasis reduced by the withdrawal of locations within 5 km of the colony, see methods). This was motivated by the fact that shearwaters may suffer from disturbance both while foraging and travelling (e.g., Rodríguez et al., 2015; Dierschke et al., 2016; Genovart et al., 2018). Yet, depending on the species and the conservation context, it is possible to select only specific locations (e.g., foraging vs. non-foraging, core-foraging areas vs. home-range). We therefore focused on ICAs based on 75% KDE (larger scale used areas), but nonetheless compared them to ICAs based on 50% KDE (considered as core used areas) which are more classically used. The ICAs based on core used areas (50% KDE) were naturally smaller than ICAs based on larger used areas (75% KDE) but they were also interestingly more divided (see Figure S9 for a graphical representation of these ICAs). ICAs based on larger used areas enabled to integrate corridors of movement between core used areas (as typically seen in Spargiotto in 2018 or Barretti in 2019, Figure S9). Therefore, for conservation actions aiming at preserving any used sites, 75% KDE might lead to more ecologically relevant ICAs.

Our study system also exemplifies the importance of deriving reliable ICAs in international contexts (here Italy and France, see also for instance Beal et al., 2021a; Davies et al., 2021), which may imply international agreements, and, here, would require a careful assessment of foraging distribution of individuals breeding in the nearby Lavezzi archipelago. Furthermore, we focused here on one species. Yet, using data from other species sharing the same foraging habitats (for instance here Yelkouan shearwaters *Puffinus yelkouan*) would also constitute a critical step to apply conservation actions benefiting multiple species.

CONCLUSION

In the context of the current biodiversity crisis, it is crucial to derive efficient tool to protect ecosystems. Yet, individual or population behavioural differences can impair the efficacy of protected areas. To derive sound conservation areas from GPS tracking data, it is essential to account for the fact that the precise individuals we sampled, at that precise moment, might not necessarily be representative of the whole target population. We show here that accounting for within-colony spatial segregation, as well as seasonal differences in foraging site selection, is key to derive ecologically representative ICAs. Besides adding to the growing body of evidence of spatial segregation at the sub-colony level, our study provides a practical and comparative guideline on how to best account for inherent heterogeneity when aiming to derive ICAs. The use of recently developed standardized statistical procedures (Beal et al., 2021b), combined with such careful consideration of the species ecology and population structure, should help improving the conservation of (marine and terrestrial) ecosystems. The growing evidence of small-scale spatial segregation also raise fascinating ecological questions regarding the biological meaning of the distinction between colonies and sub-colonies, as well as the mechanisms behind such small-scale spatial segregation.

While beyond the scope of this study, answering these questions will greatly contribute to the understanding of such spatial pattern and thus improve the conservation actions taken to protect colonial species. Considering the human-induced threats posed to the environment, future studies and predictions will be essential to adapt the current tools to rapidly changing ecosystems, in which species, populations, and individuals differ in plasticity and adaptability.

DATA AVAILABILITY STATEMENT

The tracking data are available in the BirdLife Seabird Tracking Database (<http://www.seabirdtracking.org/>).

ETHICS STATEMENT

Capture, handling, ringing and tagging procedures were performed by the Italian Institute for Environmental Protection and Research (ISPRA), under the authorization of Law 157/1992 [Art.4(1) and Art 7(5)], which regulates research on wild bird species. We were granted permission to access and work on the islets by the Parco Nazionale dell'Archipelago di La Maddalena under the agreement made with ISPRA. The authors assert that all procedures contributing to this work comply with the ethical standards of ASAB/ABS guidelines for the fair and ethical treatment of animals in behavioural research.

AUTHOR CONTRIBUTIONS

JM and JC conceived the presented idea. JM, DR, SI, and JC contributed to conception and design of the study. FP, CC, AB,

and JC collected the data. FP, AB, SI, and JC prepared the data and made preliminary analyses. JM performed the statistical analyses, wrote and revised the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.854826/full#supplementary-material>

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Exploring the Use of Seabirds as a Dynamic Ocean Management Tool to Mitigate Anthropogenic Risk to Large Whales

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Vessel strike and entanglement in fishing gear are global threats to large whales. United States management actions to reduce human-induced serious injury and mortality to large whales have been inadequate, partially due to static, spatial protection schemes that fail to adjust to distribution shifts of highly mobile animals. Whale conservation would benefit from dynamic ocean management, but few tools exist to inform dynamic approaches. Seabirds are often found in association with whales and can be tagged at lower cost and in higher numbers than whales. We explored the use of satellite-tagged seabirds (great shearwaters) as dynamic ocean management tools for near real-time identification of habitats where humpback and North Atlantic right whales aggregate, potentially increasing anthropogenic risk. We identified shearwater habitat use areas in the Gulf of Maine with 50% kernel density utilization distributions at yearly, monthly, and weekly scales using satellite-telemetry data from 2013–2018. We quantified overlap using whale sightings and whale satellite telemetry data at two spatial scales: Stellwagen Bank National Marine Sanctuary and the Gulf of Maine. Within the sanctuary, shearwaters overlapped with >50% of humpback sightings in 4 of 6 (67%) years, 15 of 23 (65%) months, and 50 of 89 (56%) of weeks. At the Gulf of Maine scale, shearwater use areas overlapped >50% of humpback sightings in 5 of 6 years (83%) and 16 of 22 (73%) months, and encompassed humpback 50% utilization distributions (based on satellite telemetry) in 2 of 3 (66%) years and 7/12 (58%) months analyzed. Overlap between shearwaters and right whales was much lower, with >50% overlap in only 1 of 6 (17%)

years and 3 of 23 (13%) months. These initial results demonstrate that satellite-tagged shearwaters can be indicators of humpback whale habitat use in both space and time. With further study, tagged shearwaters may provide near-real time information necessary to operationalize dynamic management to mitigate human impacts on humpback whales.

Keywords: great shearwaters, humpback whales, vessel strike, entanglement, climate change, tracking, biologging, Stellwagen Bank National Marine Sanctuary

INTRODUCTION

Vessel strikes and entanglement in fishing gear are global conservation concerns for baleen whales. Interactions with vessels and gear have been documented for nearly all baleen whale species (Laist et al., 2001; van der Hoop et al., 2013), are increasing in some parts of the world (Davies and Brillant, 2019; Santora et al., 2020; Saez et al., 2020) and are the leading sources of human-caused mortality (van der Hoop et al., 2013; Moore et al., 2021; NOAA, 2021a; NOAA, 2021b).

Off the NE U.S., impacts of vessel strike and entanglement to individuals and populations are best documented for humpback (*Megaptera novaeangliae*) and North Atlantic right whales (*Eubalaena glacialis*; hereafter right whales). The number of reported entanglements regularly exceed sustainable levels for both species (van der Hoop et al., 2013; Hayes et al., 2018; Hayes et al., 2021) and scar-based studies suggest that additional events go unobserved and unreported (Knowlton et al., 2012; Robbins, 2012). Lethal and non-lethal vessel strikes are consistently observed for both species (Wiley et al., 1995; Hill et al., 2017; NOAA, 2021a; NOAA, 2021b). Direct mortality and sub-lethal energetic impacts of entanglement have hindered population recovery for North Atlantic right whales (van der Hoop et al., 2016; van der Hoop et al., 2017; Corkeron et al., 2018; Moore et al., 2021).

Many U.S. management actions have been implemented to reduce entanglements and vessel strikes to large whales (NOAA (National Oceanic and Atmospheric Association), 2008; National Marine Fisheries Service, 2014; National Marine Fisheries Service, 2015). However, previous work, recent and/or ongoing Unusual Mortality Events for both species and the continued right whale population decline suggests serious shortcomings in U.S. management (Silber et al., 2012; van der Hoop et al., 2013; van der Hoop et al., 2015; Moore et al., 2021; NOAA, 2021a; NOAA, 2021b; Pettis et al., 2022). While many factors influence outcomes of management decisions, one potential factor hindering success is the spatial and temporal mismatch between management and actual whale distributions.

Mandatory U.S. spatial management schemes do not account for distribution shifts of highly mobile animals that are responding to a dynamic ocean environment. Updates to spatial management often lag years behind actual animal distribution shifts. For example, managed areas and restricted areas aiming to reduce vessel strikes and entanglements in fixed gear fisheries, respectively, off the NE U.S. are based on the historical, seasonal distributions of right whales (**Supplementary Figure 1**; NOAA (National Oceanic and Atmospheric Association), 2008; National Marine Fisheries Service, 2021).

Once established, managed and restricted areas remain in place for the duration of the regulatory period (two to five months or longer if whales remain in the area), even if no whales are present within the boundaries, and do not expand or shift to encompass whales outside the boundaries. In addition, the U.S. lacks mechanisms for implementing temporary, short-term, emergency management measures without a formal rule-making process when whales shift to unregulated areas, which will likely increase with climate-driven changes in oceanography and prey distributions (Davies and Brillant, 2019; Record et al., 2019). Mitigation of vessel strike and entanglement would benefit from a management scheme as fluid in space and time as ocean conditions, mobile species, and human users.

Dynamic ocean management (DOM) aims to meet this need by adaptively matching management strategies to the spatial and temporal scales of dynamic ocean processes, living marine resources, and users. DOM integrates near real-time biological, oceanographic, social and/or economic data to guide flexible management actions that rapidly shift in space and time (*sensu* Hobday et al., 2010). Using near real-time data to tailor management may allow temporal and spatial scales of management areas to dynamically shrink or expand, enabling the most effective protection in terms of mitigating impacts to resources and users. Coupling dynamic strategies with static management areas could preserve benefits of permanent protected areas while filling gaps in protection in response to variable species distributions (Tittensor et al., 2019). Additionally, dynamic management could occur within static protected areas, leveraging previously identified important areas but targeting management actions within them in response to real-time information. The ability to balance ecological and economic values to meet multiple objectives and reduce conflict among stakeholder groups is a major benefit of DOM (Lewison et al., 2015; Maxwell et al., 2015).

A handful of DOM tools and applications are currently in practice (Beacham et al., 2004; Howell et al., 2008; Hobday et al., 2011; Holmes et al., 2011; O'Keefe and DeCelles, 2013; Wiley et al., 2013; Howell et al., 2015; Little et al., 2015; Hazen et al., 2017; Hazen et al., 2018). All these tools collect one or more types of near real-time data and output a product to inform users and managers, but they differ in the complexity of data processing and consideration of user behavior or stakeholder input in the final product (Lewison et al., 2015; Maxwell et al., 2015). Whale Alert and EcoCast are examples of simple and more complex DOM tools, respectively (Wiley et al., 2013; Hazen et al., 2018). Other DOM tools fall within these two extremes; however, no existing DOM tools leverage near real-time locations provided by

satellite-tagged animals to gather data on animal distributions that are current and most relevant for management.

Based on their unique life-history characteristics, seabirds equipped with satellite tags could serve as valuable tools for implementing dynamic management. Procellariid seabirds are highly mobile, enabling them to respond quickly to changing environmental conditions over large spatial scales and their top position in food webs means their location may indicate areas of high forage fish abundance. Their role as ecological indicators (Velarde et al., 2019) position seabirds as attractive sentinels for monitoring changes in marine ecosystems, fluctuations in abundance and distribution of forage fishes, and for identifying areas of high productivity where top predators, including whales and ocean users may congregate. Further, tags applied to seabirds are less expensive, less invasive, and can last longer than tags on large whales.

Great shearwaters (*Ardenna gravis*; hereafter shearwaters) are one of the most common pelagic seabirds in the Gulf of Maine (GOM) (Powers, 1983), including in Stellwagen Bank National Marine Sanctuary (SBNMS), a 2180 km² federal marine protected area (MPA) (SBNMS unpublished data). In the sanctuary, shearwaters overlap with humpback whales. Both species consistently overlap with sand lance (*Ammodytes dubius*), their preferred prey in this region (Payne et al., 1986; Powers et al., 2020; Silva et al., 2020) and shearwaters are often seen foraging with surface-feeding humpback whales. Sand lance are also found in specific, sandy substrates and previous work also shows that humpbacks and shearwaters use many of the same habitats throughout the GOM (Robbins, 2007; Powers et al., 2017; Powers et al., 2020). This suggests that satellite-tagged great shearwaters could indicate humpback whale locations at wider scales, and that some of these static locations may lend themselves to dynamic management. While the idea of investigating the use of tagged shearwaters to locate humpback whale aggregations is supported by previous work, considering tagged shearwaters as indicators of right whales is also of interest for two reasons: 1) they are critically endangered and management tools to drastically reduce vessel strikes and entanglements is desperately needed and 2) right whales and sand lance in the GOM feed primarily on copepods, including *Calanus finmarchicus* (Wishner et al., 1995; Murison and Gaskin, 1989; Mayo and Marx, 1990; Suca et al., 2021), making it plausible that shearwaters feeding on sand lance may overlap with right whales.

Here, our goal was to explore the use of satellite-tagged great shearwaters as a near real-time dynamic management tool to identify habitats where humpback and/or right whales may aggregate and be at increased anthropogenic risk. To this end, we quantified spatial overlap between satellite-tagged shearwaters with both humpback and right whales at multiple spatial and temporal scales to explore potentially feasible management scales, where shearwater distributions could represent management areas.

METHODS

Datasets

We used several existing datasets in our analysis collected throughout the GOM and within SBNMS located in the SW

GOM. The Gulf of Maine represents important foraging habitat for shearwaters, humpbacks, and right whales. We also focused specifically on SBNMS based on previous work identifying strong overlap between shearwaters and humpbacks (Silva et al., 2020), availability of high-resolution sightings data, and its role in marine mammal protection as a MPA. Datasets included: 1) great shearwater satellite telemetry 2) humpback whale satellite telemetry 3) humpback whale sightings in SBNMS 4) humpback whale sightings from Gulf of Maine surveys, and 5) North Atlantic right whale sightings. A brief description of each dataset follows.

Great Shearwater Satellite Telemetry

Shearwaters were tagged off the coast of Massachusetts in the southwestern Gulf of Maine each year from 2013 to 2018 (Powers et al., 2017; Powers et al., 2020). Briefly, we used small vessels to access birds at known foraging areas and attracted birds to the vessel using cut fish and squid. Once they were close enough to the vessel, birds were caught with handled landing nets.

Solar PTT-100 tags (15 g, Microwave Telemetry, 8835 Columbia 100 Parkway, Suites K & L, Columbia, MD 21045, USA) were used with duty cycles of 24-hr [on] (i.e., continuous). Tags were attached dorsally, central to the body mass of the bird below the nape and between the wings, using four subcutaneous sutures (Prolene suture 4.0 Ethicon) as per MacLeod et al. (2008), and represented less than 3% of body mass for all tagged birds to minimize effects on flight efficiency (see Phillips et al., 2003). Tags were typically deployed in July except for 2017 when birds were tagged in August. Data from 58 birds were used in analyses.

Humpback Whale Satellite Telemetry

Humpback whales were tagged in the SW GOM in 2013, 2015, and 2018 as part of a study to evaluate the effectiveness of satellite tags and their impacts (Robbins et al., 2013). Because part of the study design involved follow-up monitoring of tagged whales to assess and evaluate impacts, individuals were prioritized for tagging based on known demographic traits and re-sighting history (Robbins et al., 2013). Therefore, tagging was not random, and we note that distributions of tagged whales may be representative of humpbacks with high fidelity to the southwestern GOM and not necessarily of the entire GOM population. Location-only, consolidated (type C, Andrews et al., 2019) implantable Argos satellite tags were deployed using a pneumatic line-thrower (Heide-Jorgensen et al., 2001) as described in Robbins et al. (2013). Tags were programmed to transmit daily from 06:00-18:00 hours GMT with a maximum of 500 transmissions per day. Data from 38 whales were used in analyses.

Humpback Sightings Within SBNMS

We used opportunistic sightings of humpback whales from whale watching trips and research cruises in SBNMS from 2013-2018. Near daily whale watching trips run from several Massachusetts ports and frequent the sanctuary. Sightings data, including identifications of individual humpbacks, are shared with and compiled by the Center for Coastal Studies

Provincetown. Research cruises are run by the Center for Coastal Studies with the goal of photo-documenting and identifying as many individual humpbacks as possible. Therefore, cruises were not standardized. To eliminate duplicate sightings and over-inflation of numbers, we chose one sighting of each individual whale, per day.

Humpback Sightings From GOM Surveys

Sightings data were collected during annual humpback whale population surveys conducted by the Center for Coastal Studies' from Nantucket, Massachusetts to Nova Scotia, Canada. We note that the survey is not standardized but designed to target historical humpback whale aggregation sites (banks, ledges, etc.) within the GOM and Bay of Fundy to photographically document as many individuals as possible. Survey effort varies somewhat each year based on weather and resources and regional effort was expended proportional to encountered whale densities. Effort was greatest in July-August and only extended into October in some years. Locations of individually identified humpback whales were used in analyses. To avoid duplicate sightings and over-inflation of numbers, we chose one sighting of each individual whale, per day. We used a 10 km buffer around ship GPS locations to create polygons to visually represent yearly survey effort.

North Atlantic Right Whale Sightings

We used right whale sightings curated by the North Atlantic Right Whale Consortium (NARWC). These data are a combination of opportunistic, aerial and shipboard sightings from 2013-2018 (North Atlantic Right Whale Consortium, 2021). Sightings data included the number of individual right whales documented at each location. To make data comparable with the humpback sightings data (number of individuals), we duplicated sightings locations based on the number of individuals recorded so that each individual whale had its own unique record.

Data Analysis

We limited our analysis to the months of July-October, months in which data were available from tagging, surveys and opportunistic platforms. Our study focused on the GOM (including Georges Bank). We defined the GOM extent as 40° - 45° latitude and west of -65° longitude and all data outside these bounds were excluded.

We included all Argos location classes from satellite telemetry data (3, 2, 1, 0, A, B) in our analysis. Bursts of points, which are common in Argos datasets when multiple location messages are received over short periods of time, were thinned to avoid bias. For each tagged individual (birds and whales), a threshold of 0.2 for the median sampling interval was used to identify a burst of points. Bursts were thinned to one location.

Utilization distributions (UDs) for 50% kernel density isopleths were derived for shearwaters and humpback whales using satellite telemetry data with the *adehabitatHR* package (Calenge, 2006) in R 3.6.2 (R Core Team, 2019) using Universal Transverse Mercator (UTM) projections. We combined shearwater data for each year, month, and week across the

study period and created 50% UD for each temporal scale. Since the computation of the kernel density UD is sensitive to the number of locations, we excluded weeks that had less than 100 shearwater locations. Range size for each UD and the number of Argos locations used to construct the UD was also calculated. We created 50% UD using the same procedure for satellite tagged humpback whales in each year and month of the study period.

We quantified spatial overlap between shearwaters and whales by calculating the percentage of humpback or right whale sightings (here, each sighting is an individual) or the humpback UD that fell within the shearwater UD. We calculated overlap between shearwaters and humpback whales in each year and month at the SBNMS and GOM scales using sightings data and satellite telemetry data. The high resolution (near-daily) of sightings data within SBNMS allowed us to also calculate weekly overlap in the sanctuary. For right whales, we calculated overlap with shearwaters for each year, month, and week throughout the GOM. We chose to quantify spatial overlap with simple percentages to accommodate multiple data types and to provide an easily interpretable metric that takes advantage of the unique strength of our whale data and their applicability to near real-time management; namely, high resolution sightings of individually identified humpback whales.

RESULTS

Numbers of shearwaters tagged each year ranged from eight to eleven (**Table 1**). However, the number of tags in the study area decreased over time for a variety of reasons, including birds leaving the area or tag failures (**Table 2**). In some years, weekly UD relied on as few as two individuals and ~ 200 Argos locations (**Supplementary Tables 1-6**). Humpbacks were tagged in only three years and numbers of tagged individuals each year ranged from seven to 20 (**Tables 1, 2**). Humpback and right whale sightings varied across years, months and weeks (**Tables 1, 2**). Only one month (GOM data) and two weeks (SBNMS data) had zero humpback sightings, while many weeks had zero, one or two right whale sightings (**Supplementary Tables 1-6**).

Annual Overlap

Annual overlap between shearwaters and humpbacks was high in SBNMS, except for 2013 and 2018. No tagged shearwaters used the sanctuary in 2013 and minimal use in 2018 resulted in no overlap for these years. From 2014 to 2017, 91-100% of sightings within SBNMS overlapped with great shearwater areas (**Supplementary Figure 2**). Similar patterns in overlap were observed in most years throughout the GOM. From 2014-2017, 77%-88% of sightings fell within shearwater UD. The lowest overlap occurred in 2018 (26%). Overlap in 2013 was much higher (80%) at the GOM scale (**Supplementary Figure 3**). While the number of humpback sightings was typically greater in SBNMS, higher number of whale sightings in the GOM in 2013 (SBNMS = 341, GOM = 808) show movement of humpbacks to the south. This is supported by telemetry data, with the entire humpback UD encompassed within the shearwater UD (**Supplementary Figure 4**).

TABLE 1 | Tagging and sightings data summaries used in annual calculations for each year 2013–2018.

	2013	2014	2015	2016	2017	2018
Great shearwaters tagged	10	11	10	10	9	8
Argos locations used to build shearwater UD	10226	12192	8900	10826	9430	7816
Area of shearwater UD (km ²)	23393	32297	24235	19805	19301	26140
Humpback whales tagged	7	–	20	–	–	11
Argos locations used to build humpback whale UD	5169	–	14033	–	–	3381
Area of humpback whale UD (km ²)	866	–	6169	–	–	21266
Humpback whale sightings (SBNMS)	341	1721	1961	2624	1400	1569
Humpback whale sightings (GOM)	808	335	1114	642	463	564
North Atlantic right whale sightings	151	541	102	584	166	42

Data are from July – October in each year. Humpback whale sightings are daily, unique sightings of individually identified whales. North Atlantic right whale sightings are the number of individuals observed at a single location. To make data comparable with the humpback sightings data, we duplicated right whale sightings locations based on the number of individuals recorded so that each individual whale had its own unique record. UD, utilization distribution.

TABLE 2 | Tagging and sightings data summaries used in monthly calculations for each month 2013–2018.

	Shearwaters tagged	Locations used to build shearwater UD	Area of shearwater UD (km ²)	Humpback whales tagged	Locations used to build humpback whale UD	Area of humpback whale UD (km ²)	Humpback whale sightings (SBNMS)	Humpback whale sightings (GOM)	North Atlantic right whale sightings
2013									
July	10	3714	10310	4	321	573	45	329	15
August	10	3178	24044	7	2914	1093	127	379	36
September	5	2438	29141	5	1731	410	58	99	88
October	3	896	20755	2	203	2594	111	1	12
2014									
July	11	1962	8020	–	–	–	765	34	99
August	11	4964	37024	–	–	–	306	269	398
September	8	3329	28365	–	–	–	440	32	36
October	5	1937	24730	–	–	–	210	0	8
2015									
July	10	2891	9109	8	744	2376	752	318	35
August	10	3253	25041	20	6964	5488	506	595	23
September	5	1609	38675	14	4517	6883	438	172	40
October	4	1147	44289	6	1808	6578	265	29	4
2016									
July	8	3142	10801	–	–	–	949	239	41
August	7	4242	15862	–	–	–	1036	213	301
September	8	2338	33729	–	–	–	479	169	210
October	4	1104	11613	–	–	–	160	21	32
2017									
July	0	0	0	–	–	–	399	135	113
August	9	3277	5244	–	–	–	555	215	45
September	8	2483	41175	–	–	–	106	69	4
October	7	3670	20296	–	–	–	340	44	4
2018									
July	8	2909	10730	9	776	34766	410	216	17
August	4	2185	47406	10	1753	31899	621	270	18
September	5	2063	27327	5	651	5539	331	66	6
October	3	659	22108	2	201	650	207	12	1

Humpback whale sightings are daily, unique sightings of individually identified whales. North Atlantic right whale sightings are the number of individuals observed at a single location. These locations were multiplied by the number of individuals to produce the sightings numbers seen here and to make the whale sightings datasets as similar as possible. UD, utilization distribution. GOM-wide humpback whale survey effort was greatest in July–August and very limited in October in all years.

Data collected throughout the GOM (surveys, telemetry) was able to capture humpback locations and overlap with shearwaters when animals were not using the sanctuary. In 2018, results from all three datasets indicate that humpbacks and shearwaters used different areas. Only 15% of the humpback UD overlapped with shearwater areas in 2018 (**Supplementary Figure 4**). Annual overlap between shearwaters and right whales was much lower. The highest overlap

occurred in 2014 at 67%. Three of six years were less than 35% and two years showed 1% overlap (**Supplementary Figure 5**).

Monthly Overlap

Monthly overlap between shearwaters and humpbacks varied more than annual overlap. In some years monthly overlap was greater than annual overlap, largely due to shifts in numbers of

tagged individuals and locations within the study areas. Highest and most consistent levels of overlap occurred throughout 2014 and 2015 in SBNMS. All months in these two years showed $\geq 95\%$ of humpback sightings within shearwater UD (Figure 1, Supplementary Figure 7). In 2016, overlap was $\geq 90\%$ from July to October, but fell to 29% in October, though many whale sightings fell just outside the shearwater UD (Supplementary Figure 8). Overlap declined slightly overall in 2017, starting at 99% in August and falling to 70% and 74% in September and October, respectively (Supplementary Figure 9). Tagged shearwaters did not use the sanctuary in any month of 2013, resulting in no overlap (Supplementary Figure 6). In 2018, a single tagged bird using SBNMS in October increased overlap from 0 (July–September) to 100% (Supplementary Figure 10).

GOM overlap showed more variability than SBNMS. Monthly overlap was highest throughout 2015, ranging from 79% to 100% (Figure 2), and lowest in 2018 with two months having $\leq 5\%$ of humpback sightings within shearwater areas (Supplementary Figure 15). While 100% of sightings overlapped in October 2018, there were only 12 sightings for comparison in this month. Satellite telemetry data also showed strong overlap in 2015 with shearwater UD encompassing 73%–100% of humpback UD (Supplementary Figure 17) and low overlap in most months of 2018 (Figure 3). Overlap ranged from

0% to 100% in 2013–2014 and 2016–2017 in the GOM with most values $\geq 50\%$ (Supplementary Figures 11–14).

Monthly overlap was much lower for right whales, except for 2014 when overlap in August, September, and October was 66%, 78% and 38%, respectively. Overlap in 2018 for right whales was relatively higher for 2 months when whales moved south of Massachusetts (Supplementary Figures 18–23).

There seemed to be no pattern in monthly overlap across years (Figure 4). Shearwater UD overlapped with SBNMS and GOM humpback sightings in most months throughout the study period (Figure 4). Overlap between shearwaters and right whales was much lower. Most right whale sightings fell outside shearwater areas in most months. Shearwaters and humpbacks showed no overlap in SBNMS and the GOM in 7 of 23 and 2 of 23 months, respectively. Six of 23 months showed no overlap between shearwaters and right whales in the GOM (Figure 4).

Weekly Overlap

We examined weekly overlap between shearwaters and humpbacks in SBNMS and shearwaters and right whales in the GOM. 2014 showed the highest and most consistent overlap in SBNMS, with shearwater UD encompassing 100% of humpback sightings in 11 of 15 weeks (Supplementary Figures 25, 30). Most weeks in 2015 and 2016 also showed high overlap

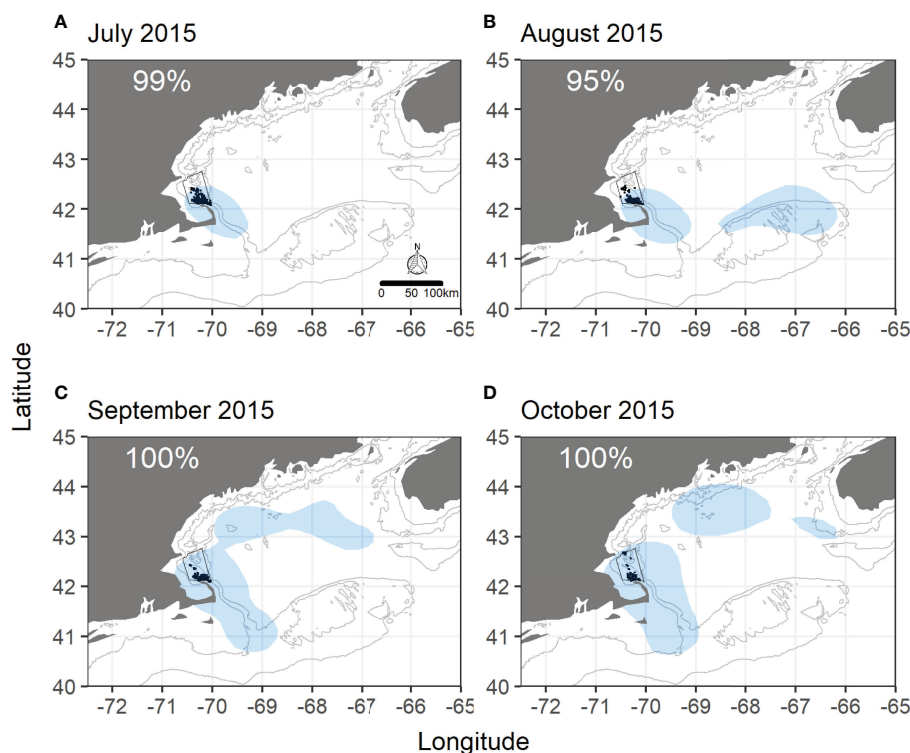


FIGURE 1 | Monthly overlap between great shearwaters and humpback whales within Stellwagen Bank National Marine Sanctuary in 2015. **(A)** July 2015, **(B)** August 2015, **(C)** September 2015, **(D)** October 2015. Shaded blue areas are shearwater utilization distributions (GOM-wide) from 50% kernel density isopleths. Black dots are daily, unique sightings of individually identified humpback whales in the sanctuary. SBNMS boundaries are in black. Gray lines represent 50m and 100m depth contours. Percentages represent the percentage of humpback sightings within SBNMS falling within the shearwater UD.

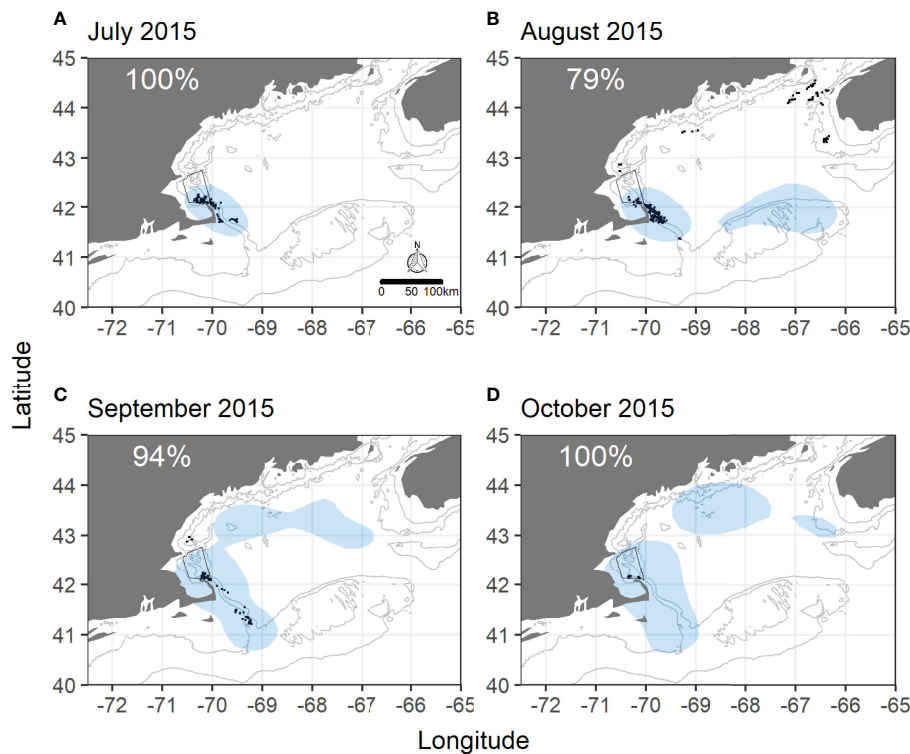


FIGURE 2 | Monthly overlap between great shearwaters and humpback whales at the Gulf of Maine scale in 2015. **(A)** July 2015, **(B)** August 2015, **(C)** September 2015, **(D)** October 2015. Shaded blue areas are shearwater utilization distributions (GOM-wide) from 50% kernel density isopleths. Black dots are daily, unique sightings of individually identified humpback whales recorded during GOM-wide humpback whale surveys. SBNMS boundaries are in black. Gray lines represent 50m and 100m depth contours. Percentages represent the percentage of humpback whale sightings falling within the shearwater UD.

(**Supplementary Figures 26–27**). All 2013 and most 2018 weeks showed no overlap between shearwaters and humpbacks in the sanctuary, though 3 weeks in 2018 showed overlap greater than 50% (**Supplementary Figures 24, 29, 30**).

Right whales showed higher levels of overlap with shearwaters at a weekly scale compared to monthly or annual scales, though 82% of weeks showed no overlap.

In 2014, 4 weeks showed >90% of right whale sightings overlapping shearwater areas starting in late August. Several weeks in 2015 showed 100% overlap, though two of these weeks only had 1 sighting (**Supplementary Tables 1–6**).

There seemed to be no patterns in terms of weekly overlap across years for humpbacks (**Supplementary Figure 30**). Considering the entire study period, $\geq 50\%$ and $\geq 90\%$ of humpback sightings were encompassed by shearwater UDs in 56% and 44% of weeks, respectively. Zero overlap occurred in 37% of weeks. For right whales, $\geq 50\%$ and $\geq 90\%$ of sightings were encompassed by shearwater UDs in 16% and 12% of weeks, respectively.

DISCUSSION

This work demonstrates that satellite-tagged shearwaters identified humpback whale aggregation areas at multiple

spatial and temporal scales, providing the near real-time information necessary for dynamic management. Our approach to use satellite-tagged seabirds as a tool to locate whale aggregations in near-real time represents a novel use of satellite-telemetry data and a new kind of DOM tool. Animal tracking data has long been recognized for its value in identifying ecologically important areas, informing management, and establishing static MPAs (Block et al., 2011; Allen and Singh, 2016; Lennox et al., 2019; Hays et al., 2019; Davies et al., 2021). More recently, dynamic habitat models using previously collected satellite-telemetry data have been developed with the goal of informing dynamic management (Żydelis et al., 2011; Abrahms et al., 2019; Barlow and Torres, 2021) and several existing DOM tools rely on tagging data in their work flows to produce end products (Hobday and Hartmann, 2006; Howell et al., 2008; Hazen et al., 2017; Hazen et al., 2018). Our work demonstrates the first potential use of animals tagged in near real-time to inform DOM.

Implementation: Considerations and Recommendations

Further study is needed to advance this work towards an operational DOM tool. Nevertheless, it is worthwhile to consider how this concept could realistically be implemented

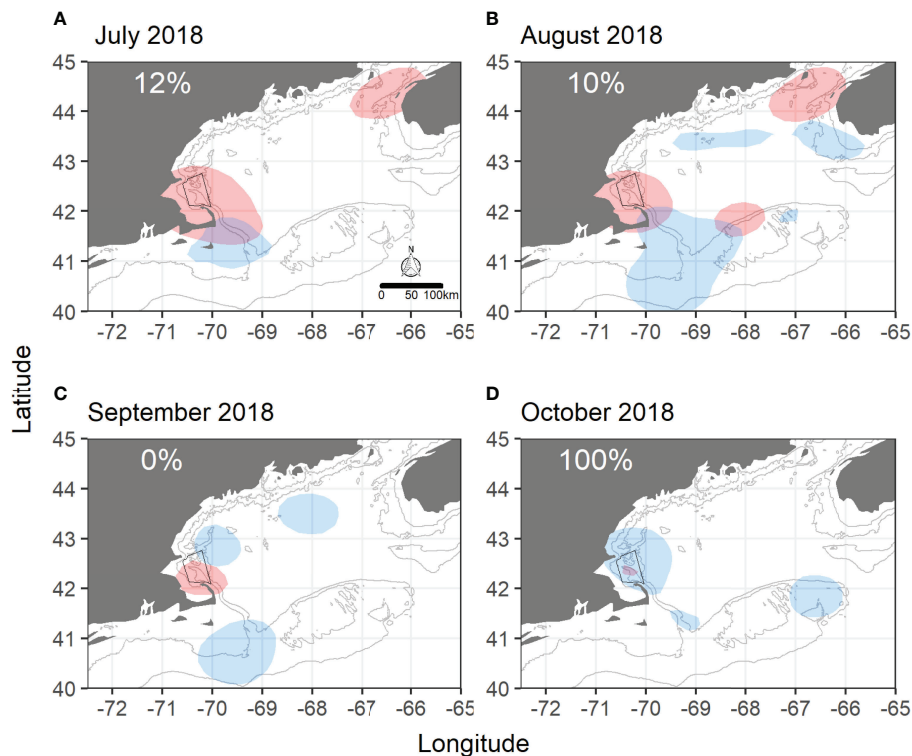


FIGURE 3 | Monthly overlap between great shearwaters and humpback whales at the Gulf of Maine scale using satellite telemetry data in 2018. **(A)** July 2018, **(B)** August 2018, **(C)** September 2018, **(D)** October 2018. Shaded blue areas are shearwater utilization distributions (GOM-wide) from 50% kernel density isopleths. Shaded red areas are humpback whale utilization distributions from 50% kernel density isopleths. SBNMS boundaries are in black. Gray lines represent 50m and 100m depth contours. Percentages represent the percentage of the humpback whale UD overlapping with the shearwater UD.

as a dynamic management strategy using the data streams and scales analyzed here.

Our regional, GOM-wide analyses (with all data types) identified high spatial overlap in areas we expected based on previous work, particularly in known foraging locations for humpbacks and shearwaters in predominantly sand habitats of high sand lance abundance (Payne et al., 1986; Clark et al., 2006;

Robbins, 2007; Powers et al., 2017; Powers et al., 2020; Silva et al., 2020; Staudinger et al., 2020). The aggregation of shearwaters and humpbacks over stable features like sand substrates lends itself well to a combination of static and dynamic management (Tittensor et al., 2019), i.e., pre-identified static areas, within which, portions could be turned on and off dynamically. For example, if areas of consistently high overlap between humpback

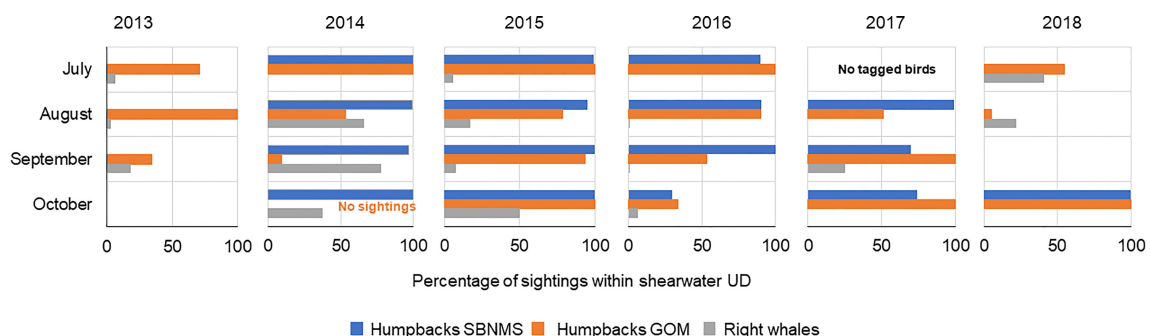


FIGURE 4 | Summary of monthly overlap across the study period showing the percentage of whale sightings overlapping with the respective shearwater utilization distribution (UD) in each month. Blue – humpback whale sightings in SBNMS, orange – humpback whale sightings in GOM, gray – North Atlantic right whale sightings. No birds were tagged in July 2017. The GOM-wide humpback whale survey did not extend into October in 2014 and was limited in that month in all years.

whales and shearwaters become recognized areas of ecological importance, detection of a tagged shearwater (or some minimum threshold of shearwater presence) in one of these areas could trigger a dynamic management action. Focusing more rigorous statistical analyses within these static areas could identify shearwater, and likely humpback, foraging hot-spots on smaller spatial scales, refining management areas and initiating dynamic management in a more targeted way.

An integrated management scheme combining static and dynamic strategies at a regional scale also makes sense based on our results and from ecological and comprehensive management perspectives. While overlap was typically higher within SBNMS, GOM-wide survey data and satellite telemetry data revealed spatial overlap in sand habitats at multiple temporal scales beyond sanctuary boundaries, highlighting the greater consistency in co-occurrence at the GOM scale and the benefit of wider scale surveillance. In addition, there is high ecological connectivity between these predominantly sand areas, including SBNMS, in terms of GOM humpback movements and source-sink dynamics of larval sand lance (Robbins, 2007; Suca et al., 2022). Further, entanglement and vessel strike are regional issues. Managing these threats at the broadest scale, which includes the full geographic range of humpback seasonal movements, provides the greatest benefits. Lastly, SBNMS is nested within the GOM and would automatically be included in a regional management approach. Prior knowledge of GOM areas where co-occurrence of humpbacks and shearwaters predictably occurs is a major advantage in focusing data collection and analysis efforts, and to operationalize a program of finer scale dynamic approaches based on near real-time co-occurrence.

While we ideally support a regional approach, several factors make SBNMS an ideal location to pilot DOM. First, co-occurrence between humpbacks and shearwaters is best understood within SBNMS (Silva et al., 2020; Silva et al., 2021); both species are often collocated on the southern portion of Stellwagen Bank where sand lance abundance is highest. Silva et al. (2021) identified site-specific probabilities of humpback aggregations on an even finer scale (~1-2 km) within SBNMS, which coincides spatially with humpback sightings and shearwater distributions in the current study. The sanctuary was included in most shearwater distributions at all scales and was consistently a high overlap area, highlighting the importance of SBNMS to humpbacks and shearwaters as foraging habitat. Second, SBNMS is a multi-use sanctuary that could benefit from additional surveillance and threat mitigation. Levels of human activities are highly concentrated and include commercial and recreational fishing and vessel traffic (Hatch et al., 2008). Entanglement and vessel strike risk have been well documented here (Wiley et al., 2003; Wiley et al., 2013; Hill et al., 2017; Office of National Marine Sanctuaries, 2020; Silva et al., 2020; Silva et al., 2021). Fourth, the sanctuary is smaller (2180 km²) than all but three shearwater use areas identified here (all at the weekly scale) which would simplify management. Fifth, existing high-resolution sightings data collection programs from research and opportunistic platforms offer unique

opportunities to corroborate analyses and assess decision making. Lastly, the sanctuary's status as a federal MPA may offer alternative management frameworks not applicable to the broader region. Pre-existing knowledge, continued monitoring and concentrated human threats suggest that piloting dynamic management could be most impactful and operational in SBNMS.

We analyzed overlap using multiple datasets and spatio-temporal scales to explore the full range of management options. In theory, dynamic management at the smallest possible spatial and temporal scales poses the least impact to stakeholders. While we demonstrate high spatial overlap between shearwaters and whales at the weekly scale within SBNMS, providing scientific support for management, managing entanglements at weekly scales may be impractical given logistics in hauling and recovering trap-pot gear (Borggaard et al., 2017), and short-term, small geographic scale management might result in gear merely being massed along the borders of the managed areas, which could increase entanglement risk. At the other extreme, an annual scale is likely too coarse and will miss pertinent dynamic shifts in animal distributions during the year. We recommend discussions on dynamic management start by considering the monthly scale. This scale is the finest, and therefore most dynamic temporal scale to more closely match animal movements and offers a more reasonable time frame for fishers, vessel operators, and managers to plan, implement and comply with management actions. Our results showed no consistent monthly patterns across years that may assist in advanced planning, though datasets currently available from July and August provided the best available insight for dynamic management. October seemed to show the most variation in overlap in all datasets (sightings, telemetry), due to limited GOM-wide whale survey effort and fewer tagged birds by this time of year due to migration or tag failure. Further analysis of trade-offs between spatio-temporal management combinations and potential impacts on feasibility of implementation is essential. Communication and engagement with stakeholders will be key in all future phases of study and development (Welch et al., 2019; Oestreich et al., 2020).

Our proposed combination of dynamic management within predefined static sand habitats relies on humpbacks and shearwaters aggregating at these sites foraging for sand lance. Fewer humpback sightings and little use of SBNMS by tagged shearwaters in 2013 and 2018 was likely driven by lower than average sand lance abundance (Silva et al., 2020). GOM survey data and satellite telemetry showed overlap in other parts of the GOM in 2013, but all data showed little to no overlap in 2018. Shearwaters and humpbacks may have targeted different prey sources in 2018, suggesting that shearwaters may be less effective indicators of humpback locations when sand lance are not abundant. Sand lance show extreme sensitivity to increasing temperatures and ocean acidification (Murray et al., 2019) and predicted abundance across the NE U.S. Continental Shelf through the remainder of the century is projected to be lower than average (Suca et al., 2021). This underscores the need for

continued innovation of dynamic management tools as climate-related oceanographic changes drive fluctuations in species' abundance and distributions.

Right Whales

Shearwaters were not reliable or consistent indicators of right whale locations. This was not unexpected, given that right whales feed on copepods (Wishner et al., 1995; Murison and Gaskin, 1989; Mayo and Marx, 1990), while humpbacks and shearwaters primarily target sand lance. The year with the highest overlap, 2014, was one where shearwaters used the Bay of Fundy in the northern GOM, historic right whale foraging habitat (Kraus et al., 1982; Murison and Gaskin, 1989; Baumgartner et al., 2003). Since 2010, coincident with an oceanographic regime shift in the GOM (Meyer-Gutbrod et al., 2021), right whales have mostly abandoned their northern GOM summer feeding grounds and are appearing in the Gulf of St. Lawrence and Southern New England (Davis et al., 2017; Leiter et al., 2017; Davies et al., 2019; Meyer-Gutbrod et al., 2021; Quintana-Rizzo et al., 2021). Interestingly, shearwaters used areas in Southern New England in 2017, just missing an aggregation of right whales. More right whale sightings were encompassed by shearwater distribution in 2018, representing the second highest yearly overlap. Analyzing more recent years may reveal increased overlap between shearwaters and right whales coincident with a shift in right whale habitat. Future work could also explore additional seabird species as better indicators of right whale presence.

Current U.S. Management

The U.S. does employ some dynamic strategies to mitigate vessel strike to whales. In addition to Whale Alert (Wiley et al., 2013), the National Oceanic and Atmospheric Administration (NOAA) can implement Dynamic Management Areas (DMAs) and Right Whale Slow Zones (NOAA, 2021c), which use near real-time visual (DMA) or visual and acoustic (Right Whale Slow Zones) detections to establish areas where mariners are encouraged to reduce vessel speed or to avoid. However, compliance in both programs is voluntary and previous work has shown voluntary rules, including DMAs, to be largely ineffective (Lagueux et al., 2011; McKenna et al., 2012; Silber et al., 2012), though Canada and New Zealand had some success with voluntary ship strike reduction measures (Vanderlaan and Taggart, 2009; Constantine et al., 2015; Ebdon et al., 2020). Mandatory, dynamic strategies may better reduce vessel strike risk to whales (Hausner et al., 2021). Further, current spatial management of vessel strikes and entanglement is designed for times and places where right whales aggregate (NOAA (National Oceanic and Atmospheric Association), 2008; National Marine Fisheries Service, 2021), providing little if any benefit to other whale species. Using satellite-tagged shearwaters to define management areas can provide a means to extend spatial protections to humpbacks and other marine mammal species that feed on sand lance.

There are currently no dynamic management strategies to mitigate entanglement in the U.S, though the data collection (Baumgartner et al., 2013; Baumgartner et al., 2019; Baumgartner et al., 2020) and dissemination (Wiley et al., 2013;

Johnson et al., 2021) infrastructure exist. NOAA made an early attempt at dynamic management of entanglement with the implementation of the Dynamic Area Management (DAM) program in 2002 (Asaro, 2012; Borggaard et al., 2017; Bisack and Magnusson, 2021). DAM zones could be created to restrict fixed gear fishing when three or more right whales were present within an area of 75 nm². When a DAM was triggered, mandatory gear removal, voluntary gear removal, or more restrictive gear modifications could be requested for 15 days. The program lasted seven years, rarely required gear removal, and ended in 2009 after much criticism from stakeholders on all sides. Notably, fishers maintained that more predictable requirements were needed for fixed gear fisheries and removal of gear required weeks to months notice (Borggaard et al., 2017). These examples provide more support for the monthly management scale recommended here. However, Canada has implemented dynamic fisheries management of the fixed gear snow crab fishery on a ~ biweekly scale. In the Gulf of St. Lawrence, acoustic or visual detection of a single right whale triggers a closed area (~2000 km²) surrounding the detection for 15 days. If no whales are detected in the closed area during days 9-15 of the closure, the area re-opens to fishing (Fisheries and Oceans Canada, 2021). While this strategy is relatively new, focuses on one specific fishery, and has not been evaluated, it does provide precedent for dynamic fisheries management at sub-monthly scales.

Limitations and Future Work

An important next step will be to evaluate how well shearwaters indicate whale locations. While spatial overlap was often high, shearwater distributions were typically much larger than humpback distributions, with many shearwater UD's greater than 20,000 km². If whale distributions account for only a small portion of shearwater UD's, implementing management areas of this size would not only be inefficient but also logistically and politically difficult. As a rough approximation for how well shearwaters locate whales, we used only telemetry datasets (GOM-wide scale) to calculate the percentage of the shearwater UD encompassed by the humpback UD, which ranged from 0-40% with most values below 20%. This suggests that establishing shearwater 50% UD's as management areas would likely ensure whale protection but managed areas would be unnecessarily large. For tagged shearwaters to be an effective and efficient DOM tool, their habitat-use areas and therefore, candidate management areas, must be refined (Dunn et al., 2016).

Future work should examine more robust statistical methods for determining home ranges using satellite telemetry data. Our method of calculating UD's was highly sensitive to numbers of Argos locations, one known bias of kernel density estimation (Winton et al., 2018). We chose this relatively simple method to examine overlap over many scales at once as proof of concept, and to accommodate differences between shearwater and humpback telemetry data collection. We also explored the use of time-based convex hulls, but found that technique to also be limited by sample size. The presence-only nature of satellite-telemetry data should also be considered in selection of future

methods. Potential biases in presence-only data are well known (Phillips et al., 2009; Elith et al., 2011; Renner et al., 2015; Winton et al., 2018). We did not account or correct for potential presence-only biases at this initial stage of exploration, but a more rigorous analysis to reduce presence-only data biases like spatial and temporal autocorrelation would likely produce smaller shearwater use areas and thus, smaller candidate management areas. We note that some whale sightings data in SBNMS were collected opportunistically and are also presence-only data, though daily effort and high resolution of these data alleviate some concern about any biases.

Incorporating environmental variables may also help refine bird use areas (Powers et al., 2017; Powers et al., 2020), particularly those that define areas of highest sand lance abundance. Species distribution modelling incorporating environmental data could also enable forecasts to predict areas of high shearwater-whale overlap. Shearwater UD's could provide a proxy for prey resources in a humpback distribution model. Forecasts could provide the advanced notice required for stakeholders to operate at weekly time scales. However, forecasts depend on strong model performance and move away from the advantages of relying on seabirds tagged in real-time. Identifying areas and times of shearwater foraging behavior where they may be more likely to overlap and associate with humpbacks may better hone in on areas for dynamic management.

Increasing sample sizes of tagged birds may better define habitat use areas and help address sources of error. Here, ~10 birds were tagged each year. Tagging additional birds may further increase and align spatial overlap. Most shearwaters in the SW GOM are likely juvenile or early subadults (0-2 years old) that use the area from July to November, suggesting age-related preferences in movements and foraging areas (Powers et al., 2017; Powers et al., 2020), but older subadults that leave the GOM by September are also common (Powers et al., 2020). Tagging more adult shearwaters, who often move north earlier in the summer, may allow us to capture more humpback or right whale locations in the northern GOM. Larger sample sizes of tagged birds could reduce error or bias in distributions, refine potential management areas, and provide data through the Fall to better support the need for entanglement mitigation throughout October.

Some caution is needed in interpretation of GOM results in light of survey purpose and effort. Surveys were not designed for spatial analyses but rather to document as many individual humpback whales as possible across the population. Effort therefore intentionally focused on historical humpback whale aggregation sites within this large area and was dependent on weather, logistics, and resources. For example, no humpback sightings on Georges Bank in these years reflects the difficulty in successfully surveying this offshore area, even though it is a known foraging area for humpback whales. Non-standardized survey effort means there could have been whales in areas or times that were not surveyed. We did not correct the data for effort and so overlap between shearwaters and humpbacks may be lower (or higher) than reported here. In addition, a temporal mismatch between survey effort and humpback presence may alter results. Regular, GOM-wide, systematic cetacean surveys (such as aerial or vessel line-transect surveys) in these months

would be valuable in further understanding overlap between humpbacks and shearwaters to inform DOM tool development.

Future work should map and quantify overlap between fixed gear locations, vessel transits, shearwater areas, and humpback aggregations to document conservation benefits to managing these areas. This has been partially done for SBNMS (Wiley et al., 2003; Wiley et al., 2013; Silva et al., 2020; Silva et al., 2021), but should be done for the entire GOM. Overlap between shearwater areas and known vessel strike and entanglement locations would be additional valuable information. Although entanglement report locations do not necessarily represent locations where entanglement occurred, high-intensity data collection programs on individual whales can sometimes clarify timing and possible location of entanglement. If entanglement locations fall within shearwater use areas, tagged birds could also inform survey effort to assess entanglement risk in other areas.

Continued investigation and investment into seabirds as potential dynamic management tools has many benefits. Tagging seabirds is cost-effective; it is cheaper than other methods to monitor whale distributions including tagging, vessel/aerial visual surveys, or passive acoustic monitoring. The sanctuary's seabird tagging program is anticipated to continue for at least the next several years, providing an existing means to continue and expand monitoring capabilities and leveraging data collection for additional applications. In addition to cost, tracking seabirds also avoids other limitations of visual and acoustic surveys for whales – daytime operations, reliance on vocalizing animals, and uncertainties in detections. Johnson et al. (2020) recommended that dynamic management areas be >10km and focus on areas used for foraging and socializing to reduce uncertainty associated with whale detection locations. While tracking seabirds has its own limitations and uncertainties in identifying whale locations, shearwater UD's and the nature of overlap with humpbacks (foraging) indicates that seabirds as dynamic tools would automatically meet these recommendations.

CONCLUSION

This work shows satellite-tagged shearwaters can serve as indicators of humpback whale locations across space and time and with further study, could increase management capabilities. As climate-related changes drive increased variability in ocean conditions and species' shifts, particularly in the GOM (Pershing et al., 2015; Pershing et al., 2021), static spatial management alone is no longer sufficient for species' protection (Runge et al., 2014). Static restricted areas and MPAs may become ineffective at serving their original purpose (Bruno et al., 2018). Dynamic management and the flexibility to respond to anomalous ocean conditions and species' shifts is necessary (Meyer-Gutbrod et al., 2018; Pinsky et al., 2018; Davies and Brilliant, 2019; Maxwell et al., 2020; Hausner et al., 2021; Meyer-Gutbrod et al., 2021). DOM tools provide the framework to meet ecological and economic objectives, making implementation of managed areas more attractive to stakeholders, while supporting ecosystem-based management (Lewison et al., 2015; Maxwell et al., 2015).

DATA AVAILABILITY STATEMENT

Data will be made available on request to the corresponding author and/or to the North Atlantic Right Whale Consortium. Requests to access these datasets should be directed to Tammy Silva - tammy.silva@noaa.gov; NARWC - <https://www.narwc.org/accessing-narwc-data.html>.

ETHICS STATEMENT

The animal study was reviewed and approved by Institutional Animal Care & Use Committee (IACUC). Shearwater tagging occurred under research permit #22055 issued by the United States Department of the Interior, #058.19SCB Issued by the Massachusetts Division of Fisheries and Wildlife and #SBNMS-2019-001 issued by the National Oceanic and Atmospheric Administration/Stellwagen Bank National Marine Sanctuary. Humpback whale surveys and tagging were conducted under NOAA permits: 14245, 20465, 16325 and the Canadian Department of Fisheries and Oceans.

AUTHOR CONTRIBUTIONS

TS, KP, JR, MT, and DW designed the study. All authors collected the data. TS and KP analyzed the data. TS wrote the initial manuscript draft. All authors edited and approved the final version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.837604/full#supplementary-material>

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The Designated Shipping Avoidance Area Around St. Lawrence Island, Northern Bering Sea, Is not Sufficient to Protect Foraging Habitat of the Island's Breeding Seabird Community

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One direct consequence of Arctic warming is the expansion of navigable portions of the Arctic Ocean. As a result, vessel traffic and the accompanying threats of spills, strikes and disturbance is intensifying throughout the Arctic. In the Bering Sea, these threats to the environment, wildlife and to the people who rely on marine resources for food and cultural continuity, are acute. We examined the spatial relevance of an Area To Be Avoided (ATBA), a shipping-risk mitigation measure, established around St. Lawrence Island with respect to seabirds, as sentinel species, habitat use. We studied four seabird species (common murre *Uria aalge*, thick-billed murre *U. lomvia*, crested auklet *Aethia cristatella*, black-legged kittiwake *Rissa tridactyla*) breeding at St. Lawrence Island in the northern Bering Sea. GPS tracking data from 47 at-sea foraging trips showed that both murre species and crested auklets distributed outside the ATBA, during at least one stage of the breeding season. A larger dataset based on the birds' red blood cell isotopic signatures confirmed that for murre, the tracked individuals covered the broad niche exploited by these species. Habitat modelling further showed that the birds' most suitable marine habitats were associated with seasonal surface chlorophyll blooms, and largely extended beyond the ATBA on the shelf north of the island. Data on the murre's diet and diving behavior emphasized the importance of the shelf as a foraging habitat for these birds. We suggest that extending the ATBA to the north by only 35 km, would include areas of maximal habitat suitability. This extension would better protect seabirds, their foraging habitats and the cultural continuity of St. Lawrence Islanders, against growing threats stemming from Arctic warming.

Keywords: Arctic, warming, GPS tracking, habitat suitability, marine spatial planning, alcids, kittiwake, subsistence harvesting

INTRODUCTION

Decreased Arctic sea ice extent has opened up new northern shipping routes (AMSA, 2009; Yumashev et al., 2017). Climate modelling indicates that these ice-free routes in the Arctic Ocean will continue to expand spatially and seasonally (Smith and Stephenson, 2013; Aksenov et al., 2017). Accordingly, vessel-based commerce has developed, and by 2025 Arctic vessel traffic is projected to triple compared to what it was a decade ago (International Council on Clean Transportation, 2015).

In particular, all vessel traffic between the Arctic and Pacific Oceans must pass through the Bering Strait, a maritime bottleneck that has become a focal point for Arctic shipping regulation and the conservation of biodiversity (AMSA, 2009; Hauser et al., 2018). The Bering Sea is known for its remarkable biological richness fuelled by high levels of surface primary productivity, and high carbon export to the benthos due to limited zooplankton grazing (Hunt et al., 2002; Grebmeier et al., 2006; Grebmeier, 2012). This results in a benthic-dominated system that supports large populations of seabirds and marine mammals (Grebmeier et al., 2015), which in turn support ancient and vibrant Indigenous cultures (Fall et al., 2013). Thus, with the increasing vessel traffic in the region, there is a potential for magnified threats to both the local marine environment and to the people who rely on this marine wildlife for food and cultural resources. Vessels in transit pose several environmental risks, such as exposure to oil, emission of gases and particles from exhausts (sulphur dioxide, nitrous oxide, ozone, black carbon), direct disturbance to wildlife including displacement and collision risks (ship strikes), noise-related impacts, discharge of contaminants and the introduction of invasive species (Huntington et al., 2015; Stevenson et al., 2019; Dehnhard et al., 2020), which may translate into the loss of biodiversity and cultural heritage (Huntington et al., 2015; Tempel et al., 2021).

In view of the magnitude, severity and rapidity of the growth of threats to the marine environment in this region, the existing network of marine areas implemented for the conservation of species and habitats is seen as inadequate and insufficient (Harris et al., 2018). Recent research in the Arctic has focused on marine mammals (e.g., Hauser et al., 2018); however, seabirds also are at risk of conflict with human activities in the Arctic (Humphries and Huettmann, 2014; Wong et al., 2018), and represent a considerable ecological and cultural component in the Bering Sea (Huntington et al., 2015). Seabirds are major secondary consumers in this ecosystem (Hunt et al., 2002; Grebmeier et al., 2015), and are a critical aspect of food security and cultural continuity for indigenous Arctic peoples in the region (Fall et al., 2013; Huntington et al., 2015; Naves, 2018; Will et al., 2020a). In particular, the importance of seabirds as subsistence resources is the highest (81%) for peoples from St. Lawrence and Diomed Islands, islands that are within or adjacent to the Bering Strait. Seabird harvesting on these islands largely relies on auklets *Aethia* spp. and murre *Uria* spp., which are among the most abundant seabird species in the region (Kuletz et al., 2015), and occurs in spring and summer (Naves, 2018).

In this context, there is an urgent need to protect both biological resources and subsistence activities from the potential impacts of increasing vessel traffic in the Bering Strait region. Implementing Areas To Be Avoided (ATBAs) for shipping offers one mechanism to help achieve these goals. Three ATBAs have recently been adopted by the International Maritime Organization (IMO) in this region. These are around King, Nunivak, and St. Lawrence islands (Huntington et al., 2019). However, there is concern that the implemented ATBA around St. Lawrence Island may not be wide enough based on initial consultation with the public (Huntington et al., 2019). This situation warrants scientific evaluation on the relevance of the current boundaries of the St. Lawrence Island ATBA to seabird habitat use. Tracking marine animals, and seabirds in particular, has strong potential to inform policy and management (Thaxter et al., 2012; Hays et al., 2019). In this paper, we use the first tracking data collected on seabird species breeding at St. Lawrence Island (three Alcidae: the common murre *Uria aalge*, the thick-billed murre *U. lomvia*, the crested auklet *Aethia cristatella* and one Laridae: the black-legged kittiwake *Rissa tridactyla*), to examine whether these species' foraging areas distributed inside the adopted ATBA's boundaries. During breeding, seabirds behave as central-place foragers (Orians and Pearson, 1979), thus their relatively restricted foraging range should provide a conservative estimate of their habitat use around the island (Oppel et al., 2018). This would ensure that we evaluated the ATBA boundaries for the seabird populations that use the island to breed, and which may be locally harvested by the islanders. We characterized habitat use by both GPS tracking, for all species, and dive behaviour and chick-diet observations, for murre only. We supplemented these data with a larger dataset from stable isotope data on the birds' blood, to evaluate how representative the individual tracking data may be. Based on these results, we discussed the options to improve the design and management of the St. Lawrence ATBA.

MATERIALS AND METHODS

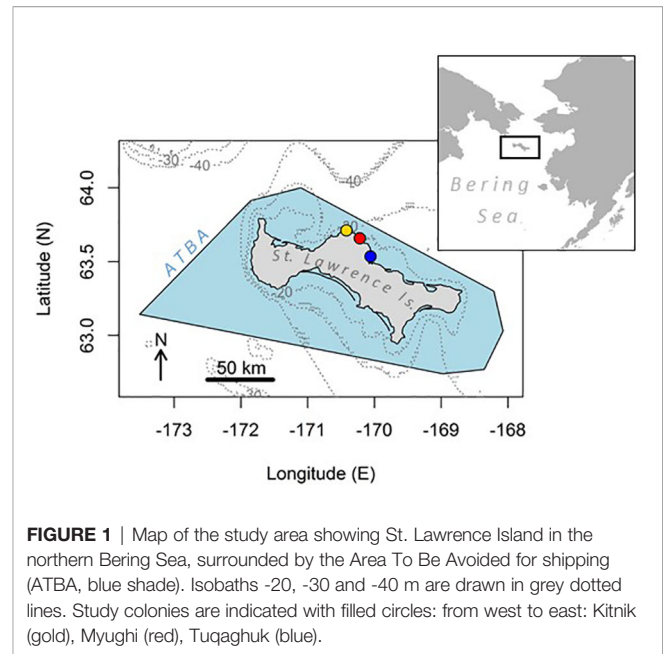
Study Sites and Species

St. Lawrence Island (Sivuqaq in Siberian Yupik) is a large island (4,640 km²) situated in the northern Bering Sea, directly south of the Bering Strait (**Figure 1**). It is surrounded by an extensive shelf, providing shallow depths (less than 30 m) around the island, especially to the east. St. Lawrence Island sits in a very dynamic hydrographic system, with two strong currents flowing northward (the Anadyr Current on the West side of the island, and the Alaska Coastal Current on the East) which supply nutrient-rich waters from the southern Bering Sea basin all the way up into the Chukchi Sea (Springer et al., 1987; Hunt et al., 1990; Piatt and Springer, 2003). The regional topography funneling the northward flow of these currents also creates a locally longitudinal current along the north coast of St. Lawrence Island, and particularly near the north-west and north-east capes (Danielson et al., 2014).

We studied seabirds from three colonies conveniently accessible from Savoonga and located on the northern coast, where the ATBA is the narrowest, a situation which may put these northern colonies at higher risk of adverse impacts from shipping. Four seabird species were studied on the island. Most of our effort focused on murres: common and thick-billed, which breed sympatrically in large numbers on seaside cliffs around the island. Current estimates of numbers on St. Lawrence Island are 337,447 and 279,219 individuals for the common and thick-billed murres, respectively (from the Circumpolar Seabird Data Portal, <http://axiom.seabirds.net/>). In the Bering Sea, common murres primarily consume pelagic schooling forage fish (Kokubun et al., 2016; Barger et al., 2016), while thick-billed murres are more generalist foragers that consume a mix of benthic prey, pelagic forage fish and large invertebrates (Harding et al., 2013; Barger et al., 2016). Earlier reports at St. Lawrence Island (Piatt et al., 1988) noted that these two species are markedly synchronous in their breeding cycle: the median laying date was between late June and early July for both species, with hatching occurring in early August and chicks fledging in late August. Murres were studied at Tuqaghuk (63.54°N; -170.06°E) and Cape Myughi (63.66°N; -170.22°E) colonies on the north shore of the island. Besides murres, two other seabird species were surveyed. First, the crested auklet was studied from Kitnik colony (63.71°N; -170.42°E). Auklets are planktivorous alcids relying predominantly on *Neocalanus* copepods during the breeding season (Gall et al., 2006; Sheffield Guy et al., 2009). They nest in burrows underneath boulders, and lay eggs on St. Lawrence around late June; hatching occurs between late July and early August, and the chicks fledge at the end of August (Gall et al., 2006). A total of 1,528,455 crested auklets are estimated to breed on St. Lawrence Island. Last, we studied the black-legged kittiwake, which similarly to murres is a cliff-nesting and piscivorous species, but feeds at the surface (Bayer, 1983); it also breeds synchronously to the murres. Kittiwakes were studied from Cape Myughi colony, and 53,937 individuals are estimated to breed on the island. Across their differences in foraging ecology, the four species studied here provide a synoptic indication of the at-sea ecology of the seabird community breeding at St. Lawrence Island.

Logger Deployments

Fieldwork was conducted in the summers of 2016 to 2019. GPS loggers were attached onto breeding birds that were caught either using a noose pole (for the cliff-nesting species) or by hand under



the boulders (auklets). The loggers were attached to the back feathers on the dorsal midline using mastic and waterproof Tesa[®] tape; the ends of the tape were locked using Loctite[®] glue. Two different types of GPS loggers were used: first, to track murres (2016 and 2017) and kittiwakes we used CatTraq loggers (CatLogTM, 16 Mb memory, 380 mA lithium-ion battery, Catnip Technologies, USA). These GPS loggers were housed in waterproof heat-shrink tubes before being deployed on the birds (final mass: 15 g, final size: 14 mm × 35 mm × 70 mm). Second, we used Ecotone GPS-UHF short-range download loggers (Alle and Uria series, Ecotone Telemetry, Gdynia, Poland) to track murres in 2019 (model Uria-100; dimensions: 35 × 16 × 11 mm; mass: 8.5 g) and auklets in all years (model Alle-60; dimensions: 26 × 16 × 10 mm; mass: 4.5 g). The attachment or recovery of loggers and associated body measurements and/or physiological samples took 10 to 20 minutes per bird. Tracking data per year, species and breeding stages are detailed in **Table 1**; no tracking data were collected in 2018 when very low breeding success was observed in all species (Will et al., 2020b).

The location acquisition was set with a 2-minute interval on the CatTraq loggers, and the loggers were retrieved after the birds made several foraging trips to sea. The Ecotone loggers were set to communicate with a base station positioned near the study

TABLE 1 | Summary of tracks available per seabird species, study year, breeding stage and model of tracking unit.

Species	Year	Colony	Breeding stage	GPS logger	Number of tracks (birds)
Common murre <i>Uria aalge</i>	2016	Tuqaghuk	Chick-rearing	CatTraq	3 (2)
	2017	Myughi	Chick-rearing	CatTraq	3 (3)
	2019	Tuqaghuk	Incubation	Ecotone	10 (2)
Thick-billed murre <i>U. lomvia</i>	2016	Tuqaghuk	Chick-rearing	CatTraq	11 (5)
	2019	Tuqaghuk	Incubation	Ecotone	9 (2)
Crested auklet <i>Aethia cristatella</i>	2016	Kitnik	Incubation	Ecotone	2 (2)
	2017	Kitnik	Chick-rearing	Ecotone	4 (2)
Black-legged kittiwake <i>Rissa tridactyla</i>	2016	Myughi	Chick-rearing	CatTraq	5 (1)

nest(s) using ultra-high frequency signal; in this case the loggers were not retrieved and the signal was acquired until the batteries died or the logger was shed. The location acquisition was set with a 5-minute interval in 2016, a 10-minute interval in 2017, and a 15-minute interval in 2019 on the Ecotone loggers. Retrieval was challenged by the fact that birds were extremely shy to human presence.

In addition, the diving behaviour of murres was surveyed using time-depth recorders. Cylindrically-shaped loggers (Little Leonardo, Tokyo, Japan; model ORI400-D3GT; dimensions: 12 mm diameter \times 45 mm length; mass: 9 g) were deployed ventrally and retrieved together with GPS units in 2016, providing depth and temperature records every second; and tri-axial acceleration data every 0.25 second. However, temperature and acceleration data were not used in this study.

Processing of the Logged Data

Data were downloaded from the loggers or the base station in the field to a computer. The first phase of analysis was to identify within each dataset the start and end points of the different trips made by the bird. Through a detailed inspection of the locations, at-sea foraging trips were separated from isolated erroneous locations or small-scale movements away from the nest reflecting recapture attempts of skittish birds. This approach identified all trips as lasting > 1 h, similar to previous studies (e.g., Kokubun et al., 2015). Second, periods at the nest between trips were removed, keeping only the start and end points of each trip at this location (or the last point recorded in the case of incomplete tracks caused by battery failure). Third, movement metrics were derived from each trip: maximum range reached from the nest (km), trip duration (h), and bearing to the furthest point (degrees, clockwise with North as 0). Fourth, each trip was linearly re-interpolated with an exact 2-minute interval, because locations were occasionally missing or were not recorded at constant intervals. The incomplete tracks were not re-interpolated past the last recorded point. This analysis was performed using the R packages “sp” and “trip”. Preliminary distribution maps derived from these tracks have been presented in Will et al. (2020b); nevertheless, these data provide the first crested auklet GPS tracks. Data on diving behaviour were analysed with Igor Pro (WaveMetrics, Oregon), with maximum dive depth and bottom time of each dive calculated as in Takahashi et al. (2008).

Statistical Analyses

An analysis of pseudo-replication was undertaken to evaluate whether successive trips made by one individual could be considered as independent trips made by distinct individuals. We followed the standard “toolkit” script provided by BirdLife International in Lascelles et al. (2016), specifically designed to account for this point, consistently across tracking analyses for conservation purposes. The pseudo-replication analysis, based on iterative Mann-Whitney U-tests, compared the intra-individual versus inter-individual proximity in core distribution areas among trips made by individuals of a same species and breeding stage. This analysis was performed only when at least two trips were collected for each of at least two

individuals, during a given breeding stage and study colony. This analysis showed that in all examined datasets (common murres during incubation, and thick-billed murres during incubation and chick-rearing), the core areas from one individual’s multiple trips were not closer to each other than that of trips from different individuals (Mann-Whitney U tests, p -value = 0.48 for common murres during incubation, 0.50 for thick-billed murres during incubation, and 0.56 for thick-billed murres during chick-rearing). Hence, individual pseudo-replication was not a significant issue and all the GPS tracks were treated as independent observations.

To count the number of tracking locations included within the ATBA for each bird trip, we used the function “over” in the R package “sp”. This function examines whether a spatial polygon (the St. Lawrence ATBA in this case) overlaps with point coordinates (the GPS tracks).

Trips were compared between species or breeding stages according to their maximum range, duration, and proportion extending beyond the ATBA. Variables were first tested for normal distribution using a Shapiro-Wilk Normality Test, and depending on the result, parametric (one-way ANOVA, t -test) or non-parametric (Wilcoxon and Kruskal-Wallis rank sum tests) comparison tests were conducted. The threshold for significance was set at $p = 0.05$. When significant differences occurred among more than two factor levels, we undertook a Tukey’s post-hoc multiple comparison test to identify which group(s) significantly differed from others. All analyses were performed using R 3.4.2 (R Core Team, 2022). Unless otherwise stated, values reported are mean \pm standard deviation. The effect of sex was not examined here, due to low sample sizes for each combination of species, year, colony and breeding stage. However, studies confirm that although the partners may segregate in time for at-sea provisioning, habitat selection and diet is similar among sexes in murres (Huffeldt et al., 2021).

Island-Wide Extrapolations

We examined whether the current ATBA limits encompassed the potential foraging distribution of seabirds from all breeding locations known around St. Lawrence Island, based on the foraging ranges measured for each species tracked in this study. To this end, we used the Circumpolar Seabird Data Portal to locate all colonies known on St. Lawrence Island for the four studied seabird species (<http://axiom.seabirds.net/maps/js/seabirds.php?app=circumpolar#z=8&ll=64.54111,-170.24739>). Using the maximum foraging range observed for the tracked birds in each species, we projected simple buffers of the seabirds’ potential distribution around the island.

Habitat Suitability

Using the Mahalanobis Distance Factorial Analysis (MADIFA, Calenge et al., 2008) approach, we quantified habitat suitability levels around the island based on habitat covered by bird tracks. Habitat selection was identified according to six environmental variables: seafloor depth (bathymetry), seafloor slope (bathymetry gradient), sea-surface temperature, sea-surface chlorophyll concentration, and zonal and meridional current velocity. The MADIFA approach is adequate for this purpose

using presence-only data, such as GPS tracking, and performs particularly well in a situation where environmental variables may be highly correlated (for a comparison of methods see Tsoar et al., 2007). In the MADIFA, two principal component analyses (PCAs) respectively summarize the information on (a) the environment described by spatial variables; and (b) the relationship (distance) between the animals' habitat niche (inferred from GPS locations) and the hypervolume described by the environmental covariates (R package "adehabitatHS"). Bathymetry data were downloaded from NOAA's ETOPO1 1 Arc-Minute Global Relief Model (<https://ngdc.noaa.gov/mgg/global/global.html>), from which the seafloor gradient was computed. For sea-surface temperature and chlorophyll concentration, monthly data were downloaded from NOAA's ERDDAP server (<https://coastwatch.pfeg.noaa.gov/erddap/griddap/jplMURSST41mday> and <https://coastwatch.pfeg.noaa.gov/erddap/griddap/erdVHNchlamday>, respectively). Specifically, the datasets were the Multi-scale Ultra-high Resolution (MUR, global, 0.01° resolution, 2002-present) temperature data, and the monthly composite rasters of chlorophyll concentration for the North Pacific (NOAA VIIRS, 750m resolution, 2015-present). Current velocity data were downloaded from the Ocean Surface Current Analysis Real-time project (OSCAR; https://podaac-opendap.jpl.nasa.gov/opendap/allData/oscar/preview/L4/oscar_third_deg/). In these datasets the currents' horizontal velocity (zonal and meridional) is directly estimated from sea surface height, surface vector wind and sea surface temperature. These data are available at a 5-day temporal resolution and one third spatial degree grid. All datasets were subsequently aggregated at this latter (coarser) spatial resolution; and the environmental variable files were subsampled to cover the time span of the tracking dataset.

Using MADIFA, we modelled the habitat suitability levels separately for each species, breeding stage and year. However, in the case of kittiwakes, the extremely small distribution range observed from the tracks precluded estimating habitat suitability, because of the insufficient number of cells used across the environmental grid. Hence, no niche modelling analysis is shown for kittiwakes. The predictions from these models were merged following three successive steps, consistently giving a similar weight to each component in the combination (following Thiers et al., 2017). First, the mapped predictions (% values in each cell) were averaged between years for the same species and breeding stage (e.g., common murre tracked during chick-rearing in 2016 versus 2017). Second, the results within each species were combined across breeding stages and years (case of the common murre in 2016/2017 versus 2019, the thick-billed murre in 2016 versus 2019, and the crested auklets in 2016 versus 2017). This step provided one prediction map per species. In the third step, the predictions were merged across species, to produce a single habitat suitability map for the locally-harvested seabird community.

We did not include distance to the colony as a spatial constraint to the potentially suitable habitats in the region. This approach was chosen deliberately so that the analysis based on the tracked birds' observed selection may also reveal

habitats deemed potentially suitable to birds from other colonies, assuming the selected habitat is comparable across colonies. Second, in this analysis our objective was to identify areas where birds may preferentially distribute at sea, but not strictly for foraging. Accordingly, all available tracking locations were included in the model, potentially reflecting any activity by the birds: commuting or resting, in addition to foraging.

Stable Isotope Analyses

The results from stable isotope analysis provide a complementary approach to the individual movement tracking data. Although it is not possible to directly translate these results into spatial context, isotopic ratios were sampled in larger numbers across species and years, and thus provided a convenient perspective to examine the representativeness of the limited individual GPS tracking data among the broader foraging niche revealed by the isotopic signatures. Thus, this comparison is used to assess how confident we may be in using the GPS tracks to represent the species' foraging strategies. In this study we re-analyzed the data presented in Will et al. (2020b), by aggregating the data across years, in contrast to the previous report which focused on interannual variability.

Blood samples were taken throughout the breeding season from 2016 to 2019, from the birds' alar vein using a heparinized syringe or a needle and heparinized capillary tubes. Samples were kept cool until centrifuged (within 12 hours of collection, as much as possible), and separated into plasma and red blood cell components. Samples were stored frozen (-80°C) until analyzed. Analysis of the samples was performed as described in Will et al. (2020b). Red blood cell samples were thawed, subsampled, and dried at 35°C in an isotherm vacuum oven. These samples have a relatively lower turnover rate than plasma, and reflect the isotopic niche of birds 1-2 months prior to the sampling date, hence during the early breeding season (Hobson and Clark, 1993). Dried red blood cell samples of 0.4 to 0.8 mg were weighed, placed into individual tin capsules, and submitted to the University of Alaska Fairbanks Stable Isotope Facility for analysis. There, they were processed in a continuous-flow isotope ratio mass spectrometer. A peptone standard was used to calibrate the ^{13}C : ^{12}C and ^{15}N : ^{14}N ratios (inter-tray SD: $\delta^{13}\text{C} = 0.02\text{‰}$, $\delta^{15}\text{N} = 0.03\text{‰}$). Sample stable isotope ratios are expressed as $\delta^{13}\text{C}$ $\delta^{15}\text{N} = [(\text{R}_{\text{sample}}/\text{R}_{\text{standard}}) - 1] \times 1000$, where R represents the ratio of ^{13}C : ^{12}C or ^{15}N : ^{14}N . These results are reported as delta values in parts per thousand (‰).

Isotopic niches (from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) are presented as relative values to the average for the year and species, and shown as Bayesian standard ellipses computed in the R package "SIAR" (Jackson et al., 2011).

Diet Observation of Murres

To further investigate the murre's habitat use, direct observations of the prey species brought back to the nest in bill loads (whole fish) were conducted as frequently as possible on the colonies of Tuqaghuk and Cape Myughi, in 2016 and 2017, using either 10 × 42 binoculars, a telescope, or photographs (Canon © digital camera with 300 mm lens). These observations were conducted over several hours during a total of 21 days: five days in 2016

(from 14 through 20 August), and in 2017 during four days in July (from 19 through 26 July) and twelve days in August (from 2 through 21 August). Identification of observed prey species was conducted to the lowest possible taxonomic level. This information on the captured prey is pertinent in our study to assess how much the birds may rely on benthic prey from the shelf to provision their offspring, and therefore, how important it may be to ensure the protection of these key foraging habitats from the development of human activities. Birds relying predominantly on pelagic prey would indicate a lower importance of the shelf habitat itself to the birds (Springer et al., 1987; Hunt et al., 1990; Piatt and Springer, 2003).

RESULTS

In total, 47 tracks were available from 19 birds: 16 tracks from 7 common murres, 20 tracks from 7 thick-billed murres, 6 tracks from 4 crested auklets and 5 tracks from 1 black-legged kittiwake (Table 1).

Bird Movements

All tracks extended to more than two km away from the nest, suggesting these were actually at-sea trips (Table 2). In all surveyed years and stages, the murres of both species moved to the northeast or east from their nest, towards the shallower area of the shelf (Figure 2). The auklets moved more northwardly towards areas with deeper waters, and performed large-scale looping or sinuous trips during incubation and more directional trips during chick-rearing. In contrast, the surveyed kittiwake remained very close to the coast throughout its five similarly small-scale trips during chick-rearing. This small-scale distribution during that stage confirmed the authors' observations in the field, feeding flocks of kittiwakes were commonly visible to the naked eye from the coast in all study years.

There was an overall significant difference in the maximum foraging range observed between species (Kruskal-Wallis $\chi^2_3 = 13.201$, $p = 0.004$), however no inter-specific difference was significant between pairs of species, with only auklets' versus kittiwake's range approaching the significance threshold (Tukey's test, adjusted $p = 0.063$; and > 0.17 in all other cases). There was no overall significant difference in the maximum foraging range between breeding stages (Wilcoxon test, $W = 325$, $p = 0.27$), even when excluding the kittiwake trips ($W = 290$, $p = 0.08$). However, within species, the maximum foraging range differed significantly between breeding stages in common murres (greater during chick-rearing than during incubation; Wilcoxon test, $W = 58$, $p = 0.003$). It was not significantly different between stages in thick-billed murres (Wilcoxon test, $W = 41$, $p = 0.55$) and due to very low sample sizes this was not statistically tested in crested auklets. Overall, in five out of the seven cases of species/breeding stages, average trip bearings were comprised between 15.3–90.5 degrees (north-east sector).

Spatial Overlap With the ATBA

In total, ten bird tracks (>21% of all tracks) extended beyond the boundaries of the ATBA: three of the 16 tracks of common murres (19%; all of them during chick-rearing), four of the 20 tracks of thick-billed murres (20%; all of them during incubation), and half of the six auklet tracks. There was no significant difference between the proportion of common versus thick-billed murre trips extending outside the ATBA (Fisher's exact test for count data, $p = 1$). However, there was a significant effect of the breeding stage in murres on the proportion of trips extending outside the ATBA, with significantly more trips extending outside the ATBA during chick-rearing in common murres (Fisher's exact test for count data, $p = 0.036$), versus more during incubation in thick-billed murres ($p = 0.026$). Auklets were the only tracked birds to extend trips beyond the ATBA during both incubation and

TABLE 2 | Summary of trip metrics per categories of species and breeding stage.

Species	Breeding Stage	Maximum range; absolute max. (km)	Trip duration (h)	Bearing to furthest point (°)	Number of trips beyond ATBA	% points outside ATBA; (range)	Bathymetry distribution (m)
Common murre <i>Uria aalge</i>	Incubation	5.5 ± 3.9; 14.0	12.5 ± 5.5	85.5 ± 12.1	0/10 (0%)	0	-7.0 ± 5.0
	Chick-rearing	34.7 ± 24.8; 68.9	16.7 ± 15.5	84.7 ± 8.6	3/6 (50%)	27.3 ± 39.1 (0–84.2)	-17.0 ± 16.4
Thick-billed murre <i>U. lomvia</i>	Incubation	22.8 ± 9.0; 36.0	7.2 ± 1.8	90.5 ± 56.5	4/9 (44%)	22.3 ± 30.1 (0–73.7)	-18.8 ± 7.0
	Chick-rearing	19.1 ± 6.3; 27.4	8.7 ± 4.6	87.7 ± 5.8	0/11 (0%)	0	-15.7 ± 6.3
Crested auklet <i>Aethia cristatella</i>	Incubation	47.9 ± 1.0; 48.6	37.8 ± 6.9	15.3 ± 92.0	2/2 (100%)	66.2 ± 12.0 (57.7–74.7)	-27.5 ± 15.5
	Chick-rearing	18.5 ± 12.7; 34.9	10.6 ± 16.6	332.1 ± 38.1	1/4 (25%)	17.3 ± 34.6 (0–69.2)	-30.2 ± 14.2
Black-legged kittiwake <i>Rissa tridactyla</i>	Chick-rearing	5.5 ± 0.8; 6.4	3.5 ± 1.8	109.2 ± 14.1	0/5 (0%)	0	-0.8 ± 18.2

Range and trip duration are given as mean ± SD. The bearing to the furthest point reached is measured clockwise (with 0° being the North). The number of trips extending at least one point outside the ATBA is indicated relative to the total number of trips available in this category, and as a percentage. The mean ± SD (range) percentage of the trips' locations falling outside the ATBA is indicated for each category.

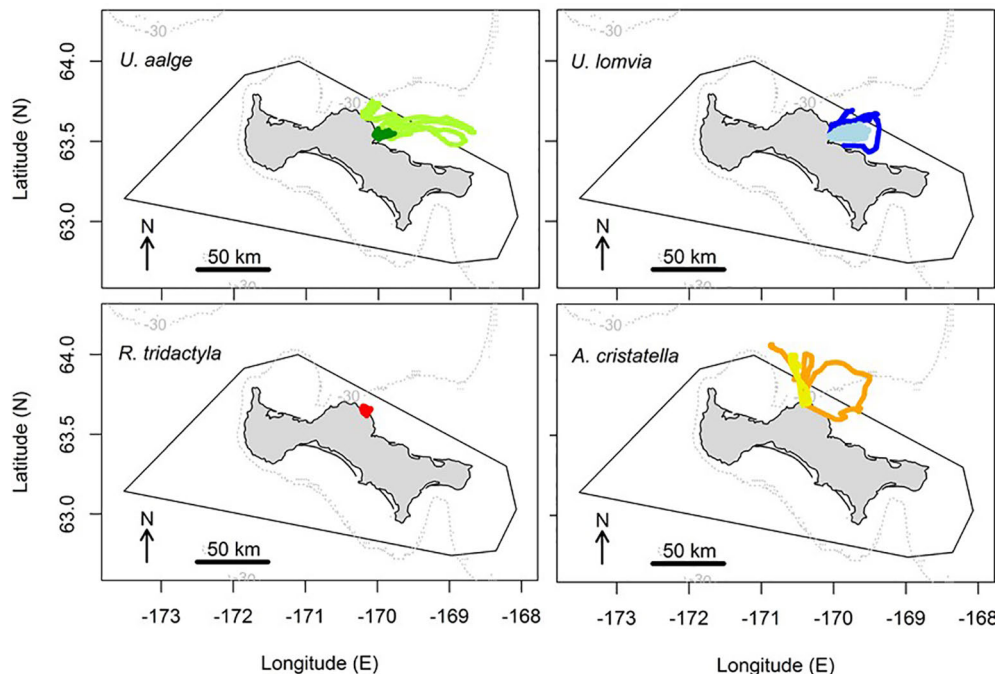


FIGURE 2 | At-sea distribution of the birds tracked from St. Lawrence Island (common murres *U. aalge*: $n = 16$ tracks, thick-billed murres *U. lomvia*: $n = 20$ tracks, black-legged kittiwake *Rissa tridactyla*: $n = 5$ tracks, and crested auklets *Aethia cristatella*: $n = 6$ tracks), relative to the contour of the Area To Be Avoided (black line). The tracks collected during the incubation versus chick-rearing stages are shown in darker versus lighter colors, respectively. The -30 m isobath is drawn in grey dotted line.

chick-rearing stages. None of the kittiwake tracks extended beyond the ATBA.

The proportion of locations falling outside the ATBA for each trip varied between 0 and 84.2% for common murres, and between 0 and 73.7% for thick-billed murres. This represented an average portion of $10.2\% \pm 26.4$ of each trip's locations for common murres (both stages pooled), and $10.0\% \pm 22.6$ for thick-billed murres (no significant difference between species, Wilcoxon test, $W = 159$, $p = 0.98$). In common murres, the three trips extending outside the ATBA had $54.6\% \pm 39.8$ (range: 9.4 – 84.2) of their locations outside the area; in thick-billed murres, that was $50.1\% \pm 23.6$ (range: 24.8 – 73.7) for the four trips extending outside the area.

Island-Wide Extrapolations

There are 25 sites where the four seabird species surveyed in this study are known to breed on St. Lawrence Island. Projected foraging ranges around these locations extended beyond the boundaries of the ATBA in virtually all directions: in the north, west, south and east (**Figure 3**). However, only in the north, where the ATBA boundary is closer to the shore, did the three species (the common and thick-billed murres and the crested auklet) have their foraging range extend markedly beyond this limit. The foraging distribution of black-legged kittiwakes, based on the maximum foraging range measured for single individual, did not seem to extend outside the ATBA.

Habitat Suitability Analysis

The MADIFA adequately summarized on a single principal component the relationship between the birds' habitat use and the environmental covariates, with generally 80–90% of variance

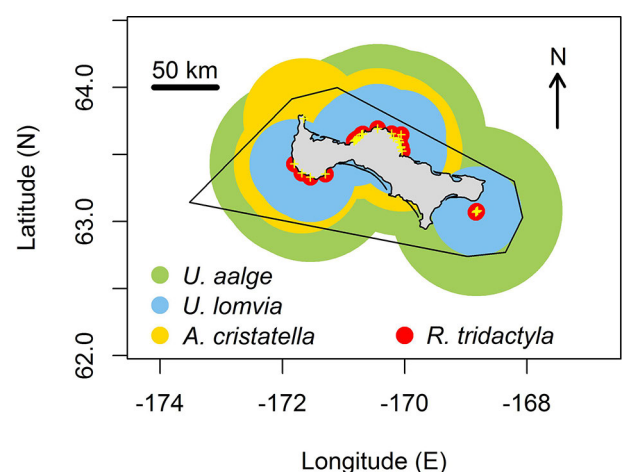


FIGURE 3 | Projected foraging range of seabirds, based on foraging tracks collected in this study, for 25 colonies (yellow crosses) around St. Lawrence Island for common murres (green areas), thick-billed murres (blue areas), crested auklets (gold areas) and black-legged kittiwakes (red areas). The contour of the ATBA around the island is indicated in black.

explained by the first component (**Supplementary Figure 1**). Sea-surface chlorophyll concentration was the highest scoring variable in most models (5 out of 7, with absolute scores on the first principal component >0.90 in four out of these five cases), and was the second-best variable in another case (thick-billed murre data from 2019, absolute score: 0.49). In the latter case, bathymetry was the best explanatory variable (absolute score: 0.65), and this variable was the second-best in three other cases: common murre data from 2017 and 2019, and crested auklets from 2017 (absolute scores: 0.45, 0.63, and 0.47, respectively). Zonal current velocity (longitudinal, noted U) was the best explanatory variable in one case (common murre data from 2016, score: 0.96), when both sea-surface chlorophyll concentration and bathymetry showed extremely low scores. Zonal current velocity was the second-best score for thick-billed murre data from 2016 (score: 0.65). These three variables (sea-surface chlorophyll concentration, bathymetry and zonal current velocity) were the only ones with predominant scores on the first principal component in at least one instance, and had low scores <0.10 occurring in only one model for each of these variables. SST was never the highest scoring variable in any model, but showed absolute scores ranging from 0.31–0.58 except in two cases when it was <0.1 . SST was only the second-best explanatory variable in two cases:

for common murre and crested auklet data, both from 2016. The two other variables used in the habitat model (meridional current velocity and the bathymetry gradient) were never among the higher-scoring factors. Meridional current velocity showed absolute scores ranging 0.18–0.35 except in two cases when it was <0.1 ; for bathymetry gradient, the absolute scores were 0.10 or less in three models, and reached only 0.17 at most.

In each case-specific projection (**Supplementary Figure 1**), the highest levels of habitat suitability were found off the north-eastern coasts of the island, whereas lower levels usually appeared off the southern coast.

This pattern was particularly evident in the years 2016 and 2019 across species, when high levels of suitability were generally found from 63 to 66°N; whereas this was less marked in 2017 (common murre and crested auklet datasets), when the distribution of high suitability areas tended to be more balanced off the north and south coasts.

When merging predictions at the species level (**Figure 4**), it was clear that highly suitable foraging habitats were available for the birds off the north-east coasts of the island. However, projections for thick-billed murres were unique in predicting large favourable areas to the north up to the Bering Strait, whereas suitable areas for common murres were in a relatively narrow band north-east from the island to the continent. For

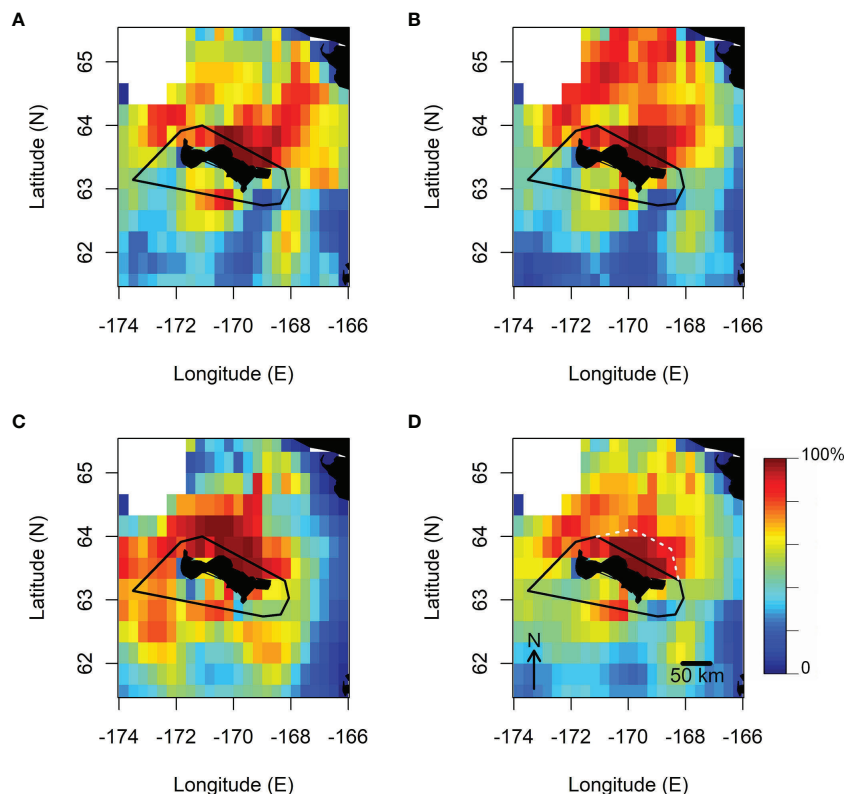


FIGURE 4 | Results of the Mahalanobis Distance Factorial niche analysis, showing the projected habitat suitability levels (expressed in %) of common murres (**A**); thick-billed murres (**B**); crested auklets (**C**), and for the three species combined (**D**). The boundaries of the ATBA around St. Lawrence Island is shown in black lines, and the white dashed lines indicate the suggested 35 km extension of the ATBA. These projection maps do not account for distance from the tracked colony as a covariate to evaluate regional habitat suitability.

crested auklets, the marine areas predicted as suitable did not extend as far to the north as it was predicted for the murres, however these areas spread more to the western sector of the island.

Overall, across species, the most suitable marine habitats for the seabird community breeding on St. Lawrence Island were projected to be concentrated off the north-east coasts of the island. However, this relatively small patch of high suitability (>90%) extended from the island to about 50 km offshore, more than twice as much as the ATBA.

Murres' Diving Behaviour and Diet

Data collected through time-depth recorders retrieved from two thick-billed murres indicated shallow diving behaviour during daytime, up to 41 m depth (Figure 5), and shallower than 10 m during the Arctic summer twilight. Dive bouts exhibited by murres during daytime often showed typical benthic dive behaviour (constant maximal dive depth to specific depths between 37 and 41 m). These benthic dives were not numerous

(7.6 and 4.0% of 236 and 330 dives recorded), nevertheless contributed disproportionately to total bottom time recorded by the two birds (17.0 and 9.5% of 101 and 143 min. of total bottom time, respectively). These results indicate that the birds likely relied, at least partially, on the benthic shelf habitat for provisioning.

This was supported by the direct observations made on the murres' diet. Prey brought to the nest by both species of murres consisted of fish species only (Table 3). Capelin *Mallotus villosus* and Pacific sand lance *Ammodytes hexapterus* were the only identified species of pelagic prey; whereas three identified taxa of benthic prey were observed, among which the Pricklebacks (Stichaeidae) were the most often found. A substantial proportion of the observed prey could not be identified, in both murre species and years ($35.5 \pm 19.6\%$). Considering only the identified prey species, the diet of common murres consisted of benthic fish at 33.3 and 77.9% in 2016 and 2017, respectively, and that was 70.0 and 94.9% for the thick-billed murres.

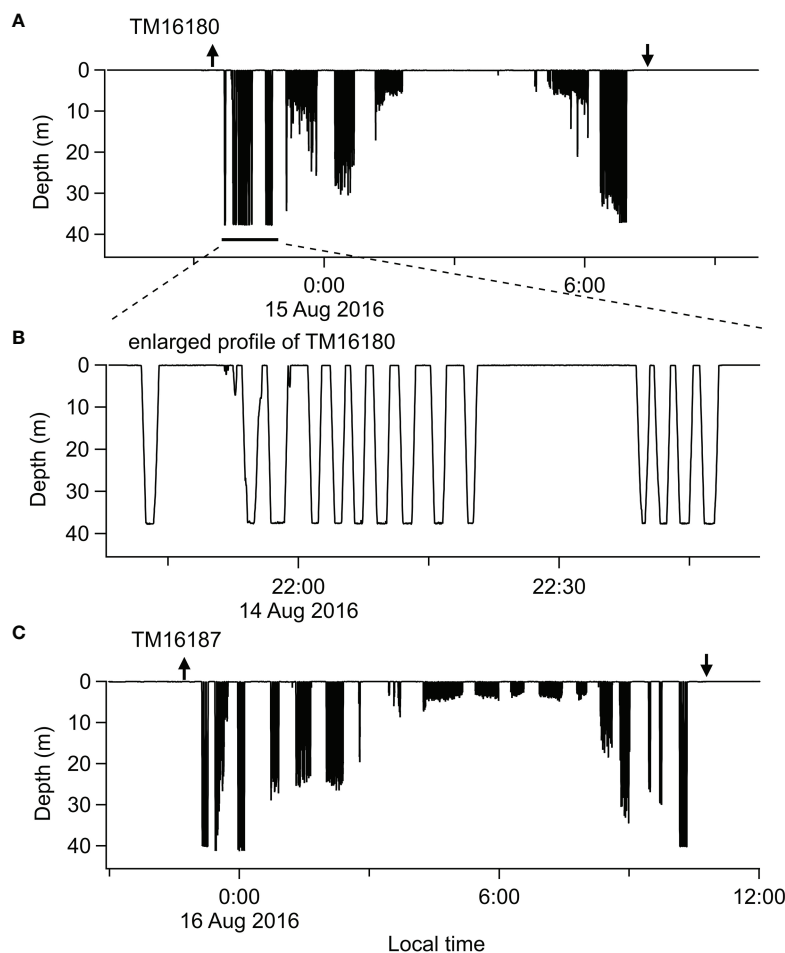


FIGURE 5 | Time-depth records collected from two thick-billed murres *U. lomvia* (TM16180 and TM16187) (A, C) surveyed from Tuqaghuk colony during the chick-rearing stage in 2016. The arrows indicate trip departure (up arrow) and return (down arrow) based on acceleration and temperature. The middle panel (B) is detailed profiles of dives reaching to constant depth (37.6–37.8 m), showing characteristic benthic diving behaviour.

TABLE 3 | Food items delivered to the chicks by common and thick-billed murres at St. Lawrence Island in 2016 and 2017.

Food item	Common murre <i>Uria aalge</i>				Thick-billed murre <i>Uria lomvia</i>			
	2016		2017		2016		2017	
	n	%	n	%	n	%	n	%
Capelin <i>Mallotus villosus</i>	2	15.4	17	11.3	2	9.5	0	0.0
Pacific sand lance <i>Ammodytes hexapterus</i>	6	46.2	4	2.7	1	4.8	2	2.8
Total Pelagic fish	8	61.6	21	14	3	14.3	2	2.8
Pricklebacks (<i>Stichaeidae</i>)	2	15.4	72	48.0	2	9.5	33	46.5
Sculpins (<i>Cottoidei</i>)	2	15.4	0	0.0	5	23.8	1	1.4
Cod (<i>Gadiformes</i>)	0	0.0	2	1.3	0	0.0	3	4.2
Total Benthic fish	4	30.8	74	49.3	7	33.3	37	52.1
Unidentified fish prey	1	7.7	55	36.7	11	52.4	32	45.1
Total	13	100.0	150	100.0	21	100.0	71	100.0

Fish species was identified during direct observation (2016) or from photographs (2017). Unidentified fish prey likely include those species or groups listed above.

Isotopic Niche Variability

Isotopic data were available for all studied species and years, with 52–96 samples available per species (see **Table 4** for sample sizes per species and year). In common and thick-billed murres, the stable isotope signatures of birds with GPS data overlapped the broad spectrum of year-species-specific isotopic niches (**Figure 6**). This indicates that the diets and foraging behaviour of GPS-sampled birds were representative of species-specific foraging patterns typical for the breeding murre populations sampled on the island. However, in black-legged kittiwakes, the one bird that had both GPS and isotopic samples, appeared outside the ellipses (**Figure 6D**); indicating that the behaviour of that single individual likely represents a smaller portion of the population foraging trips in the nearshore habitat, while the majority of birds are likely to have different foraging patterns that we were not able to document through GPS tracking. Finally, no crested auklet with isotopic sample had concomitant GPS data, and thus it was not possible to assess representativity in this case.

DISCUSSION

Spatial Distribution

Using the first individual GPS tracking data collected on four seabird species breeding on St. Lawrence Island, our study revealed that three of these species exploited at-sea habitats outside the ATBA: the common and thick-billed murres, and the crested auklet. Movements extending beyond the ATBA boundaries were repeatedly observed in these species despite the limited number of tracks that were collected.

The results from murres are particularly illustrative of a mismatch between ATBA and birds foraging distributions.

Specifically, the murre foraging ranges measured in our study are relatively small compared to other study sites. Common murres from the Bering and Chukchi Seas showed foraging ranges reaching up to more than double the values measured in our study (e.g., Hatch et al., 2000; Kokubun et al., 2016), whereas values from the Atlantic sites were more similar to those recorded in our study (e.g., Cairns et al., 1987; Gulka et al., 2019; Delord et al., 2020). In thick-billed murres, foraging ranges were greater both in the Atlantic (e.g., Benvenuti et al., 2002; Gaston et al., 2013) and Pacific (Hatch et al., 2000; Kokubun et al., 2016) regions than we recorded at St. Lawrence Island. Yet, despite their comparatively small foraging ranges, the ATBA north to the island was too narrow to contain the at-sea distribution of both species of murres breeding at St. Lawrence Island (**Figure 2**). Whether habitat use from the other colonies on the island are the same as predicted here, or remain within the ATBA is not known. Tracking studies on murres from the south-eastern Bering Sea showed dramatically divergent foraging distribution and habitat selection, depending on the colony location on the same island (Paredes et al., 2015). Thus, the fact that areas predicted as the most suitable (>90%) extend from the ATBA to the north only (**Figure 4**), should be considered a minimum region to be included in the ATBA.

For auklets, the high levels of predicted suitability expanded more widely than murres, to the west on the northern side of the island. These predictions match the density of at-sea observations of this species in this sector (Kuletz et al., 2020), probably mirroring the existence of large auklet colonies on the west side of the island (Piatt et al., 1988). Again, this indicates that at least a fraction of the auklets breeding on the north and west sides of the island, may largely distribute outside the ATBA during the breeding season (**Figure 3**; **Figure 4**), while this may not be true for the southern colonies.

TABLE 4 | Sample sizes available for the isotopic data in each studied species and year.

Year	Common murre <i>Uria aalge</i>	Thick-billed murre <i>U. lomvia</i>	Crested auklet <i>Aethia cristatella</i>	Black-legged kittiwake <i>Rissa tridactyla</i>
2016	20	28	17	11
2017	29	38	35	18
2018	10	7	16	11
2019	18	23	27	12
TOTAL	77	96	95	52

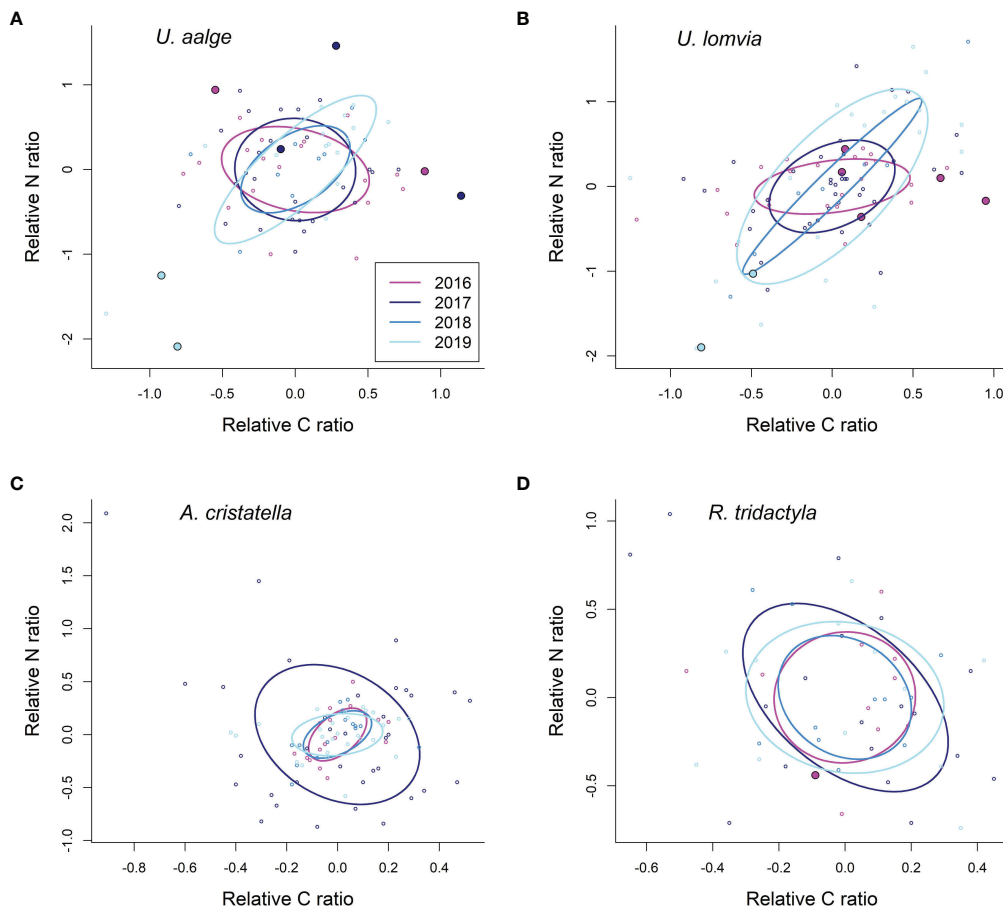


FIGURE 6 | Standard Bayesian ellipse areas (solid lines) corrected for small sample sizes **(A)**: common murres; **(B)**: thick-billed murres; **(C)**: crested auklets; **(D)**: black-legged kittiwake. The axes show the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic ratios relative to the average values per species and year. Points show individual values; the larger points represent isotopic signatures of birds for which GPS data was also available (no GPS data available among crested auklets with isotopic samples).

Areas selected by the three bird species were characterized by chlorophyll blooms, high longitudinal current, as well as deeper depths and slightly colder waters. These characteristics are congruent with the oceanographic conditions associated with higher densities of foraging seabirds observed around St. Lawrence Island in recent years (Nishizawa et al., 2020), providing observational support for the model prediction that the area north of St. Lawrence Island is an important habitat for these three seabird species during the breeding season.

Our study did not provide a sufficient record to evaluate whether foraging black-legged kittiwakes distributing beyond the ATBA during the breeding season. The foraging range measured here for a single individual breeding at St. Lawrence Island appears very small compared to values recorded elsewhere in the region. For example, tracking studies on this species in the Pribilof Islands in the Bering Sea have repeatedly measured bimodal foraging ranges averaging 27.2 and 201.4 km, respectively, during the chick-rearing period (Paredes et al., 2014). While our results correspond with repeated field observations of flocks of birds feeding a few hundred meters from the island during the

breeding season, it is likely they do not represent the full range of kittiwake foraging movements at this colony, as inferred from the isotopic niches occupied by kittiwakes breeding on St. Lawrence I. For instance, tracking data collected from breeding kittiwakes on Middleton Island in the Gulf of Alaska, also exhibit bimodal foraging ranges (Kotzerka et al., 2010): about half of the foraging trips recorded by GPS ($n=7$ among 15) ranged within 10 km of the breeding site (average 5.0 km, similarly to our study), but the others were 45.0 km on average (up to 92 km). At-sea surveys conducted concurrently with our at-colony work also indicate large numbers of kittiwakes (of unknown breeding status and colony of origin) during the breeding season outside the St. Lawrence Island ATBA (Nishizawa et al., 2020), hence suggesting potentially greater foraging ranges than what we measured from a single bird. However, in the absence of further quantitative evidence that kittiwakes breeding on St. Lawrence Island might forage outside of the current ATBA boundaries, we conservatively report that during chick-rearing at least a portion of their foraging trips occur within the current boundaries.

Effect of Environmental Variability

Despite fundamental differences in their at-sea ecology, the four studied species all highlighted the utilization of the shelf area immediately north-east of the island. For murres, the importance of this habitat was further emphasized by the high ratio of benthic prey in their diet, and coherently by a clear benthic-diving behaviour for the thick-billed murres. However, we argue that the importance of these benthic foraging areas to the St. Lawrence Island seabird community may not be as consistently important as it was suggested here.

First, murre diet observations were conducted in 2016 and 2017, which are considered relatively “warm” years (above the long-term survey mean) in the northern Bering Sea, with low winter sea-ice extent and warm summer water temperatures affecting the latitudinal distribution of high-biomass seabird prey species as well as their recruitment success (Stevenson and Lauth, 2019). This situation may have caused the low occurrence of pelagic fish in the diet observations, especially in 2017 which is considered the first extreme anomalous year in the recent regime shift (Huntington et al., 2020; **Table 3**), and this would in turn over-emphasize the importance of benthic habitats for murres. Common and thick-billed murres, as well as black-legged kittiwakes previously exhibited increased foraging on shelf-based prey during warm oceanographic conditions in the southeastern Bering Sea, in contrast to a higher reliance on pelagic prey during cold conditions (Will and Kitaysky, 2018). In this context, it is remarkable that 2017 is the only year in our habitat suitability model predictions where there is no clear segregation between the habitat suitability levels north and south of St. Lawrence Island (**Supplementary Figure 1**). This situation occurred at a time when common murres from this island showed a significant increase in their nutritional stress levels, and a shift in their isotopic niche indicating higher reliance on benthic prey coincided with a decline in the abundance of pelagic forage fish in the region (Will et al., 2020b). The other two summer seasons in our survey, 2018 and 2019, were even warmer in the northern area, and are among historical lows in winter sea-ice formation (Duffy-Anderson et al., 2019; Huntington et al., 2020). These years were associated with increased nutritional stress in all seabird species studied here (Will et al., 2020b). Hence, the recent regime shift to warmer conditions in the northern Bering Sea may cause additional nutritional stress to seabirds, with an observed response to further rely on benthic food sources for the common murre.

Second, multiple studies have shown that murres and kittiwakes from the Bering Sea exhibit variable foraging ranges in response to changes in food resources availability in their immediate environment. For instance, in years of low levels of local food resource, black-legged kittiwakes switched to substantially longer-distance foraging trips to the oceanic basin (Paredes et al., 2014). Similarly, thick-billed murres prolonged their foraging trip duration and enlarged foraging radius in years when they fed less on pelagic fish (Kokubun et al., 2018). This comparison, together with the result that sea-ice loss in the northern Bering Sea was associated with increased nutritional

stress in all seabird species studied from St. Lawrence Island (Will et al., 2020b), indicates that seabirds from this island may also show variable foraging habitats and ranges (and thus, variable propensity to reach outside the ATBA), in different food resource conditions. Considering the shift to a warm regime during our study years (Stevenson and Lauth, 2019; Huntington et al., 2020; Will et al., 2020b), and thus potentially to further reliance on benthic foraging habitat for murres, it is possible that the seabird community of St. Lawrence Island may have shown different foraging ranges than what may occur under other environmental regimes. Specifically, with the long-term trend to northward distribution shifts in marine benthic resources under the effect of regional warming (Grebmeier et al., 2015; Zhang et al., 2022), and a general reduction in the availability of Arctic Cod (*Boreogadus saida*) for seabirds in the region (apparently unavailable to murres in our study), it would be plausible that such unusually warm conditions may drive the St. Lawrence Island birds at-sea distribution further north too. However, none of the murre species' foraging range increased from 2016 to 2019, and it even decreased in common murres. This indicates that these birds may be switching to benthic foraging, after reaching the limits of their ability to target north-shifting pelagic resources in the current warm regime. Thus, they may not be primarily benthic specialists, and instead may rely less on benthic resources during colder oceanographic regimes. Further tracking studies under different regimes would be needed to formally test this point and quantify how the foraging range variability may affect the exploitation of habitats beyond the ATBA.

Recommendations for ATBA Design and Management

The at-sea distribution of breeding murres and other seabirds including kittiwakes has been used as an indicator to quantify the impact of anthropogenic marine activities on the environment (e.g., Eastern Canadian Arctic: Gaston et al., 2013; southern North Sea: Peschko et al., 2020). Using tracking techniques, it has also been possible to guide the implementation of ATBAs based on distribution hotspots of seabird communities (e.g. in the South Atlantic: Requena et al., 2020). According to the seabird tracking data collected from St. Lawrence Island, the current ATBA boundaries do not fully encompass the marine habitats used by seabirds during the breeding season. Instead, the tracking data provide support for the initial boundaries based on recommendations from St. Lawrence Islanders (Huntington et al., 2019). During the review process at the IMO these boundaries were reduced for fear that a large ATBA would hinder navigation in the region, an argument used to reduce ATBA's elsewhere as well (e.g., Peninsula de Osa off the Pacific coast of Costa Rica, Huntington et al., 2019). Specifically, the current ATBA polygon coordinates were chosen to accommodate for the neighboring shipping routes, as well as the limits of the contiguous Exclusive Economic Zones of the USA and Russia (Huntington et al., 2019). Based on the results presented here, in order to adequately protect important ecological and cultural marine resources, the ATBA around St.

Lawrence Island should be extended further to the north-northeast, by about 35 km (18.9 nautical miles), to capture most of the predicted area of maximal habitat suitability (**Figure 4**). Such an extension would address the following shortcomings in the current ATBA boundaries.

First, the current ATBA design inadequately sets boundaries close to the island's north-eastern shores, where most of the seabird breeding sites are located (Piatt et al., 1988; **Figure 3**), making it more likely that seabirds from these northern colonies may distribute beyond the ATBA. Moving this northern boundary further offshore, would maximize conservation benefits on these bird-rich northern shores which are a focal point for murre egg harvesting by the islanders (Will et al., 2020a).

Second, an extended ATBA would encompass the entirety of the high suitability (>90%) area predicted for the breeding seabird community that is immediately north of the current ATBA boundary. This high suitability area highlighted from our model relates mostly to alcids (murres and auklets), which, as diving birds, may be particularly susceptible to impacts from oiling (Wiese et al., 2004; Hedd et al., 2011), as they spend more time in contact with seawater (more so than the kittiwakes, King et al., 2021).

Besides, and more generally, the wider the regulation zone, the stronger the buffer effect to dilute acute threats (including noise, displacement, atmospheric pollution, oil, discharge) in a wildlife-rich area. Such an approach involving buffer zones along shipping routes has recently been suggested to better protect Arctic marine megafauna (Pirota et al., 2019), and is particularly useful near areas with large aggregations of animals. Similarly, a general outcome of extending the ATBA into an area where shipping traffic is reduced may also improve safety at sea for local fishing activities operated from small boats (Huntington et al., 2015).

And finally, this highlighted area of maximal habitat suitability for seabirds is similar to an area of high ecological importance to other harvested resources (marine mammals, fish) computed for St. Lawrence Island in the absence of tracking data on seabirds (Krenz, 2014). Hence, this area is not specific to seabirds but is also an important one for fish and marine mammals, adding support to including this key region in the ATBA.

To balance marine conservation with shipping safety, a hybrid solution is to implement a dynamic ATBA (Huntington et al., 2019). In the present case, the most practical version of this would be a seasonal extension of the ATBA, as described above, such that during the seabird breeding season (May–August) foraging areas are well-protected, given that this same time-frame is when shipping traffic is likely to be the most intense (Hauser et al., 2018; Stevenson et al., 2019). Then, during the rest of the year when sailing conditions are more hazardous the boundaries would be reduced, giving ships more room to maneuver. Seasonal adjustments could also be made for the presence of spectacled eiders, whales and walrus in winter and early spring at the documented aggregation sites (Noongwook et al., 2007; Lovvorn et al., 2009; Grebmeier, 2012; Grebmeier

et al., 2015). Alternatively, if a vessel management system were in place, a more adaptive ATBA could be implemented which would be able to account for the variability in habitat use indicated by the stable isotope standard ellipses in this study (Maxwell et al., 2015; Maxwell et al., 2020). Natural environmental variability and current transformations underway in the Pacific Arctic (Grebmeier et al., 2015; Stabeno and Bell, 2019; Huntington et al., 2020) may result in shifts in habitat suitability, corresponding to interannually different seabird distributions (e.g., Nishizawa et al., 2020; Kuletz et al., 2020). For instance, we suggest that a dynamic management of the St. Lawrence ATBA could be based on surface isotherms to reflect ecological habitat distributions (Stevenson and Lauth, 2019). Such mobile areas have been implemented effectively elsewhere and allow managers to quickly adjust boundaries based on near-real time information (hazardous sea-ice conditions for example, or quick feedback on recent ship strikes or other accidents; Maxwell et al., 2015; Huntington et al., 2019; Maxwell et al., 2020).

Study Limitations

This study's primary objective was to evaluate the effectiveness of the current St. Lawrence Island ATBA boundaries at separating vessel traffic from seabird foraging habitat. Here we identify the shortcomings of the study and discuss whether or how they may affect our ability to draw conclusions about seabird habitat use during the breeding season as it relates to the ATBA boundary north of St. Lawrence Island. Although our tracking data set is based on a small number of individuals, we repeatedly observed individuals from three species and across two breeding stages travel beyond the ATBA boundaries, indicating that birds from these northern colonies may come into contact with increased shipping-related threats in the region. To evaluate how representative these few individuals were of their respective species we used stable isotopic data, dive behavior and diet observations to complement our knowledge on the birds' foraging niche. While these approaches do not directly translate into spatial distribution or inform us on the proportion of birds reaching beyond the ATBA boundaries; the details gained on habitat use at their foraging locations are crucial elements to evaluate population sensitivity to threats and ultimately to adjust conservation policies.

Representation of seabird colonies as well as seabird species may also be considered somewhat limited in our study. Foraging range may vary across colonies due to competition-induced effects, habitat availability, and colony size (e.g., Ballance et al., 2009; Gaston et al., 2013). Hence the island-wide extrapolations shown in **Figure 3** should be taken with caution. However, by keeping the observed distribution radius constant across colonies, we highlight that the current ATBA's design with inconsistent width from the shore is likely to create a discrepancy in the birds' protection level across the island. We acknowledge that because we tracked seabirds from colonies situated on the island's northern coasts only, our results do not necessarily imply that a similar proportion of birds reach outside the ATBA boundaries at all colonies around the island. Rather,

we make the case that where the ATBA is the narrowest (northern side), it does not cover the relatively small at-sea distribution radius measured for three species during the breeding season. Thus, in line with this limitation in our sampling set-up, our recommendation to extend the ATBA applies only to the northern shore of the island. Although our study focused on some of the most numerous and culturally important species, several other species may remain to be studied to fully encompass the seabird community. These include other locally abundant species (e.g., the least auklet *Aethia pusilla*), or those that also have traditionally been or still are harvested by the islanders (pigeon guillemot *Cephus colomba*, horned puffin *Fratercula corniculata*, pelagic cormorant, *Phalacrocorax pelagicus*; Naves, 2018). Thus, further tracking surveys may still be warranted, however smaller GPS tags would need to be developed (e.g., for least auklets), and the issue of small sample sizes, due both to low accessibility to the colony and high sensitivity of St. Lawrence birds to human disturbance, would still persist.

CONCLUSIONS

As sea ice is rapidly lost in the Arctic, the region is threatened by risks from emerging industrial activity, such as the development of commercial shipping traffic. Proactive strategies are necessary to safeguard the marine environment for the people and wildlife that rely on it. Implementing area-based management tools such as ATBAs based on ecological and culturally important wildlife areas requires reliable information on animals' at-sea distribution (Hays et al., 2019). The scientific data from our study contributes concrete quantitative and conservative measurements of the St. Lawrence Island seabird community's habitat use that were missing at the time of implementing the local ATBA. Based on these data and our modelling results, we recommend extending the northern boundary of this ATBA 35 km to the north-northeast. Due to the variability observed in isotopic niches and in environmental conditions during our study period, we further advise that a more dynamic approach to the St. Lawrence Island ATBA boundaries be considered. Depending on the region's capacity these boundaries could be based on key environmental features monitored in real-time, or be seasonally proscriptive to maximize wildlife protection and minimize risks to ships. Regular re-evaluation of the boundaries should be undertaken given the rapid environmental changes occurring in this region.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: ADS (Arctic Data archive System) of the National Institute of Polar Research:

Behavioral and ecological data on seabirds in St. Lawrence Island, 2016: <https://ads.nipr.ac.jp/data/meta/A20191227-002/>

Behavioral and ecological data on seabirds in St. Lawrence Island, 2017: <https://ads.nipr.ac.jp/data/meta/A20191227-003/>

Behavioral and ecological data on seabirds in St. Lawrence Island, 2018: <https://ads.nipr.ac.jp/data/meta/A20191227-004/>

Behavioral and ecological data on seabirds in St. Lawrence Island, 2019: <https://ads.nipr.ac.jp/data/meta/A20191227-005/>.

ETHICS STATEMENT

The animal study was reviewed and approved by University of Alaska Fairbanks Institutional Animal Care and Use Committee protocol #471022, USFWS scientific collection permit #MB70337A, Alaska Department of Fish and Game's permits #19-140, 18-131, 17-104, 16-089.

AUTHOR CONTRIBUTIONS

J-BT, AW, AK, and AT lead the writing. J-BT, AW, and AT conducted the analysis. AK, AT, and AW organized the funding. J-BT, AW, ST, AK, and AT conducted field work. All contributed writing and final edits.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.875541/full#supplementary-material>

Supplementary Figure 1 | Results of the second Principal Component Analysis in the MADIFA computed from bird tracks for each dataset (species: COMU):

common murre, TBMU: thick-billed murre, CRAU: crested auklet; and year and breeding stage). Results show % of variance explained by the two first principal components, and correlation coefficients between the MADIFA components and the variables (bathymetry, bathymetry gradient, sea surface temperature, sea surface chlorophyll concentration, and zonal and meridional current velocity). In each case, the two variables with the highest scores are highlighted in red. A map with projected habitat suitability (expressed as %; the boundaries of the ATBA

around St Lawrence Island is shown in black lines); and histograms of the available (open bars) versus utilized (shaded bars) range of relative values for each environmental variable are presented for each species and stage.

Supplementary Figure 2 | A flowchart detailing the steps followed in this study from the case-by-case habitat suitability models to the final projections accounting for all studied species, years and breeding stages.

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Predicting the Foraging Habitats of Sympatrically Breeding Gadfly Petrels in the South Pacific Ocean

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Gadfly petrels (genus *Pterodroma*) are one of the most threatened groups of birds. They are exceptionally well adapted to forage over enormous areas to maximize chances of encountering prey. Their wide-ranging travel, extensive use of oceanic habitats beyond national jurisdictions (the high seas), and limited information on their at-sea distributions and foraging ecology pose several management challenges. Here, we examined the foraging distributions and habitat preferences of three gadfly petrels that breed on Phillip Island (Norfolk Island Group), in the southwest Pacific Ocean, and tested the ability of species distribution models (SDMs) to predict important marine habitats. GPS loggers were deployed in 2018 and 2019 on chick-provisioning black-winged petrels (*P. nigripennis*) and white-necked petrels (*P. cervicalis*) and in 2020 on Kermadec petrels (*P. neglecta*), and hidden Markov models (HMMs) were used to estimate behavioral states across 387 foraging trips. SDMs were built using six algorithms and the predictive performance of models constructed using conventional random cross-validation (CV) was compared to those constructed with spatially independent CV. All three species demonstrated dual-foraging strategies with short trips closer to the colony and longer, presumably self-provisioning, trips with maximum distances from the colony of several thousand kilometers for black-winged and white-necked petrels. Foraging areas of each species were distinctly partitioned across the Tasman Sea during long trips, but there was high overlap during short trips. Black-winged and white-necked petrels exhibited area-restricted search foraging behavior throughout their foraging ranges which spanned almost the entire Tasman Sea and into the western Pacific, whereas the foraging range of Kermadec petrels was restricted closer to the colony. Approximately half of each species' foraging range extended into the high seas. Response curves and variable importance between the two SDM CV approaches were similar, suggesting that model fitting was robust to the CV approach. However, evaluation using spatially independent CV indicated that generalizability of ensemble SDMs to new data ranged from poor to fair

for all three species. This suggests that the maximal-area foraging strategy of gadfly petrels (whereby they search opportunistically for resources across expansive oceanic habitats) results in weak or wide associations with environmental features making predicting important habitats extremely challenging.

Keywords: seabirds, seabird conservation and management, High Seas, Australia, *Pterodroma* petrels, at-sea distribution, foraging behavior, species distribution modeling (SDM)

1 INTRODUCTION

Seabirds are top predators that play important functional roles in marine and terrestrial ecosystems (Stapp et al., 1999; Sánchez-Piñero and Polis, 2000; Smith et al., 2011; Graham et al., 2018) and are widely recognized as valuable bioindicators of changes in the state of ocean ecosystems (Diamond and Devlin, 2003; Boyd et al., 2006; Parsons et al., 2008). Despite their ecological importance, seabirds are among the most threatened groups of birds with many populations having undergone rapid declines over recent decades (Croxall et al., 2012; Paleczny et al., 2015). Seabird conservation is often confounded by a lack of basic information about life histories and distributions at sea. This is especially true of seabirds in the tropics and subtropics (Bernard et al., 2021), regions which support diverse seabird communities, and which have received little research effort (Mott and Clarke, 2018). There is a particular lack of information about at-sea distributions for many South Pacific seabird taxa, despite this region representing the largest expanse of ocean on Earth (Croxall et al., 2012; Rodríguez et al., 2019). Such fundamental ecological knowledge is key to achieving effective conservation and enables researchers and policy makers to more accurately identify current and future threats (Burger and Shaffer, 2008; Lescroël et al., 2016; Bernard et al., 2021).

While the lack of information on many seabirds persists, anthropogenic pressures continue to degrade marine habitats and transform the integrity and stability of marine ecosystems, including the extent, availability, and predictability of prey resources for marine predators (Halpern et al., 2008; Hoegh-Guldberg and Bruno, 2010; McCauley et al., 2015). Obtaining information about the foraging distributions of wide-ranging seabirds has historically been logistically and financially challenging and biased towards shipboard surveys in coastal or nearshore habitats. Furthermore, studies using tracking technologies have been restricted by device sizes that could be deployed only on larger-bodied species (Burger and Shaffer, 2008). However, recent advancement in electronic tracking technology has led to miniaturized devices and transformed what can be learned about the ecology and distributions of even the smallest of seabirds (Nathan et al., 2008; Block et al., 2011; Halpin et al., 2018; Fischer et al., 2021). Furthermore, the advancement of the biologging field presents new opportunities to investigate the importance of seabird habitat on the high seas (i.e., marine areas extending beyond the 200 nautical mile limit of countries' Exclusive Economic Zones) (Beal et al., 2021; Davies et al., 2021). Although the high seas are classically considered important for migratory seabirds (Harrison et al., 2018), for many wide-ranging species,

particularly those in the order Procellariiformes, the high seas also represent critical foraging habitat during breeding stages (Ramírez et al., 2013; Clay et al., 2017; Ramos et al., 2017). Although a lack of global coordination for managing the high seas makes conservation challenging, growing awareness of the need for a global governance framework presents opportunities to implement appropriately planned conservation measures in the near future (Davies et al., 2021).

Procellariiform seabirds in the genus *Pterodroma* ("gadfly petrels") are among the most threatened of all seabirds (Croxall et al., 2012). Yet, there is often a lack of basic information about their biology, foraging behavior and at sea distributions (Rodríguez et al., 2019). Gadfly petrels are colonial-breeding species that generally nest on isolated oceanic islands (Warham, 1996; Brooke, 2004). These long-lived, monogamous, and strongly philopatric seabirds exhibit low fecundity, raising one altricial offspring per breeding season over an extended nesting period (Warham, 1996; Brooke, 2004). Gadfly petrels are highly pelagic, undertaking long foraging journeys over vast oceanic areas during both reproductive and migratory life stages (Rayner et al., 2012; Ramírez et al., 2013; Priddel et al., 2014; Rayner et al., 2016; Ramos et al., 2016; Clay et al., 2017; Ramos et al., 2017; Ventura et al., 2020). Among seabirds, gadfly petrels have especially high aspect ratio relative to wing loading, which makes them especially well-adapted for optimal use of wind conditions, enabling fast and efficient flight with low energetic costs (Spear and Ainley, 1997; Ventura et al., 2020). Although there is some evidence that gadfly petrels forage around oceanographic features such as seamounts (Rayner et al., 2012) and frontal regions (Rayner et al., 2008), the few existing studies on gadfly petrels that use high resolution GPS tracking (e.g., Ventura et al., 2020; Raine et al., 2021) tend to demonstrate that these species often do not have distinct preferences for, or rely completely on, one or two static or dynamic oceanographic features when foraging and make some of the longest foraging trips in the animal kingdom (Clay et al., 2019; Taylor et al., 2020; Ventura et al., 2020). Through optimal use of ocean basin-scale prevailing wind patterns, gadfly petrels appear to adopt a maximal-area foraging strategy to cover extremely large areas thereby increasing their chances of encountering food resources (Adams and Flora, 2010; Ventura et al., 2020). For example, Ventura et al. (2020) demonstrated that Desertas petrels (*Pterodroma deserta*) do not concentrate foraging in highly productive regions with predictable resources, and Clay et al. (2017) established that Murphy's petrels (*P. ultima*) do not have clear preferences for oceanographic or topographic features.

Here, we present the first Global Positioning System (GPS) tracking datasets for three species of gadfly petrel: black-winged petrel (*P. nigripennis*; IUCN status: Least Concern), white-necked petrel (*P. cervicalis*; IUCN status: Vulnerable) and Kermadec petrel (*P. neglecta*; IUCN status: Least Concern). We sought to first identify the hitherto unknown foraging behavior and at-sea distributions of these species using GPS loggers over multiple years at a single colony in the South Pacific Ocean. Second, we constructed ensemble species distribution models (SDMs) with three main goals: 1) to determine how these three sympatric species partition the environment when foraging; 2) to test if foraging habitat of the gadfly petrels in the present study could be generalized to new data using a spatially independent model evaluation approach; and 3) to consider how important foraging areas can be identified in the event that SDMs poorly predict foraging habitat in chick-provisioning gadfly petrels.

2 MATERIALS AND METHODS

2.1 Field Methods

2.1.1 Study Site and Species

Fieldwork was conducted on Phillip Island (29°07'S, 167°57'E, **Figure 1**). Phillip Island is a small (207 ha) and uninhabited

subtropical island in the Norfolk Island Group, an Australian external territory in the South Pacific Ocean. Phillip Island is a globally important colony for seabirds and supports considerable diversity with 13 species breeding there annually. The island is particularly important because it supports breeding populations of four gadfly petrel species. The most abundant of the four species is the black-winged petrel (15,000 – 19,000 breeding pairs; Priddel et al., 2010; N. Carlile, unpublished data). The colony also supports the only Australian population of white-necked petrels [20 – 30 breeding pairs (Halpin et al., 2021)]; one of only two Australian populations of Kermadec petrel [56 breeding pairs (Carlile et al., 2021a; Carlile et al., 2021b)]; and a remnant population of the formerly abundant providence petrel [*P. solandri*; 10 – 100 breeding pairs (Carlile et al., 2021a; Carlile et al., 2021b)]. Elsewhere, established black-winged petrel breeding colonies occur in New Zealand on the Kermadec Islands, Manawatawhi/Three Kings (Great King, South West), Motuopao, Motupia, Simmonds, Motukokako (Piercy), East (Whangaokeno), Portland and Chatham Islands and on an islet off Cape Brett; in Australia on Lord Howe Island; in New Caledonia, Tonga and in French Polynesia on the Austral Islands (Gill et al., 2010; Priddel et al., 2010; Miskelly et al., 2019). White-necked petrel colonies occur on the Macauley Island (Kermadec Islands) (Miskelly et al., 2019); and Kermadec petrel colonies occur on the Kermadec Islands, Lord Howe

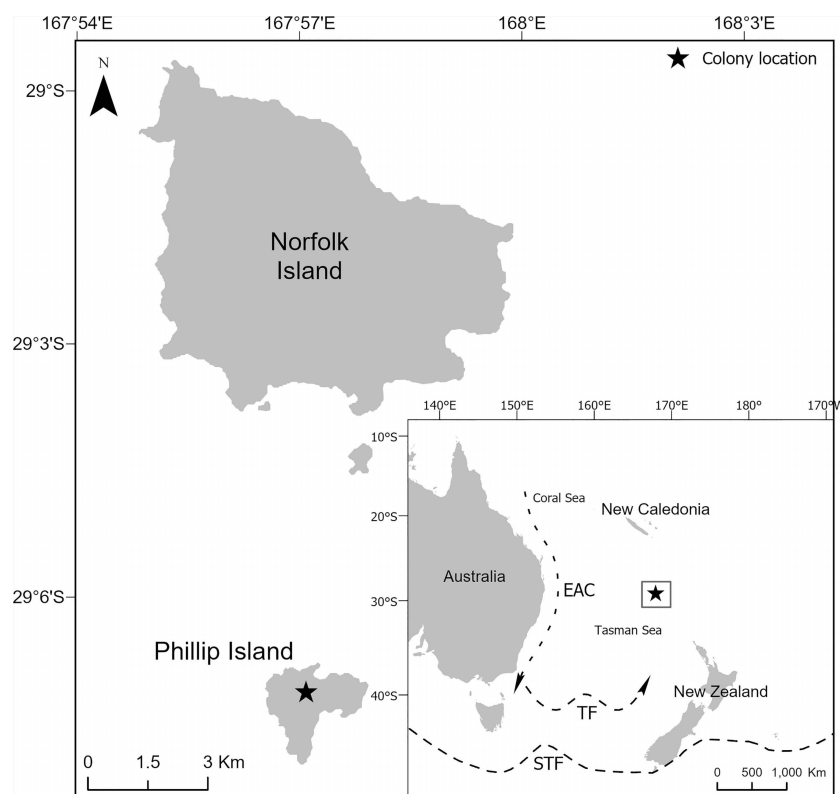


FIGURE 1 | The location of the Norfolk Island Group in relation to Australia, New Zealand and New Caledonia. Included are the approximate locations and direction of flow of the East Australian Current (EAC), the Tasman Front (TF) and the Subtropical Front (STF).

Island; in French Polynesia on the Austral Islands and Tuamotu Islands; in Chile on Easter Island, Juan Fernandez Island and San Ambrosio Island.; and in Mauritius on Round Island (Priddel et al., 2010; Miskelly et al., 2019).

All gadfly petrels produce a maximum of one offspring per year per pair. Adult black-winged petrels weigh on average 171 g ($n = 48$; this study) and nest predominantly in burrows, but occasionally deep crevices. Breeding occurs on Phillip Island from October to May with chicks hatching approximately in late January and fledging occurring in approximately May (Priddel et al., 2010). Little is known about white-necked petrel breeding biology, however, on Phillip Island adults weigh on average 464 g ($n = 27$; this study) and generally nest beneath stands of mature white oak (*Lagunaria patersonia*) among boulders, in rocky crevices, artificial cavities, and occasionally on the ground where dense vegetation cover is present. Breeding occurs on Phillip Island from approximately November to May or June (Priddel et al., 2010). White-necked petrel chicks generally hatch in January and February and fledge approximately in May and June. Adult Kermadec petrels weigh on average 444 g ($n = 52$; this study) and nest on the ground in sheltered areas between roots of mature white oak trees, or in dense thickets of introduced African olive (*Olea europaea*). More protracted breeding occurs in Kermadec petrels with egg laying occurring from September to May with a peak in November. The population tracked in the present study is the summer-breeding group which breeds approximately from September with chick fledging occurring from March. Black-winged and white-necked petrels are strongly faithful to their nest sites, returning to the same nest site each year, but Kermadec petrels often use different nests within the same general area each year.

2.1.2 Seabird Capture and Sampling

Capture and tracking of gadfly petrels occurred exclusively during the chick-provisioning period for black-winged and white-necked petrels from February to April in 2018 and 2019 and in January 2020 for Kermadec petrels. All tracked birds were provisioning chicks at a similar stage of chick development. Adult birds were captured by hand in their nests during the early to middle chick-provisioning periods from February to April in 2018 and 2019 (black-winged and white-necked petrels) and in January 2020 (summer-breeding Kermadec petrels). Black-winged petrels, were captured by hand at their nests both during the day and at night because they exhibit cathemeral nest site attendance. Due to the unpredictable timing of black-winged petrel nest attendance, we fitted one-way trapdoors to their nest entrances and checked for returning adults approximately every three to four hours while traps were installed. White-necked petrels, which display strictly nocturnal colony attendance, were captured by hand at their nest sites at night. Kermadec petrels, which display crepuscular colony attendance, were captured by hand at nests from early dusk to night.

All three study species are sexually monomorphic. To sex birds we collected 1–2 μ L of blood from the brachial vein using a sterile 26-gauge needle and whole blood was then placed onto FTA classic cards (Whatman International Ltd., Maidstone, UK).

Sex of individuals was determined using PCR reactions following Griffiths et al. (1998) by DNA Solutions (Wantirna, Victoria, Australia). Prior to attachment of GPS loggers, birds were weighed using Pesola scales ($\pm 0.3\%$, Pesola Präzisionswaagen AG, Switzerland) and fitted with a metal leg band supplied by the Australian Bird and Bat Banding Scheme.

We fitted petrels with custom Pathtrack Nanofix[®] archival GPS loggers (Pathtrack Ltd., Otley, United Kingdom) programmed to record position data every ten minutes and attached them to the two central rectrices using Tesa[®] tape (4651, Tesa Tape Inc., Charlotte, NC, USA). We fitted GPS loggers to 27 black-winged petrels in 2018 and 25 in 2019. In 2018, one GPS logger failed to record data, one was lost from the bird, and one was not retrieved before our departure from the colony. In 2019, one GPS logger was not retrieved before our departure from the colony. In 2018 we fitted 13 GPS loggers to white-necked petrels and 16 in 2019. One GPS logger in each year was not retrieved before our departure from the colony. In 2020 we deployed 9 GPS loggers on Kermadec petrels. All GPS loggers were retrieved. GPS loggers weighed an average of 3.23 ± 0.07 (g \pm SD; range: 3.1–3.38 g; $n = 34$). Average percentages of body mass for GPS loggers were 1.88% for black-winged petrels (range: 1.22–2.32%; $n = 48$), 0.70% for white-necked petrels (range: 0.59–0.88%; $n = 27$), and 0.72% for Kermadec petrels (range: 0.64–0.88%; $n = 9$), lower than the 3% threshold that is thought to negatively affect procellariiform seabirds (Phillips et al., 2003). The average duration (days \pm sd) between GPS logger attachment and removal on individuals was 14.6 ± 9.2 , 27.9 ± 11 and 12.1 ± 4.9 , respectively, for black-winged, white-necked and Kermadec petrels.

2.2 Data Processing and Analysis

2.2.1 GPS Tracking Data

All data were processed in the R programming language, version 4.1.2 (R Core Team, 2021), and spatial measurements were calculated on the World Geodetic System (WGS 1984) ellipsoid. Maps were produced in ArcGIS Pro (version 2.4.0; ESRI Inc., CA, United States) and data were projected in the Lambert Azimuthal Equal Area projection, centered on the breeding colony. GPS data were filtered to remove erroneous locations where successive relocations would require flight velocities exceeding 27.8 m.s^{-1} (100 km.h^{-1}) (Lascelles et al., 2016). GPS tracks were linearly interpolated using the package adehabitatLT (version 0.3.25; Calenge, 2006) by resampling all locations to an equal 10 min interval. We gap-filled GPS tracks except when periods of more than 1 hour occurred between location fixes.

2.2.2 At-Sea Distribution and Behavior

To determine foraging characteristics, we split tracking data into individual foraging trips originating from and returning to the colony using the 'tripSplit' function in the package, track2KBA (version 1.0.1; Beal et al., 2021). For each complete foraging trip, we used the 'tripSummary' function in track2KBA to calculate the duration (days) from departure to return to the colony and the maximum distance from the colony (foraging range, km).

We tested for differences in foraging trip duration and maximum distance from the colony between species in complete foraging trips using linear mixed effects models in the lme4 package (Bates et al., 2015) and a *post-hoc* Tukey's HSD test for multiple comparisons. To account for repeated trips made by the same individual we included individual identity as a random effect. We considered that sex-related differences in foraging behaviors would be highly unlikely because birds were tracked exclusively during chick-provisioning. Gadfly petrels share parental duties equally, with sex-related differences in foraging absent in chick-provisioning adults (Pinet et al., 2012; Clay et al., 2017). Nonetheless, we tested for intraspecific sex-related differences in maximum foraging range and trip duration using linear mixed effects models using the package lme4 with individual identities as random effects to account for repeated trips made by the same individual.

To identify important at-sea areas for each species, we first calculated the spatial scale of area-restricted search (ARS) using the function 'findScale' in the package track2KBA (Lascelles et al., 2016; Beal et al., 2021) for black-winged petrels (18 km), white-necked petrels (17 km) and Kermadec petrels (18 km). We then computed 50% kernel utilization

distributions using the R package adehabitatHR (Calenge, 2006) and used the scale of each species' ARS as the kernel smoothing parameter (h). Following previous studies, we define the 50% utilization distribution as the 'core' foraging area where birds spent 50% of their time (Ford and Krumme, 1979; Soanes et al., 2013; Lascelles et al., 2016). We estimated the representativeness of each species' core foraging area as a function of sample size to ensure that data were sufficiently representative of the foraging distributions of the colony-level populations. To do this we used the bootstrapping approach described in Lascelles et al. (2016) using the function 'repAssess' in the track2KBA package (Beal et al., 2021). We classified foraging trips according to whether they were short or long. To do this, we first qualitatively determined the distance classifications for each species by examining histograms of the frequency distribution of maximum trip distances (Figure 2). We then classified short trips as those with a maximum distance from the colony of < 1000 km for black-winged petrels; < 500 km for white-necked petrels and < 200 km for Kermadec petrels. We then produced a map of the short and long trips to demonstrate bimodal foraging strategies exhibited by each species.

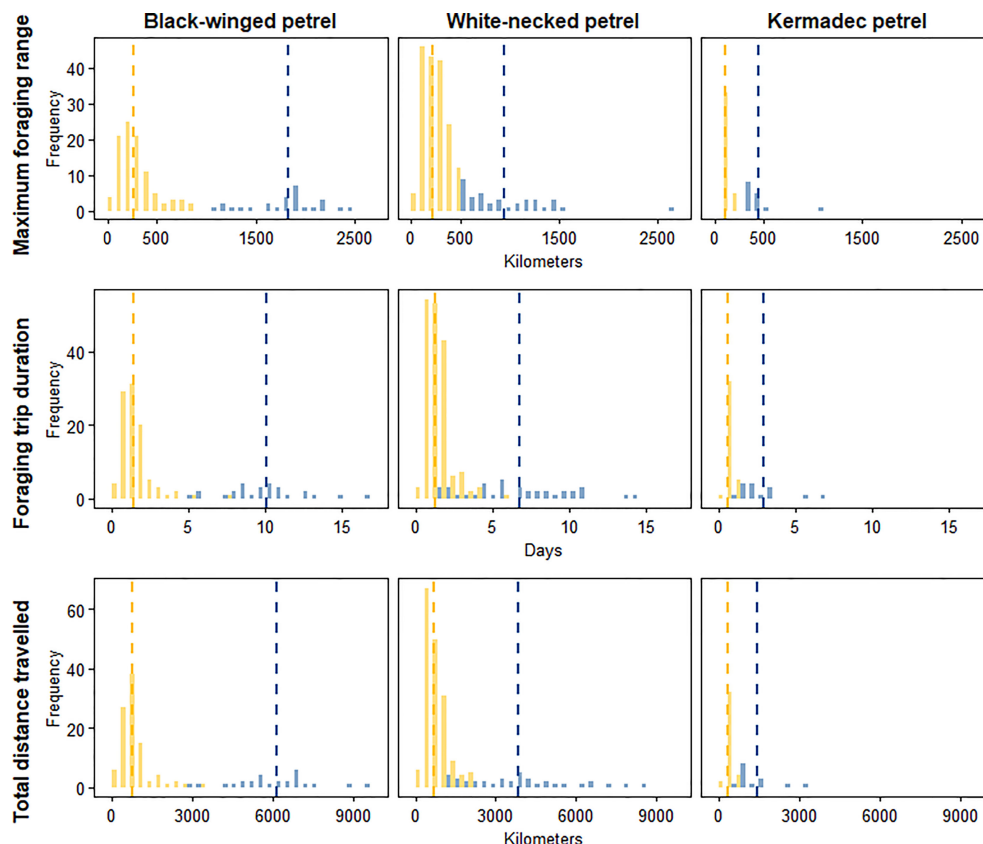


FIGURE 2 | Frequency distributions of maximum foraging range (km; upper row), duration of foraging trips (days; center row) and total distance traveled (km; lower row) for short trips (yellow) and long trips (blue) for black-winged petrels (left column), white-necked petrels (center column) and Kermadec petrels (right column). The dashed lines represent the mean of the frequency for short trips (yellow) and long trips (blue).

To distinguish the behavioral states of individuals during their foraging trips, we used hidden Markov models (HMMs). For each species, we fitted a three-state HMM to the interpolated GPS tracks using the momentuHMM package (version 1.5.4; McClintock and Michelot, 2018). Following Clay et al. (2020), to determine choice of initial values for step length and turning angle distributions, we selected these values randomly 100 times from within a range of biologically plausible values, then determined the most appropriate values as those that were closest to the most frequent estimation. We then estimated three behavioral states in the GPS tracks using two input variables: step lengths and turning angles. We considered directed flight (i.e., travel) to be associated with high flight speeds and shallow turning angles, area-restricted search (i.e., foraging) to be associated with moderate flight speeds and moderate to wide turning angles; and rest associated with low speeds and shallow to moderate turning angles. We used a gamma distribution for step lengths and a von Mises distribution for turning angles. We used the Viterbi algorithm in the package momentuHMM to estimate the most likely sequence of behavioral states from fitted models (Rabiner, 1989). Performance of the HMM behavioral state assignment was assessed by examining histograms of step lengths and turning angles for each species (**Supplementary Figures 1–3**), and each track was then visually assessed to ensure that state-space assignments were plausible. For each trip we calculated the percentage of time ($\% \pm \text{SD}$) that birds spent in each behavioral state and averaged the proportion across all trips to understand activity budgets. To test for differences between species in the proportion of time spent in ARS, we performed a one-way ANOVA test and a *post-hoc* Tukey’s HSD test for multiple comparisons. For each trip we also calculated the average duration (hours $\pm \text{SD}$) that birds spent in each behavioral state before switching to another state during a foraging trip. To determine whether nocturnal foraging might be an important feature of the species we tracked, we tested for differences in the proportion of time that each species spent foraging in daylight versus darkness using Student’s *t*-tests.

Lastly, to evaluate the extent of foraging across the species’ ranges we mapped the occurrence of locations inferred to be foraging (i.e., area-restricted search) by the HMMs on a 50 x 50 km grid cell size for each year of tracking and, for black-winged and white-necked petrels, which were tracked in more than one year, we overlaid gridded rasters to produce maps showing repeated grid cell use between years.

2.2.3 Species Distribution Modelling

We used SDMs to both characterize important foraging habitats for gadfly petrels and to assess the generalizability of models between spatial regions. We modeled the foraging locations identified by the HMMs against a suite of environmental predictors (**Table 1**). Environmental predictors were selected based on ecological knowledge of the drivers of subtropical pelagic seabirds’ foraging activity (Ballance et al., 2006; Hyrenbach et al., 2006; Ramos et al., 2015; Clay et al., 2017; Miller et al., 2018; Waugh et al., 2018). We used three static environmental predictors and seven dynamic environmental

TABLE 1 | Static and dynamic oceanographic variables, resolutions, measurement units and sources used in models to predict the foraging habitat of gadfly petrels.

Variable	Unit	Native resolution	Description and data source
Chlorophyll <i>a</i> (chl- <i>a</i>)	mg/m ³	4 × 4 km	Monthly mean chlorophyll <i>a</i> concentration. Chlorophyll <i>a</i> , Aqua MODIS, NPP, L3SMI, Global, 2003-present. (https://coastwatch.pfeg.noaa.gov/erddap/griddap/erdM11chl4mday.html)
Distance to colony	km	1 × 1 km	Static. Grid cell transit distance to the colony. Calculated in the present study. Accounts for transit distances around land.
Distance to seamount	km	NA	Static. Grid cell transit distance to the nearest seamount. Calculated in the present study. Accounts for transit distances around land. Global distribution of seamounts and knolls inferred, using a searching algorithm, from bathymetric data at 30 arc-sec resolution. (https://data.unep-wcmc.org/datasets/41)
Finite-sized Lyapunov exponent (FSLE)	day ⁻¹	1 _{/25} × 1 _{/25} °	Monthly mean backward-in-time FSLE and Orientations of associated eigenvectors. (https://www.aviso.altimetry.fr/en/data/products/value-added-products/fsle-finite-size-lyapunov-exponents.html)
Sea surface temperature front	°C	0.01 × 0.01°	Monthly mean sea surface temperature front. Calculated in the present study as the standard deviation over a 3 × 3 grid of the 1 km resolution sea surface temperature data using the Multi-scale Ultra-high Resolution (MUR) SST Analysis fv04.1, Global, 2002-present. (https://coastwatch.pfeg.noaa.gov/erddap/griddap/jplMURSST41mday.html)
Sea surface temperature	°C	0.01 × 0.01°	Monthly mean sea surface temperature. Multi-scale Ultra-high Resolution (MUR) SST Analysis fv04.1, Global, 2002-present. (https://coastwatch.pfeg.noaa.gov/erddap/griddap/jplMURSST41mday.html)
Sea level anomaly (SLA)	m	0.25 × 0.25°	Monthly mean sea level anomaly. National Oceanic and Atmospheric Administration (NOAA) CoastWatch, Sea Surface Height Anomalies from Altimetry, Global, 2017–Present. (https://coastwatch.pfeg.noaa.gov/erddap/griddap/needssSH1day.html)
Bathymetric slope	degrees	15 arc seconds	Static. Grid cell angle of depth slope. Calculated in the present study using the GEBCO Compilation Group 2021 gridded bathymetry data set (https://www.gebco.net/data_and_products/gridded_bathymetry_data/)
Wind speed	m/s ⁻¹	0.25 × 0.25°	Monthly mean horizontal speed of wind at 10 meters above sea level. ERA5 European Centre for Medium-Range Weather Forecasts (ECMWF) global reanalysis for the global climate and weather (https://cds.climate.copernicus.eu/cdsapp#/dataset/10.24381/cds.f17050d7?tab=overview)
Thermocline depth	m	0.083° × 0.083°	Monthly mean ocean mixed layer thickness (GLOBAL_MULTYEAR_PHY_001_030). Copernicus Marine Service (https://doi.org/10.48670/moi-00021)

predictors in our models (**Table 1**). Static predictors were: 1) the bathymetric slope, represented in degrees, and 2) distance (km) to seamounts and knolls as indicative of shelf-breaks and bathymetric features that could represent productive areas of upwelling; and 3) transit distance (km) from the colony as a proxy for the importance of accessibility to foraging habitat given that all birds were centrally-placed (i.e., had an intrinsic requirement to regularly return to the colony to provision nestlings). The seven dynamic oceanographic variables were: 1) sea surface temperature ($^{\circ}\text{C}$), and 2) sea surface temperature fronts measured by calculating the standard deviation of the sea surface temperature ($^{\circ}\text{C}$) within a 10 km buffer of the original 1 km resolution of the sea surface temperature grid as an indicator of frontal regions; 3) sea level anomaly (m) as an indicator of mesoscale eddies and ridges; 4) wind speed (m.s^{-1}) as an indicator of optimal transit conditions for gadfly petrels (i.e., Ventura et al., 2020); 5) chlorophyll *a* concentration (mg.m^{-3}) as a proxy for ocean productivity; 6) the finite-size Lyapunov exponent (FSLE; days^{-1}) to test the preference of birds for foraging in sub-mesoscale transport fronts; and 7) the depth of the thermocline layer (m). FSLE is based on Lagrangian reanalysis of satellite altimetry-derived surface currents (d'Ovidio et al., 2004; Cotté et al., 2015). Further information on the original spatial resolution and sources of environmental variables is provided in **Table 1**. Predictor variable rasters were scaled to a 1×1 km grid cell resolution using bilinear interpolation and were projected in the Lambert Azimuthal Equal Area projection centered on the breeding colony. Predictor variables were standardized using the 'scale' function in the raster package (Hijmans and van Etten, 2021) to improve the spread of the data. We applied a variance inflation factor test to ensure that predictor variables were not collinear and found no collinearity problems among the ten predictor variables.

We used a multi-model ensemble approach to test whether the environmental features could predict gadfly petrel foraging habitat. Using the biomod2 package (version 3.5.1; Thuiller et al., 2009; Thuiller et al., 2021) we fitted six algorithm types: Artificial Neural Networks (ANN), Classification Tree Analysis (CTA), Generalized Additive Models (GAM), Generalized Boosted Models (GBM), Multiple Adaptive Regression Splines (MARS) and Random Forests (RF). We used the default model parameters in biomod2 for all models except GBM where the bag fraction was set to 0.75 and maximum number of trees was set to 3000 (e.g., Elith et al., 2008). GAMs were specified to use Restricted Maximum Likelihood (REML); and the number of learning trees in Random Forests was set to 1000. We modeled the GPS locations that were inferred by HMMs to be foraging behavior as the response variable. For each foraging location we randomly sampled a single matched pseudo-absence because a ratio of 1:1 presence:pseudo-absence is most suited to the learning algorithms that we used to model the characteristics of foraging habitat (Barbet-Massin et al., 2012). Pseudo-absences were generated within foraging extents, which we separately defined for each species, by computing a minimum convex polygon around all available tracking locations.

To evaluate the ability of the models to predict the probability of foraging on new data, we compared two approaches, 1) conventional random *K*-fold cross-validation (CV) with 80% of each species' data for model fitting and the remaining 20% for testing (Elith et al., 2008) and 2) spatially independent *K*-fold CV (Roberts et al., 2017) using the blockCV package (Valavi et al., 2019). The latter approach to assessing model predictive performance is more robust because it ensures spatial independence of testing and training data thereby accounting for spatial structure in cross-validation data. Conventional random selection of training and testing folds that are not spatially independent commonly leads to underestimated error in spatial predictions and overestimated model performance and predictive power (Telford and Birks, 2009; Roberts et al., 2017; Hao et al., 2019; Valavi et al., 2019). Five folds were specified for both approaches. Spatially-independent CV used a spatial blocking size of 800 km for black-winged and white-necked petrels but had to be reduced to 250 km for Kermadec petrels due to their much smaller range size. Spatial blocks were randomly assigned using 200 iterations to find evenly dispersed folds and were generated based on the extent of each species' foraging range. Block size was chosen as the approximate range over which observations become spatially independent and was determined by constructing empirical variograms using the function 'spatialAutoRange' in the package blockCV. Predictive performance of both approaches was then evaluated using the True Skill Statistic (TSS) and Area Under the Receiver Operating Characteristic curve (AUC_{ROC}). AUC_{ROC} is a widely used measure of a model's predictive performance and its ability to differentiate presence and absence locations (Lobo et al., 2008). AUC_{ROC} values and associated performance evaluations range from 0 to 1, with excellent AUC_{ROC} : > 0.90 ; good AUC_{ROC} : $> 0.80 \leq 0.90$; fair AUC_{ROC} : $> 0.70 \leq 0.80$; poor AUC_{ROC} : $> 0.60 \leq 0.70$; very poor AUC_{ROC} : $> 0.50 \leq 0.60$; and AUC_{ROC} : ≤ 0.50 indicating predictive performance that is no better than random (Hosmer et al., 2013). We averaged the respective TSS and AUC_{ROC} values across model folds for each algorithm type and model. Due to the robust spatial independence of the blocked cross-validation approach we took the model evaluation metrics of this method as superior to those of conventional *K*-fold random CV models. We therefore interpreted the AUC_{ROC} values of the spatially blocked models as the more statistically credible approximation of model generalizability to new data for gadfly petrels.

Total consensus ensemble models were constructed based on all models for each CV method (so that fair comparisons between the performance of formal and ensemble models could be made). The conventional CV ensemble was built with an evaluation metric threshold applied such that models with $\text{AUC}_{\text{ROC}} < 0.8$ were excluded, but no evaluation metric threshold was applied to the spatial blocking ensemble due to the inherently low AUC_{ROC} values. Species-specific ensemble model response curves were constructed from the spatially blocked models and calculated as the median response across 10 replicate model runs within the biomod2 package using the algorithm-independent evaluation strip method following Elith et al. (2005), which facilitates direct

comparison of predicted responses from different statistical approaches on the same data.

We used multivariate environmental similarity surfaces (MESS; Elith et al., 2010) to check that differences in behavior of Kermadec petrels were not likely to have been caused by divergent environmental conditions in the year that they were tracked (January 2020) versus the years that black-winged and white-necked petrels were simultaneously tracked (February to April in 2018 and 2019). We computed MESS grids for each dynamic predictor for each month in which black-winged and white-necked petrels were tracked and used the overall MESS grid to assess the percentage of cells with negative values (cells with negative values represent those with conditions outside of the range present in the reference time period).

3 RESULTS

Over three breeding seasons, we obtained 387 complete foraging trips from 80 individuals of three species of sympatrically breeding gadfly petrels (**Table 2**). Core foraging areas (i.e., 50% utilization distributions) used by the sampled individuals were estimated to be highly representative of the core foraging areas of the respective colony-level populations for black-winged petrels (87.5%) and white-necked petrels (93.5%), but representativeness was lower for Kermadec petrels (68.5%) due to the lower sample size.

3.1 Foraging Characteristics

We found no sex-related differences in maximum foraging ranges and durations of trips made by black-winged petrels (foraging range: $F_{122} = 0.738$, $p = 0.541$; trip duration: $F_{122} = 0.613$, $p = 0.462$), white-necked petrels (foraging range: $F_{208} = 0.533$, $p = 0.595$; trip duration: $F_{208} = 0.198$, $p = 0.843$) and Kermadec petrels (foraging range: $F_{6.1} = -0.773$, $p = 0.469$; trip duration: $F_{5.8} = -0.59$, $p = 0.577$). Therefore, we pooled the data from both sexes within each species. When accounting for random effects of individuals making repeated trips, maximum foraging ranges differed between black-winged and white-necked petrels and black-winged and Kermadec petrels (Tukey's *post-hoc* test: $p < 0.001$ for both relationships; **Table 2**), but not between white-necked and Kermadec petrels (Tukey's *post-hoc* test: $p = 0.098$). Similarly, the duration of foraging trips was different between black-winged and white-necked petrels (Tukey's *post-hoc* test: $p = 0.0105$) and between black-winged and Kermadec petrels (Tukey's *post-hoc* test: $p < 0.001$), but not between white-necked and Kermadec petrels (Tukey's *post-hoc* test: $p = 0.0679$). Tracking data also indicated that all three species exhibited bimodal foraging strategies, alternating between short and long foraging trips (**Figures 2, 3**).

Behavioral state space modeling revealed that although all three species demonstrated area-restricted search foraging behavior throughout the entire range of their breeding distributions, they tended to concentrate foraging activity nearer (< 500 km) the colony (**Figures 4–6**). On average all species spent more than half of their time traveling, and a relatively small proportion of their

TABLE 2 | Summary of the GPS tracking dataset for birds that returned data (i.e., tracking device was recovered and remained functional for at least one trip).

Species	Year	No. of individuals (males/females)	No. of complete trips (short/long)	Sample rep. (%)	Trip duration (days)		Foraging range (km)		Cumulative trip distance (km)	
					Short	Long	Short	Long	Short	Long
Black-winged petrel <i>Pterodroma nigripennis</i>	2018	24 (14/7)	44 (33/11)	87.5	1.4 (0.1 – 7.6)	10.4 (5.9 – 16.9)	237 (19 – 846)	1,764 (1,168 – 2,214)	691 (29 – 3,161)	6,186 (4,154 – 9,642)
	2019	23 (13/10)	80 (64/16)		1.3 (0.3 – 4.3)	9.9 (5.2 – 15)	276 (29 – 807)	1,865 (1,131 – 2,487)	759 (102 – 2,509)	6,094 (3,004 – 8,929)
White-necked petrel <i>Pterodroma cervicalis</i>	2018	12 (3/9)	116 (96/20)	93.5	1.4 (0.1 – 5.6)	7.0 (2.1 – 10.8)	234 (25 – 433)	1,063 (546 – 2,680)	712 (38 – 2,141)	4,065 (1,559 – 8,565)
	2019	15 (2/13)	94 (76/18)		1.2 (0.1 – 3.9)	6.6 (1.9 – 14.7)	206 (30 – 480)	810 (520 – 1,451)	642 (59 – 2,117)	3,610 (1,181 – 7,833)
Kermadec petrel <i>Pterodroma neglecta</i>	2020	9 (5/4)	53 (37/16)	68.5	0.6 (0.2 – 1.2)	2.9 (1.2 – 6.9)	109 (57 – 229)	445 (331 – 1,086)	320 (125 – 583)	1,432 (812 – 3,298)

Data indicate foraging trip characteristics for complete trips and sample representativeness of sympatrically breeding gadfly petrels from Phillip Island (Norfolk Island Group) during chick-provisioning in 2018 & 2019 (black-winged and white-necked petrels) and 2020 (Kermadec petrels).

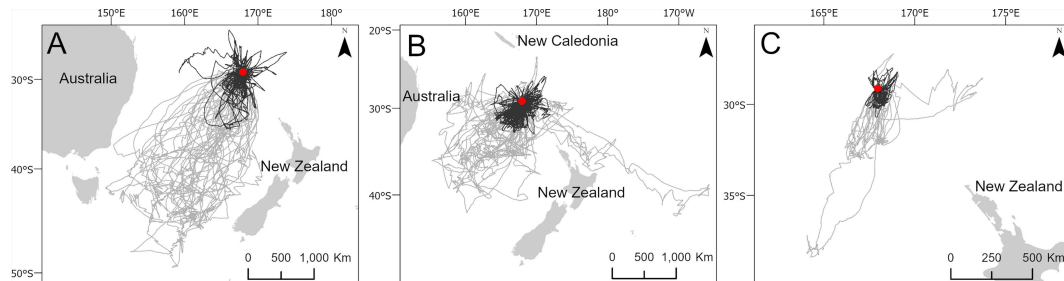


FIGURE 3 | Maps demonstrating the short (black) and long (grey) foraging trips of black-winged petrel **(A)**, white-necked petrel **(B)** and Kermadec petrel **(C)** bimodal foraging strategies. The colony location is indicated by a red circle. The number of trips in each category are detailed in **Table 2**.

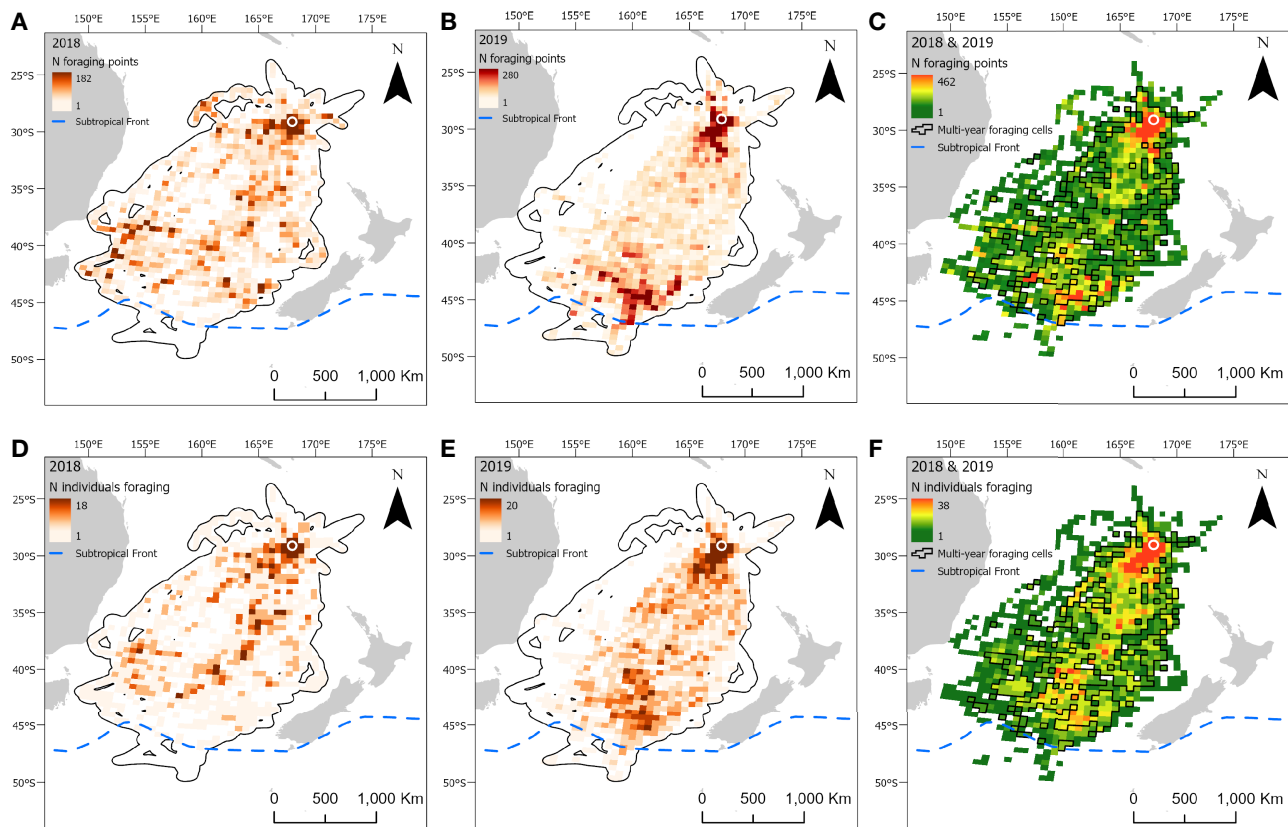


FIGURE 4 | At-sea distribution and locations of foraging behavior in chick-provisioning black-winged petrels (*Pterodroma nigripennis*). Grid cells (50 x 50 km) depict the number of foraging locations in 2018 **(A)**; $n = 24$ individuals) and 2019 **(B)**; $n = 24$ individuals) and combined number of foraging locations in 2018 and 2019 **(C)**. Number of individuals foraging in each grid cell in 2018 **(D)** and 2019 **(E)**; and the combined number of individuals foraging in each grid cell in both 2018 and 2019 **(F)**. Polygonised cells in C and F represent grid cells in which birds foraged in both years. The location of the breeding colony is represented by a white circle. Black polygons around the foraging areas **(A, B, D, E)** represent the home range (99% utilization distribution). The approximate location of the Subtropical Front is represented by a dashed blue line.

time resting during foraging trips (**Table 3**). We found significant between-species differences in the proportion of time spent in ARS behavior ($F_2 = 10.98$, $p = < 0.001$). Black-winged petrels spent proportionally less time in ARS than white-necked ($p < 0.001$, 95%

C.I. = [0.02 – 0.09]) and Kermadec petrels ($p < 0.001$, 95% C.I. = [0.04 – 0.14]), but there was no difference between white-necked and Kermadec petrels ($p = 0.2$, 95% C.I. = [-0.08 – 0.01]). We found no significant difference in the proportion of time spent

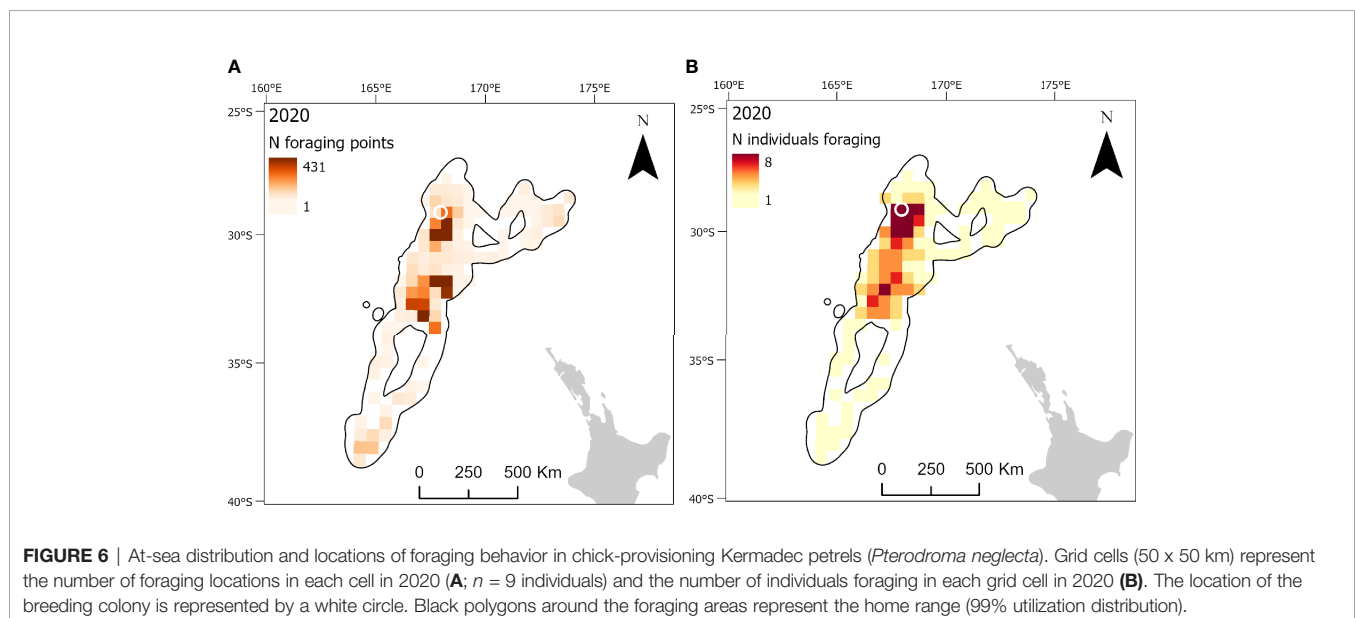
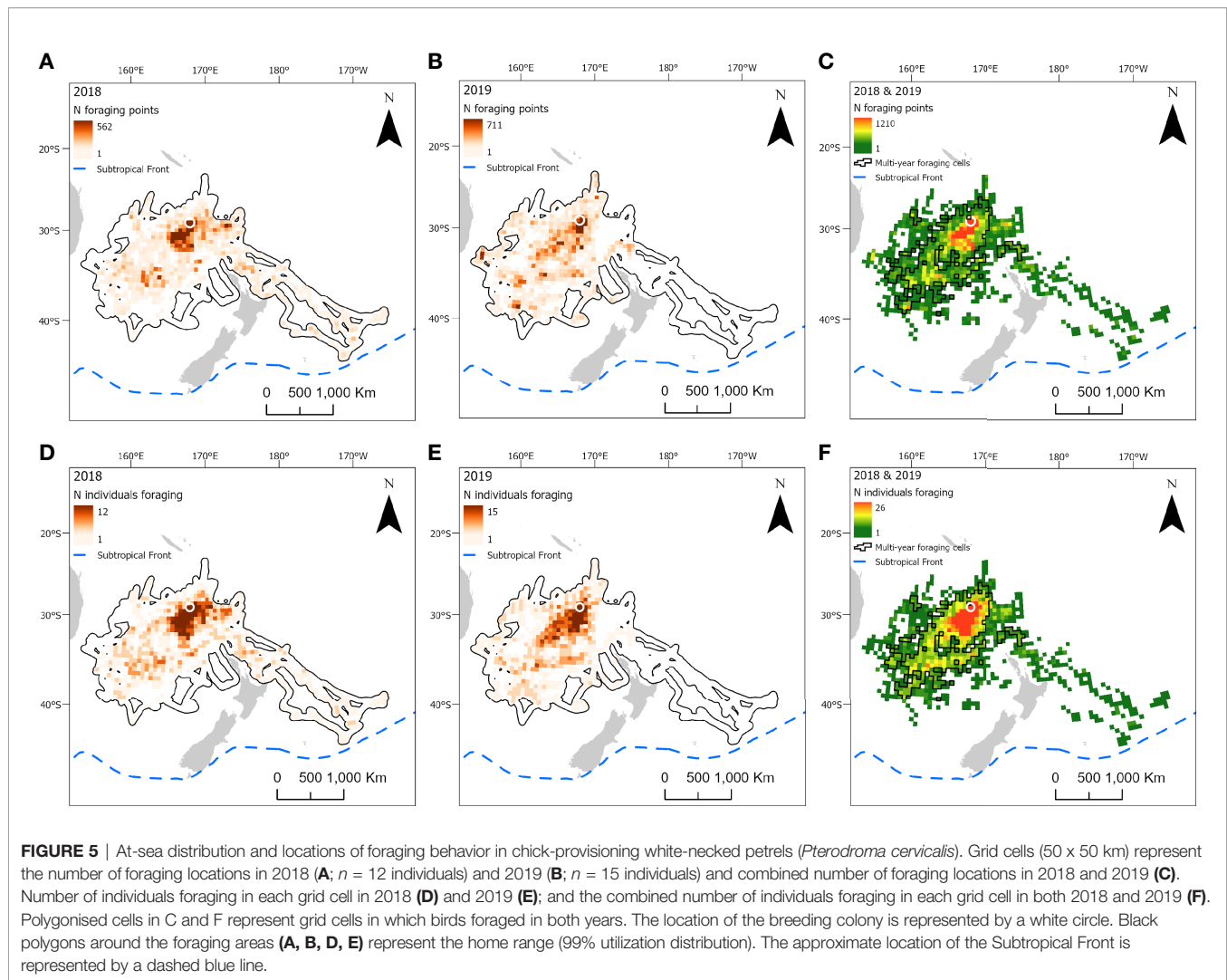


TABLE 3 | Average duration and percentage that gadfly petrels spent in travel, area-restricted search (ARS) and rest during foraging trips. Behavioral states were inferred from hidden Markov models (HMMs).

Species	Behavioral bout duration (hours/trip)						Percentage of time per trip					
	(Mean \pm SD)						(Mean \pm SD)					
	Travel		ARS		Rest		Travel		ARS		Rest	
	Short	Long	Short	Long	Short	Long	Short	Long	Short	Long	Short	Long
Black-winged petrel <i>Pterodroma nigripennis</i>	17.9 \pm 9.3	20.0 \pm 6.6	9.2 \pm 4.5	9.6 \pm 4.8	9.5 \pm 5.6	9.1 \pm 2.9	60.7 \pm 18.8	69.7 \pm 7.7	32.2 \pm 14	25.3 \pm 6.7	7.1 \pm 8.3	5.0 \pm 3.1
White-necked petrel <i>Pterodroma cervicalis</i>	17.9 \pm 9.3	20.0 \pm 6.6	9.2 \pm 4.5	9.6 \pm 4.8	9.5 \pm 5.6	9.1 \pm 2.9	52.7 \pm 16.7	55.1 \pm 13.1	35.4 \pm 15.9	34 \pm 9.1	11.9 \pm 11.8	10.9 \pm 10.1
Kermadec petrel <i>Pterodroma neglecta</i>	14.6 \pm 5.5	21.3 \pm 8.3	10.7 \pm 5.3	11.7 \pm 5.6	5.3 \pm 2.8	7.5 \pm 3.1	52.2 \pm 17.1	54.0 \pm 13.1	40.8 \pm 12.2	36.3 \pm 8.7	7.0 \pm 11.3	9.7 \pm 8

foraging during daylight and darkness in black-winged petrels (daylight: 30.4 ± 14.2 , darkness: 28.6 ± 17.1 ; t -test: $t_{(258)} = -0.986$, $p = 0.325$) and Kermadec (daylight: 37.9 ± 17.7 , darkness: 37.8 ± 20.8 ; t -test: $t_{(102)} = -0.013$, $p = 0.989$), but found that white-necked petrels spent proportionally more time foraging during daylight (daylight: 40.4 ± 15.4 , darkness: 28.5 ± 21.2 ; t -test: $t_{(400)} = -6.72$, $p < 0.001$).

3.2 At-Sea Foraging Distribution

Foraging ranges extended over vast oceanic areas including, for black-winged (Figure 4) and white-necked petrels (Figure 5), almost throughout the entirety of the Tasman Sea and, to a lesser extent, at the southern limits of the Coral Sea at its 30° south limit. Approximately 55%, 35% and 42%, respectively, of black-winged, white-necked and Kermadec petrel area-restricted search foraging locations occurred in international waters (outside of EEZs). All three species foraged broadly within the warm waters of the wind-driven, southward flowing East Australian Current (EAC) and to the southern extent of the eastward-flowing Tasman Front (TF), which separates the Coral Sea to the north and the Tasman Sea to the south and flows from the east coast of Australia into the western Pacific Ocean. Black-winged petrels made use of areas bordering the Subtropical Frontal Zone in the south of the Tasman Sea and foraged over an area of almost 4 million km², white-necked petrels over approximately 5 million km² including to the east of New Zealand bordering the Subtropical Frontal Zone, but Kermadec petrels (Figure 6) remained relatively close to the colony with a foraging range that spanned almost 0.5 million km². Grid cell analysis of foraging behavior revealed that gadfly petrels engaged in area-restricted search behavior throughout their entire foraging ranges. However, most grid cells occupied by foraging black-winged petrels on long trips were concentrated in the south of the Tasman Sea (Figure 4). Foraging ranges of both black-winged and white-necked petrels were larger in 2018 than in 2019 (Figures 4, 5). There was a high degree of overlap in foraging ranges of all three species, but black-winged petrels appeared to concentrate their long foraging trips considerably further south than the other species (Figures 4–6).

3.3 Species Distribution Modeling

Evaluation metrics for habitat models constructed with spatially independent CV were substantially poorer (AUC_{ROC} of 0.55 – 0.77; Table 4) than of models fit using conventional random CV (AUC_{ROC} of 0.93 – 0.95; Table 4). Despite these apparent differences in model performance, response curves and relative importance of predictor variable contributions of conventional CV and spatially independent CV ensemble models were similar (Supplementary Figures 4, 5) indicating consistent environmental relationships, regardless of the CV method. Both methods are likely to have poor generalizability to new spatial and temporal environment data because the spatially independent CV method is specifically designed to evaluate how well model predictions transfer to new environmental contexts. Ensemble model predictive performance for black-winged petrels was approximately equivalent to random

TABLE 4 | Number of presences and pseudo-absences used to build ensemble species distribution models (SDM) and the average values of fivefold conventional random cross-validation and spatially independent cross-validation for the two calculated model evaluation measures including true skill statistic (TSS) and area under the receiver operating characteristic curve (AUC_{ROC}).

Species	Presences	Pseudo-absences	Evaluation measures (ensemble models)			
			Conventional random cross-validation		Spatially independent cross-validation	
			TSS	AUC _{ROC}	TSS	AUC _{ROC}
Black-winged petrel <i>Pterodroma nigripennis</i>	20,513	20,512	0.70	0.93	0.19	0.55
White-necked petrel <i>Pterodroma cervicalis</i>	28,002	28,082	0.73	0.94	0.39	0.71
Kermadec petrel <i>Pterodroma neglecta</i>	4,456	4,437	0.78	0.95	0.48	0.77

classification (AUC_{ROC} = 0.55; TSS = 0.19), and performance was fair for white-necked (AUC_{ROC} = 0.71; TSS = 0.39) and Kermadec petrels (AUC_{ROC} = 0.77; TSS = 0.48) (Araujo et al., 2005; Hosmer et al., 2013). Distance from the colony (**Figure 7**) was the most important predictor, with all three species demonstrating a high probability of foraging closer to the colony. All species showed a preference for foraging in warmer sea-surface temperatures, and for black-winged and white-necked petrels SST was the second most important environment variable for predicting the location of foraging. Black-winged and white-necked petrels preferred to forage in areas with higher wind speeds (albeit wind speed had only low (3.1%) variable importance for white-necked petrels), but Kermadec petrels preferred lower wind speeds (**Figure 7**). Models presented some evidence that black-winged petrels expressed preference for foraging in areas with shallower thermocline depths (i.e., 9.9% variable importance; **Figure 7**), whereas white-necked petrel foraging was associated with deeper thermocline depths (i.e., 6% variable importance; **Figure 7**). Thermocline depth had weaker contribution to the Kermadec petrel models (i.e., 3.1% variable importance) with no obvious preference for foraging in waters with shallow or deep thermocline layers.

We found no evidence of any of the species showing preferences for foraging close to seamounts. Conversely, the probability of foraging was uniformly higher among all species at greater distances from seamounts; and birds did not appear to target bathymetric slopes. Kermadec petrels demonstrated some preference for foraging in areas with higher chlorophyll *a* concentration compared to black-winged and white-necked petrels. Additionally, for all three petrels, species distribution models could not determine any clear preferences for foraging near sub-mesoscale sea-surface temperature fronts, nor transport fronts (i.e., areas with lower FSLE values that represent the outer parts of transport fronts) or areas with higher sea level anomalies. However, black-winged petrels appeared to make some general use to the north of the Subtropical Frontal Zone (Bostock et al., 2015; **Figure 4**) during long foraging trips. In 2019, only two white-necked petrels traveled to the east of New Zealand, possibly making use of productive waters to the north of the Subtropical Frontal Zone (**Figure 5**).

MESS grids indicated that only $0.04 \pm 0.08\%$ (mean \pm SD) of the foraging area during the time period when Kermadec petrels were tracked had environmental conditions outside the range of those during the time period when black-winged and white-necked petrels were tracked (**Supplementary Figure 6**).

4 DISCUSSION

4.1 Foraging Characteristics

Our tracking data and analyses demonstrate that summer-breeding gadfly petrels from the Norfolk Island Group use waters of the East Australian Current and the Subtropical Frontal Zone. Behavioral state-space modeling demonstrated that while they do use some oceanographic features, they also travel very widely, foraging throughout most of the Tasman Sea, apparently opportunistically exploiting resources as they travel (e.g., Ventura et al., 2020). These results support the hypothesis that, while gadfly petrels do make some broad use of oceanographic features, they also use a maximal-area foraging strategy, travelling over large areas to maximize chances of encountering unpredictable resources in relatively unproductive marine ecosystems (e.g., Clay et al., 2017; Ventura et al., 2020).

Among seabirds, gadfly petrels undertake some of the most extensive foraging movements during breeding when they must travel repeatedly to and from their nests to incubate eggs or provision themselves and their altricial offspring (Clay et al., 2019; Taylor et al., 2020). The three species we studied all demonstrated bimodal foraging strategies (e.g., Weimerskirch et al., 1994) whereby birds made both short and long foraging journeys. Concentrated foraging around seabird colonies depletes local resources, which forces individuals to journey further in search of food: a phenomenon known as ‘Ashmole’s halo’ (Ashmole, 1963; Oppel et al., 2015; Weber et al., 2021). Seabirds exhibiting bimodal foraging strategies do so in response to near-colony resource depletion, whereby short foraging trips are used to provision their dependent young, whereas parents need to travel to more distant foraging grounds to meet their own energetic requirements (Weimerskirch et al., 1994; Oppel et al., 2015; Weber et al., 2021). Gadfly petrels appear exceptionally well suited to

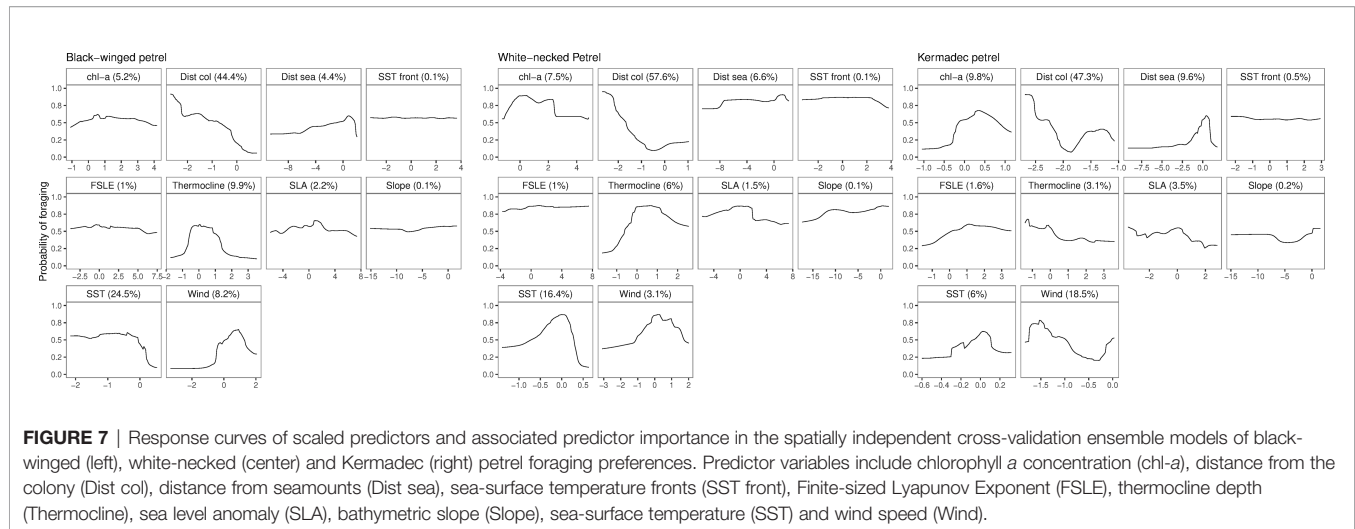


FIGURE 7 | Response curves of scaled predictors and associated predictor importance in the spatially independent cross-validation ensemble models of black-winged (left), white-necked (center) and Kermadec (right) petrel foraging preferences. Predictor variables include chlorophyll *a* concentration (chl-*a*), distance from the colony (Dist col), distance from seamounts (Dist sea), sea-surface temperature fronts (SST front), Finite-sized Lyapunov Exponent (FSLE), thermocline depth (Thermocline), sea level anomaly (SLA), bathymetric slope (Slope), sea-surface temperature (SST) and wind speed (Wind).

making long-distance self-provisioning journeys due to their unique morphological adaptations for fast, and energy efficient flight relative to other seabirds (Spear and Ainley, 1997; Ventura et al., 2020).

4.2 At-Sea Foraging Distributions

Tracking data collected over multiple years highlighted that some areas experience more intensive foraging than others. This is true for both the number of individuals foraging in a given region as well as the intensity of foraging activity of individuals within that region. All three species had high foraging activity immediately surrounding the colony, with other hotspots of foraging activity relatively diffusely spread over the remaining large foraging extent, which is typical of other central place foraging seabirds that display dual foraging strategies (Magalhães et al., 2008; Raine et al., 2021). Hotspots of black-winged petrel foraging activity occurred between approximately 40°S – 47°S. The large spatial area over which gadfly petrels foraged encompasses areas of the Exclusive Economic Zones (EEZs) of Australia and New Zealand with a large proportion of foraging ranges encompassing the high seas, a “global commons” for which no country holds sovereign jurisdiction. In this study, approximately 55%, 35% and 42%, respectively, of black-winged, white-necked and Kermadec petrel foraging locations occurred outside of EEZs, which highlights the importance of internationally coordinated efforts to conserve gadfly petrel foraging habitat (e.g., Davies et al., 2021).

We demonstrated a large degree of spatial overlap in foraging areas among all three species, suggesting that competition for resources may be mediated over finer spatial scales through differences in prey acquisition methods, presumably as a result of morphological differences (e.g., body size), instead of large-scale spatial or habitat segregation (Spear et al., 2007). Diet diversity in pelagic tropical seabirds is generally low (Diamond, 1983) with most species restricted to foraging on squid and flying fish, which results in high diet overlap (Ashmole and Ashmole, 1967; Harrison et al., 1983; Ballance et al., 1997). Indeed, observations of stomach regurgitations and of parents feeding young during fieldwork of the

present study suggest that the three species provisioned chicks with unidentified squid (Decapodiformes) and flying fish (Exocoetidae) and, in black-winged petrels, unidentified zooplankton (L. Halpin, personal observations, 2018–2021). Kermadec petrels are reported to be partially kleptoparasitic (Spear and Ainley, 1993). That Kermadec petrels foraged closer to the colony and spent on average proportionally more time in area-restricted search behavior may be indicative of a kleptoparasitic foraging strategy, whereby birds do not need to travel far to find prey, but instead may harass other species close to the colony that have acquired food. This species also demonstrated preferences for foraging in areas with higher chlorophyll *a* concentration, suggesting that within their smaller foraging range, which encompasses more oligotrophic areas, they may need to seek patches with higher productivity to obtain sufficient prey resources. All three species intensively used the areas surrounding the colony in short foraging trips, but during long trips black-winged petrels tended to forage in cooler waters much further south than white-necked petrels. This may be indicative of black-winged petrels having increased flight proficiency relative to white-necked petrels thus enabling them to exploit resources further afield.

4.3 Foraging Habitat

Model predictive performance was generally poor to fair as is often the case for habitat generalists that lack strong affinity to a particular habitat type or feature (Elith et al., 2006; Andrew and Fox, 2020). We believe that the poor predictive performance was due in part to the behavioral characteristics (i.e., more generalist habitat requirements) of gadfly petrels rather than factors such as the choice of environmental variables used to predict foraging habitat. Furthermore, the response curves and relative importance of the predictor variables to model predictions were very similar between conventional cross-validation and spatially independent cross-validation approaches, demonstrating that birds have weak or wide preferences for available habitat, regardless of the cross-validation method. While the predictive performance of the Kermadec petrel species distribution model was within range of what is generally considered acceptable, we

suggest that the performance of this model should be taken with caution due to the lower representativeness of the sample size (68.5%) to foraging movements of the colony-level population. MESS grids indicated a general similarity in environmental conditions experienced by Kermadec petrels compared to the other two species. We therefore do not believe that differences between the foraging characteristics of Kermadec petrels compared to the other two species were driven by differences in environmental conditions due to the different time periods in which the species were tracked.

Our results suggest that black-winged petrels target waters with shallower thermocline depths, which may indicate a more varied diet that includes zooplankton since planktivorous species tend to prefer waters with shallower thermocline depths (e.g., Spear et al., 2001; Ballance et al., 2006). Conversely, the preference for foraging in waters with deeper thermoclines expressed by white-necked petrels may indicate that the species is more piscivorous than black-winged and Kermadec petrels. That black-winged and Kermadec petrels spent almost equal proportions of their time foraging during darkness compared to daylight suggests that nocturnal foraging is likely to be an important feature of their behavior. These results are consistent with other studies indicating that tropical and subtropical seabirds often rely on deep water prey that perform diel vertical migrations to the sea surface at night (e.g., Hays, 2003). Such prey includes mesopelagic squid, fish and zooplankton (Ashmole, 1971; Imber et al., 1995; Dias et al., 2012). Similar to a closely related species, the Bonin petrel (*Pterodroma hypoleuca*; Harrison et al., 1983), black-winged petrels may be well-adapted for night time foraging and may rely substantially on diel migrant prey, possibly including bioluminescent squid (Ommastrephidae; Harrison et al., 1983) and zooplankton. Kermadec petrels are known to feed on diel migrant squids, particularly Onychoteuthidae (Imber et al., 1995).

Previous studies have suggested that, unlike many other pelagic seabirds, gadfly petrels have less clear habitat preferences, especially when engaged in long foraging trips during the breeding season (Clay et al., 2017; Clay et al., 2019; Ventura et al., 2020). Our study provides support for this hypothesis with evidence to suggest that the foraging strategy is likely based on opportunistic prey encounters rather than targeting of specific habitat features. For example, foraging occurred throughout the species ranges, and travel accounted for a disproportionately large percentage of time allocation within foraging trips. Additional support for this hypothesis is that, across all three species, the most important model predictor of probability of foraging behavior was the distance from the colony. From a species distribution modeling perspective, this suggests that, like other centrally placed foragers, breeding gadfly petrels' foraging ranges are mainly constrained by their need to return to nests to provision chicks.

Possible evolutionary drivers of this lack of habitat specificity are that (sub)tropical waters and open ocean regions are less predictable than temperate and polar regions, and inshore waters. Indeed, it has been hypothesized that as ocean productivity decreases – which results in reduced prey abundance – seabird flight proficiency becomes more

important because those with low flight costs will be able to reach more distant resources (Ballance et al., 1997). Furthermore, gadfly petrels' high mobility and large foraging ranges allows birds to be less reliant on specific oceanographic features associated with moderate to high productivity, such as fronts or eddies, which can be ephemeral and are highly dynamic in marine systems (Weimerskirch, 2007), and instead allows birds to opportunistically target prey items or patches they encounter while in flight.

Gadfly petrels tracked in the present study showed no affinity for foraging near seamounts, similar to Raine et al. (2021). Several studies (e.g., Haney et al., 1995; Thompson, 2007; Morato et al., 2008) demonstrate that some seabirds – including gadfly petrels – occur in higher abundance near seamounts, particularly in the North Pacific and Atlantic. However, these studies have generally occurred during gadfly petrels' non-breeding stages (i.e., in the austral winter) when birds are not constrained to routinely return to the colony. Given the low energetic costs of long-distance travel, it could be that for chick-provisioning gadfly petrels, targeting foraging at seamount locations yields lower foraging success than ranging widely across the Tasman Sea. Furthermore, little is known about seabird prey distributions in the oceanic Pacific (Ballance et al., 1997). It is thus also possible that the squid and flying fish prey targeted by gadfly petrels during chick-provisioning occur in no higher abundances at accessible seamounts within the species' foraging ranges than in pelagic waters.

4.4 Implications for Conservation

The opportunistic foraging strategies of gadfly petrels and the enormous areas over which they forage mean that it may be challenging or impractical to use traditional approaches to identifying and protecting key foraging habitats, such as static marine protected areas (Oppel et al., 2018). Conservation of gadfly petrel foraging habitat may therefore require focus on maintaining functional and healthy marine ecosystems and reducing generalized threats (e.g., commercial fisheries that cause high seabird bycatch, marine pollution) to birds in these areas, which will ensure long term food supplies for these oceanic wanderers. Lack of generalizability of habitat suitability models poses a challenge for conservation planners. If it is not possible to predict where suitable habitat is under current environmental conditions, then spatially dynamic conservation measures, which have been proposed and enacted in other marine contexts, may be impossible to implement (Hobday et al., 2011; Maxwell et al., 2015). However, our analysis of at sea distribution presents some opportunities. Our tracking dataset identifies some areas of high foraging activity by multiple individuals between years. This approach to examining areas with repeated use between years is likely more useful for determining important foraging areas for gadfly petrels and other seabirds that may lack predictable foraging preferences for any static and dynamic oceanographic features. Moreover, the dual foraging strategy that we identified also creates potential for different conservation strategies to provide protection for the different trip types. The short foraging trips cover a much smaller area, meaning that

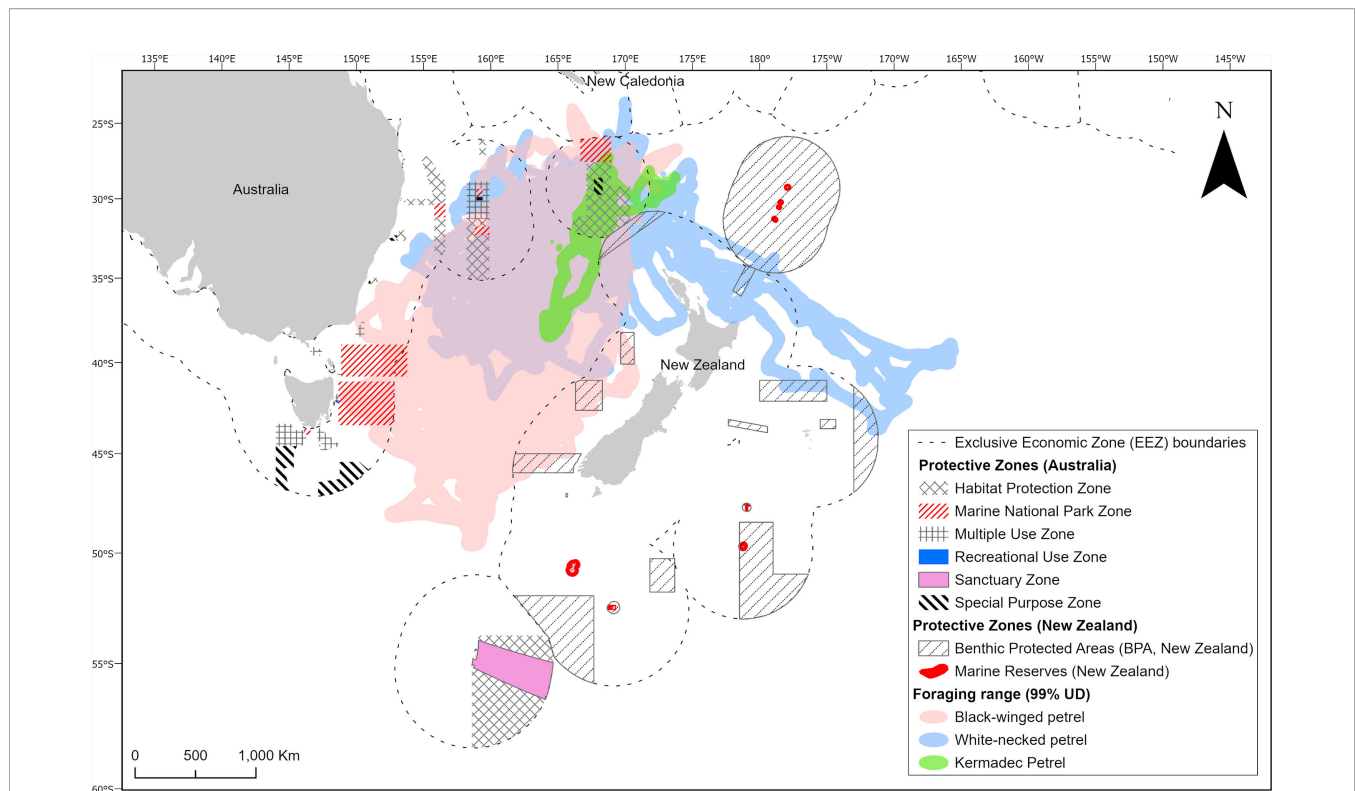


FIGURE 8 | Foraging ranges of black-winged petrels (*Pterodroma nigripennis*), white-necked petrels (*P. cervicalis*) and Kermadec petrels (*P. neglecta*) in relation to existing protected areas and areas outside of national jurisdictions.

methods such as marine protected areas could be effective at this spatial scale (Oppel et al., 2018). Some existing protections that prohibit commercial fishing occur in the Norfolk Island National Park Zone to the north of the Island (**Figure 8**), which encompasses a small portion of the areas used by gadfly petrels during short trips. Conversely, the vast extent covered during longer foraging trips by self-provisioning gadfly petrels means that policy-based methods such as fisheries regulation (e.g., quotas and more comprehensive enforcement) or management of marine plastic pollution will likely represent the best tools for conserving birds undertaking these long-distance trips (Oppel et al., 2018). While the risk of interactions with commercial fisheries is considered low for the small to medium sized gadfly petrels in our study (Vaugh et al., 2012), their populations will benefit from increased efforts to prevent the degradation of marine ecosystems through pollution, over-fishing, and climate change both within and outside of EEZs. Although the conservation of the high seas is much more challenging than within EEZs, several large high seas areas of the Tasman Sea – which are frequented by gadfly petrels in the present study – have been identified as ecological or biologically significant marine areas (EBSAs) by Parties to the Convention on Biological Diversity (Bax et al., 2016). These areas have been the topic of discussions initiated by a United Nations call to establish marine protections beyond national jurisdictions. Provided that their nesting colony on Phillip Island remains free of introduced

predators, conservation efforts for these gadfly petrels should focus on collaborative multinational cross-border efforts to conserve and restore marine ecosystem function in the Tasman Sea and the wider South Pacific.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in the Seabird Tracking Database (<https://seabirdtracking.org>) online repository (dataset IDs: 1499, 1453, 1422, 1452, 1423).

ETHICS STATEMENT

This animal study was reviewed and approved by Monash University School of Biological Sciences Animal Ethics Committee and New South Wales Department of Planning, Industry and Environment (DPIE) Animal Ethics Committee.

AUTHOR CONTRIBUTIONS

LH conceived the project idea, acquired funding and scientific permits, conducted field expeditions, collected field data,

analyzed the data, and led the writing of the manuscript. RM assisted with formulation of ideas, data analysis and contributed to project development. TCl and GH assisted with data analysis. TCh assisted with field expeditions and data collection. NC and RC contributed to fieldwork, project development and ideas, acquisition of scientific permits and funding. All authors contributed critically to manuscript drafts and gave final approval for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.853104/full#supplementary-material>

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Sympatric Seals, Satellite Tracking and Protected Areas: Habitat-Based Distribution Estimates for Conservation and Management

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Marine predator populations are crucial to the structure and functioning of ecosystems. Like many predator taxa, pinnipeds face an increasingly complex array of natural and anthropogenic threats. Understanding the relationship between at-sea processes and trends in abundance at land-based monitoring sites requires robust estimates of at-sea distribution, often on multi-region scales. Such an understanding is critical for effective conservation management, but estimates are often limited in spatial extent by spatial coverage of animal-borne tracking data. Grey (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) are sympatric predators in North Atlantic shelf seas. The United Kingdom (UK) and Ireland represents an important population centre for both species, and Special Areas of Conservation (SACs) are designated for their monitoring and protection. Here we use an extensive high-resolution GPS tracking dataset, unprecedented in both size (114 grey and 239 harbour seals) and spatial coverage, to model habitat preference and generate at-sea distribution estimates for the entire UK and Ireland populations of both species. We found regional differences in environmental drivers of distribution for both species which likely relate to regional variation in diet and population trends. Moreover, we provide SAC-specific estimates of at-sea distribution for use in marine spatial planning, demonstrating that hotspots of at-sea density in UK and Ireland-wide maps cannot always be apportioned to the nearest SAC. We show that for grey seals, colonial capital breeders, there is a mismatch between SACs (where impacts are likely to be detected) and areas where impacts are most likely to occur (at sea). We highlight an urgent need for further research to elucidate the links between at-sea distribution during the foraging season and population trends observed in SACs. More generally, we highlight that the potential for such a disconnect needs to be considered when designating and managing protected sites, particularly for species that aggregate to breed and exhibit partial

migration (e.g. grey seals), or spatial variation in migration strategies. We demonstrate the use of strategic tracking efforts to predict distribution across multiple regions, but caution that such efforts should be mindful of the potential for differences in species-environment relationships despite similar accessible habitats.

Keywords: animal-borne telemetry, marine spatial planning (MSP), marine vertebrate predators, regional habitat preference, partial migration, place-based conservation, special area of conservation (SAC), use-availability

INTRODUCTION

Marine ecosystems are facing an unprecedented biodiversity crisis, with multiple compounding impacts such as overfishing, climate change, and anthropogenic habitat modification (Worm et al., 2006; Brook et al., 2008; Maxwell et al., 2013; McCauley et al., 2015). Quantifying the effects of human activity on marine systems and prioritising conservation efforts is a complex, multifaceted yet pressing concern (Parsons et al., 2014; Venegas-Li et al., 2018; Nelms et al., 2021). Marine predators are often considered sentinels of ecosystem health (Hazen et al., 2019) or indicators of environmental change (Croxall et al., 2002), and hotspots of predator abundance are assumed to represent areas of ecosystem-level importance (Worm et al., 2003; Raymond et al., 2015; Hindell et al., 2020). Understanding what characterises important habitat for marine predators is therefore critical to prioritising conservation efforts and informing marine spatial planning.

Species that return to land between foraging trips and/or to breed such as seabirds, sea turtles and pinnipeds offer a unique opportunity to monitor trends in abundance (Nel et al., 2013; Sherley et al., 2018; Russell et al., 2019). However, linking any observed changes in abundance at land-based monitoring sites to potential threats occurring at sea requires robust estimates of at-sea distribution (Witt et al., 2011; Hindell et al., 2017; Fauchald et al., 2021). This is especially pertinent for protected sites on land, where observed population trends may inform conservation efforts and influence marine spatial planning (Nel et al., 2013). Animal-borne tracking technology allows ecologists to reconstruct the at-sea movements of marine predators, and gain insights into their behaviours and habitat associations (Hazen et al., 2012). Tracking data can be used in habitat preference models to investigate the environmental drivers of distribution and identify areas of suitable or important offshore habitat (Aarts et al., 2008; Raymond et al., 2015; Reisinger et al., 2018). When combined with spatially resolved abundance data (e.g. land counts), these models can be used to predict the spatial variation in density of a population at sea (Wakefield et al., 2017; Fauchald et al., 2021). Such habitat-based distribution maps are integral to effective marine spatial planning, and often inform environmental impact assessments for proposed activities. However, a limiting factor for providing such distribution estimates across a large spatial scale is the requirement of a large sample size of tagged individuals, often covering multiple centres of abundance in different regions (Wakefield et al., 2017; Fauchald et al., 2021). This is further complicated by the fact that a predator population may occupy different habitat types

throughout the study range, yet studies often assume one species-environment relationship. Indeed, recent research suggests that in such cases regional habitat preference models are more appropriate than single models (Torres et al., 2015; Mannocci et al., 2020). Nevertheless, species distribution estimates across multi-region study areas are generally restricted to predictions from single models (Wakefield et al., 2017; Fauchald et al., 2021), or predictions for discrete areas from regional models (Huon et al., 2021), and no framework exists to combine predictions from regional models into a continuous distribution map.

The need for robust species distribution estimates is especially pertinent given the widespread and rapidly changing extent of anthropogenic activity on marine predator habitat, alongside efforts to reduce biodiversity loss (McCauley et al., 2015). Against a backdrop of decommissioning of offshore oil and gas infrastructure, the drive to reduce reliance on fossil fuels is leading to extensive planning and construction of offshore marine renewable energy installations around the world (Magagna and Uihlein, 2015; Borthwick, 2016; Wright et al., 2020). Installations such as windfarms and tidal turbine arrays often overlap with predator foraging areas or travel routes, raising concerns about collision risk for flying seabirds with wind turbines (Bradbury et al., 2014) or marine mammals and diving seabirds with tidal turbines (Waggitt and Scott, 2014; Onoufriou et al., 2019), as well as fitness consequences of avoidance behaviour (Masden et al., 2010; Russell et al., 2016; Palmer et al., 2021) and auditory damage for aquatic species (Bailey et al., 2010; Hastie et al., 2015; Whyte et al., 2020) associated with construction and operation. Special Areas of Conservation (SACs) are part of the marine spatial planning toolkit used in the European Union (EU), allowing member states to designate areas for protection that are expected to make a significant contribution to habitats and species conservation targets laid out in the EU Habitats Directive (European Council Directive 92/43/EEC). In the EU and United Kingdom (UK) – which retained the fundamental requirements of the Habitats Directive in domestic law after leaving the EU in January 2021 – as part of the consenting process developers must consider potential impacts on protected species such as marine mammals and seabirds, and the potential for such impacts to propagate to sites designated for their conservation. Consequently, there has been a drive to quantify the connectivity between offshore anthropogenic activities and designated conservation areas (such as SACs and Special Protection Areas (SPAs) for seabirds). One such approach is to “apportion” at-sea species density estimates in a given area (e.g.

impact zone or footprint of a development) to specific designated conservation areas. However, to date this work has largely focussed on linking seabird at-sea distributions during the breeding season to land-based SPAs (Butler et al., 2017; Fauchald et al., 2021), or individual tagged seals to land-based SACs.

Grey (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) are high trophic level predator species listed on Annex II of the Habitats Directive, meaning that EU member states (and the UK) have an obligation to designate SACs, monitor their populations and maintain them in a “Favourable Conservation Status” (FCS). The UK and Ireland represents an important population centre for both species, with ~37% of global grey seal pup production (i.e. number of pups born), and ~36% of the Eastern Atlantic subspecies of harbour seals (*P. vitulina vitulina*) (SCOS, 2020). Both species co-occur around much of the UK and Irish coastline (Jones et al., 2015), but their breeding and moult cycles are asynchronous, and harbour seals can undertake foraging trips during lactation, whereas grey seals are typical capital breeders which aggregate in colonies during the breeding season (Bonner, 1972). Grey seal population monitoring (largely focussed on pup production) over the past 40 years has revealed a steady increase in numbers, but the rate of growth varies regionally (SCOS, 2020). Indeed, abundance appears to be at carrying capacity in the west and north of Scotland; pup production plateaued between 1990 and 2000 (Russell et al., 2019). In contrast, pup production along the UK mainland coast of the North Sea, which holds a substantial proportion (~62%) of the UK and Ireland abundance (SCOS, 2020), has continued to grow exponentially since the 1980s (Russell et al., 2019). Although harbour seal abundance in the UK and Ireland (monitored during the annual moult) in 2019 was comparable to in the late 1990s, there was marked variation in regional population trends, with some areas experiencing catastrophic declines (e.g. Orkney and East Scotland), while others were stable or increasing (Thompson et al., 2019). As yet these declines are unexplained, but are likely related to processes occurring at sea (Thompson et al., 2019). There is evidence of dietary overlap in some areas (Wilson and Hammond, 2019), and grey seals are known to predate harbour seals (van Neer et al., 2015; Brownlow et al., 2016), but the extent of predatory and competitive interactions between the two species, and their contribution to population trends, remains unknown.

Previous work has predicted the at-sea distributions of grey and harbour seal populations in the UK and Ireland using a model-supervised kernel smoothing approach applied to tracking data (Matthiopoulos et al., 2004; Jones et al., 2013; Jones et al., 2015; Russell et al., 2017). Although these “usage maps” have been widely used in marine spatial planning, they now require updating in light of recent changes in regional population trends and the existence of new higher resolution satellite tracking datasets. Moreover, although the track smoothing approach is highly effective for mapping distribution emanating from haulout sites in areas with a wealth of tracking data, it does have certain limitations. Firstly, it does not provide ecological insights into the environmental

drivers of distribution, which could help to elucidate the causes of species-specific regional variation in population trends. Secondly, estimates were based on the distribution of tagged individuals, and only a subset of all haulouts used by grey and harbour seals were visited by tagged individuals. Thus, for the remaining haulouts predictions were based on “null usage”; the assumption that usage declines with distance from the haulout (Jones et al., 2013; Russell et al., 2017). Hotspots of important foraging habitat are likely to be heterogeneously distributed offshore, and if none of the tracked seals visited a certain foraging patch, this approach would underestimate or overlook density in that area. Other studies have modelled tracking data in a habitat preference framework and predicted seal distribution in specific discrete areas of the UK and Ireland (Aarts et al., 2008; Bailey et al., 2014; Jones et al., 2017; Huon et al., 2021), but no study has used habitat preference to generate distribution estimates for the whole of the UK and Ireland. Given the regional differences in habitat characteristics (Huon et al., 2021), population dynamics (Thomas et al., 2019; Thompson et al., 2019), diet (Gosch et al., 2019; Wilson and Hammond, 2019), and foraging trip characteristics (Huon et al., 2021) of both seal species, a single habitat preference model would likely produce unrealistic results when used to generate predicted distributions across multiple regions. Therefore, updated distribution estimates are required for the entire populations for both species, based on regional habitat preference.

In the UK and Ireland, grey and harbour seals are primary or qualifying features for 23 and 25 SACs respectively (Natura 2000 data - the European network of protected sites, European Environment Agency, 2021), yet these sites are focussed entirely on coastal haulout sites or breeding colonies and adjacent waters, and do not consider important foraging habitat offshore. Moreover, links between grey and harbour seal distribution at sea and use of land-based SACs have not been explored in detail. In the absence of such information, developers may assume that high at-sea density is attributable to individuals from the nearest SAC. However, foraging areas may be hundreds of kilometres from coastal haulout sites (McConnell et al., 1999). Moreover, grey seals exhibit partial migration; some move between different regions for breeding and foraging, meaning that seals that breed in a given SAC do not necessarily forage nearby (Russell et al., 2013). Understanding how seal density at sea during the foraging season relates to SAC use is therefore an important step in providing effective tools for marine spatial planning.

In this study we utilise an extensive, high resolution (GPS) satellite tracking dataset, unprecedented in both size (114 grey and 239 harbour seals) and spatial extent (covering most major centres of abundance across the UK and Ireland), to build regional habitat preference models. We then use these models, combined with spatially resolved abundance data (haulout counts), to predict the at-sea distribution of all grey and harbour seals hauling-out in the UK and Ireland, and provide updated distribution maps for use in marine spatial planning. We also provide the first SAC-specific estimates of distribution, demonstrate their application to real world planning scenarios,

and examine the spatial coherence between SACs and areas of high at-sea density for each species in the context of conservation management. Lastly, we examine the seasonal movements of grey seals in relation to SACs and consider to what degree SAC-specific distribution estimates are indicative of where the SAC population is distributed outside of the breeding season.

MATERIALS AND METHODS

Study Area

The study area comprised the whole of the UK, Ireland and Isle of Man. This area was divided into regions for habitat preference modelling (**Figure 1**). Regional boundaries were broadly based on the Seal Monitoring Units (SMUs) used in UK seal conservation and management (SCOS, 2020), but with some alterations to incorporate Ireland and the Isle of Man, and to maximise the predictive power of the models, accounting for the availability of tracking data (**Figure 2**), as well as spatial differences in movement patterns and the heterogeneity of habitat, and ensuring that clusters of haulout sites were not split by regional boundaries. Each region was assigned a sequential number, used here throughout (**Figure 1**).

Tracking Data

Grey ($n = 114$: 45 M, 69 F) and harbour seals ($n = 239$: 107 M, 132 F) were tagged at 26 sites in the UK and Ireland between 2005 and 2019 (**Supplementary Material S1**). All seals were estimated to be >1 year old based on mass and body length. Seals

were captured on, or close to, haulout sites using seine, pop-up, tangle, or hand nets. Seals were instrumented with Fastloc[®] GPS phone tags or dual tags (GPS-GSM-ARGOS) (SMRU Instrumentation, UK), glued to fur at the base of the skull following the procedure outlined by Sharples et al. (2012). For analysis in habitat preference models, data were cleaned following Russell et al. (2016) to remove erroneous location estimates and data during the breeding and moulting seasons (grey seals: September – April, harbour seals: June – August), regularised to a constant 2 h time step and partitioned into trips at sea. Trips were then assigned to one of the ten regional designations for habitat preference models (see **Figure 1**) based on the location of the haulout sites used at the start and end of each trip. At-sea locations were only included in the analysis if they belonged to trips that originated and terminated at haulout sites in the same region (grey seals: 93% of locations, harbour seals: 99.5% of locations). For detailed data cleaning and processing protocol, see **Supplementary Material S2**. The resulting dataset for grey seals comprised 3,276 trips (61,296 temporally regularised at-sea locations) throughout the summer foraging season (May – August) (**Figure 2A**). The dataset for harbour seals comprised 8,579 trips (99,159 temporally regularised at-sea locations) throughout the autumn-winter-spring foraging season (September – May) (**Figure 2B**).

Use-Availability Design

Under a “use-availability” study design (Johnson, 1980; Aarts et al., 2008; Matthiopoulos et al., 2020), accessibility polygons were generated for each haulout location in the tracking datasets,

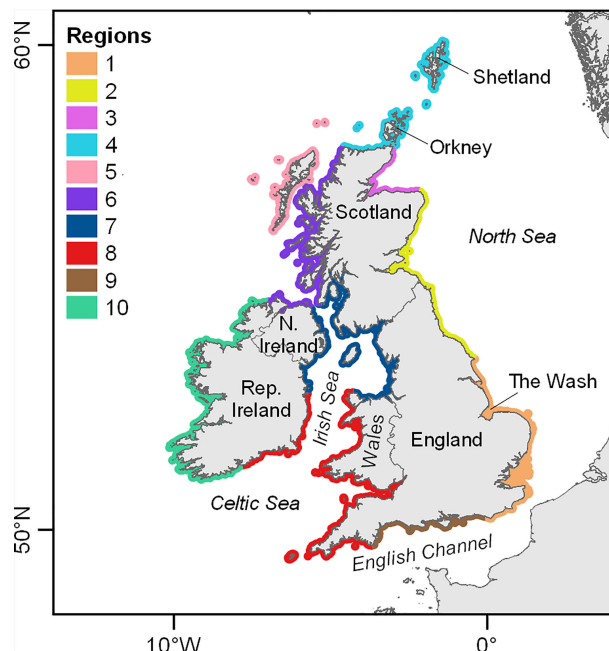
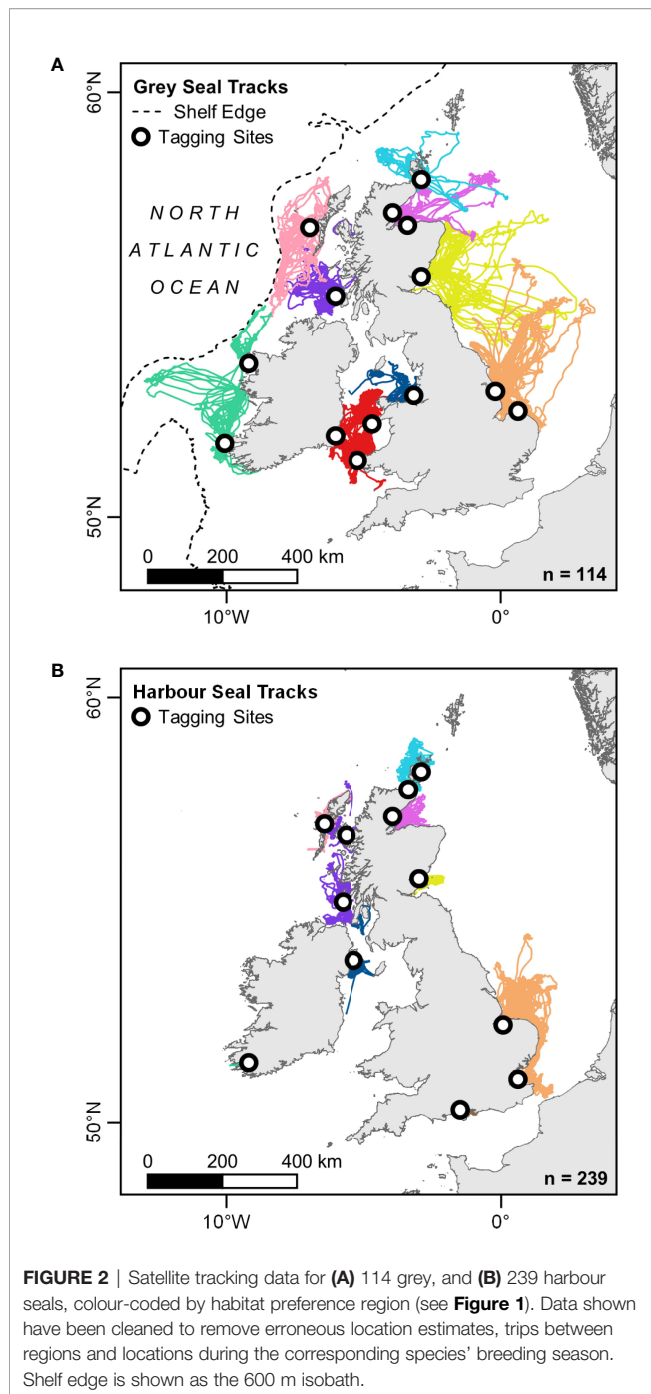


FIGURE 1 | Map of the study area showing regional designations for habitat preference models. 1: Southeast England, 2: East Coast, 3: Moray Firth, 4: North Coast & Northern Isles, 5: Western Isles, 6: West Scotland & Ireland North, 7: Irish Sea North, 8: Celtic Sea & Irish Sea South, 9: English Channel. 10: West Ireland.



with a radius based on the maximum geodesic distance (shortest path at sea without crossing land) from a haulout by any seal in the cleaned tracking dataset (Russell et al., 2016) (grey seals: 448 km, harbour seals: 273 km), thus representing the species' maximum foraging range (Wakefield et al., 2009). For each regularised seal location, a random sample of control points was generated within the corresponding accessibility polygon, representing the available habitat that is accessible to the tagged seal (Aarts et al., 2008; Beyer et al., 2010). The ratio of control points to presences was set using model coefficient stability

analysis (Beyer et al., 2010; Ventura et al., 2019), and varied between the species and among regions from 15:1 to 25:1 (see **Supplementary Material S3** for more details). In this use-availability framework, areas where seals go (presences; seal location data) are modelled alongside areas where they *could* go (control points) (Matthiopoulos, 2003). Preference for a particular habitat type is inferred where its use is disproportionate to its availability (Johnson, 1980; Matthiopoulos et al., 2020).

Environmental Covariates

A range of static and seasonally dynamic environmental variables were extracted for each seal location and control point and included as candidate explanatory covariates in a maximal model for each species in each region (**Figure 3**). These covariates included: distance to haulout site, water depth, substrate type, mean winter sea surface temperature (SST) lagged by one year, water column vertical stratification, Δ stratification (spatial variation in stratification values, analogous to frontal intensity), seabed slope, rugosity and proximity to the continental shelf break (see **Supplementary Material S4** for more detail). Covariates were chosen because of known or potential biological relevance to seals and/or their prey, or to account for the effects of accessibility on habitat selection.

Habitat Preference Modelling

For each species-region combination, a binomial response term (0/1; control/presence) was modelled as a function of environmental covariates in a generalized additive mixed model (GAMM) using the package “mgcv” (Wood, 2020) in R (R Core Team, 2020). Individual seal ID was included as a random intercept. This meant that the relationships in the models were estimated across individuals rather than data points, ensuring that data-rich individuals did not have a disproportionate influence on the overall trends. Control points were weighted in the models according to the ratio of control points to presences, such that each set contributed the same as one presence. I.e., if the ratio of control points to presences was 20:1, then each control point would be weighted at 0.05 (1/20). Each continuous covariate was fitted as a smoothed term with shrinkage, such that uninformative terms can be penalised to zero, effectively making them linear (Wood, 2020). To ensure smooth functions reflected plausible biological relationships, the number of knots (k) was determined for each smooth by trialling different values ($2 \leq k \leq 10$) and selecting that which minimised the model Akaike Information Criterion (AIC) score whilst still returning a relationship that was biologically interpretable. Maximal models were simplified to a minimal adequate model using a two-stage approach comprising: (i) backwards model selection by AIC score and (ii) k -fold cross validation (**Supplementary Material S5**).

Seal Haulout Counts

Haulout count data were used to weight model spatial predictions (**Figure 3**; see below). These data comprised counts of grey and

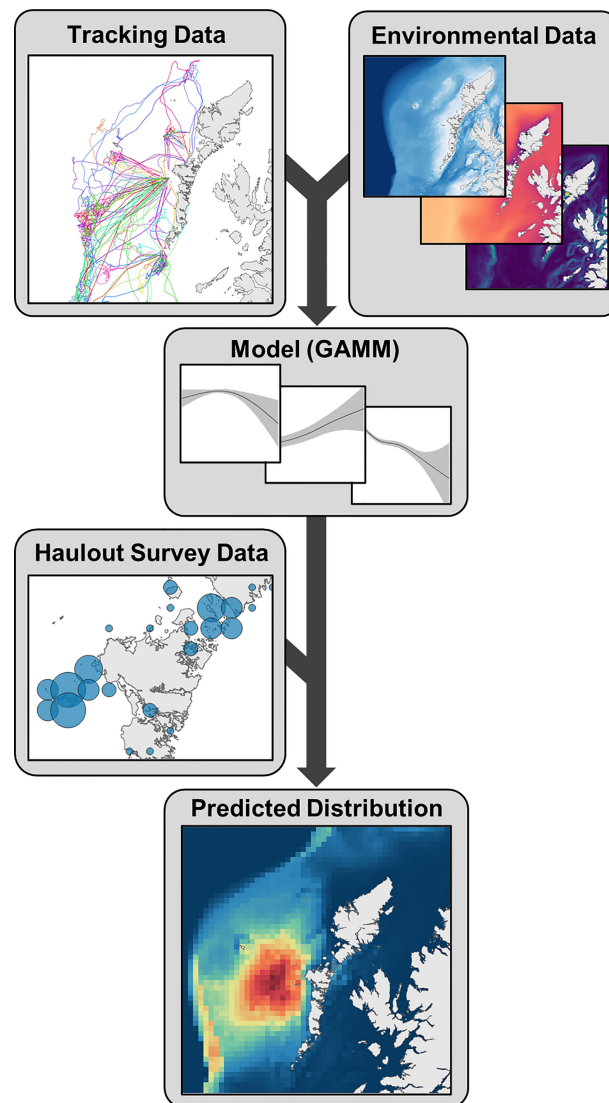


FIGURE 3 | Schematic representation of the methods relating to distribution estimation. Environmental data are extracted for seal tracking locations and availability sample and modelled in regional Generalized Additive Mixed Models (GAMMs). Model predictions are weighted by most recent haulout counts to generate at-sea density estimates. Regional estimates are then combined into one distribution map for the UK and Ireland.

harbour seals on terrestrial haulouts from aerial and ground survey platforms, conducted during August (**Supplementary Material S6**) (Morris and Duck, 2019; SCOS, 2020). In brief, Scotland (SCOS, 2020), Northern Ireland (SCOS, 2020), eastern England (with the exception of the Tees Estuary) (Cox et al., 2020; SCOS, 2020), and Republic of Ireland (Morris and Duck, 2019) were surveyed aerially. Data for the remaining areas (rest of England, Isle of Man and Wales) were comprised of ground and boat counts from multiple organisations (see **Supplementary Material S6** for full list of sources). Counts were aggregated to 5 km x 5 km grid cells (hereafter 'haulout cells'). Survey effort varied spatially; for this study the most recent available counts were used for each haulout cell. The vast majority of counts (94.4%) were recorded from 2015 - 2018 (**Figure S6.1**).

UK and Ireland Distribution Estimates

A prediction grid was generated on a 5 km x 5 km cell resolution encompassing the at-sea area accessible to seals from all haulout cells in the study area (UK, Isle of Man and Ireland). Environmental data corresponding to the modelled covariates were extracted for each cell (see **Supplementary Material S7.1**). Data for non-static covariates were extracted for 2018. Spatial predictions of relative at-sea density (mean and associated lower and upper 95% confidence intervals) were generated per species using the corresponding region-specific habitat preference model (**Figure 3**). Predictions were made emanating from each haulout cell with a non-zero count in the most recent survey (**Figure S6.2**). Raw predictions (on the logit scale) were exponentiated, then normalised (Manly et al., 2002; Matthiopoulos et al., 2020).

Haulout-specific prediction surfaces were then weighted by the number of individuals counted on the most recent survey. These weighted prediction surfaces were then summed into a multi-region surface and normalised. The mean distribution estimates therefore represent the percentage of the at-sea population for the UK and Ireland (i.e. excluding hauled-out animals) estimated to be present in each cell at any one time (see **Supplementary Material S7.2** for more detail). Thus, cells in the mean relative density distribution map sum to 100%. Cell-wise lower and upper 95% Bayesian credible intervals (hereafter confidence intervals) were generated using a posterior simulation approach (Wood, 2006; Augustin et al., 2013) (**Supplementary Material S7.3**). For some applications, estimates of absolute density (i.e. number of seals) are favourable to relative density. Here, we present distribution maps as relative density (see “Technical Considerations” in Discussion for rationale). However, the mean prediction can be converted to absolute density using population scalars derived from telemetry data, and this process is explained in **Supplementary Material S7.4**. In brief, haulout counts are scaled to total population size for UK and Ireland using the mean estimated proportion of the population hauled-out during the survey window (and thus available to count). Total population size is then scaled to at-sea population size using the mean estimated proportion of time seals spend at-sea during the months that the maps represent (i.e. excluding breeding and moulting). Relative density estimates (percentage of the at-sea population) can then be converted to absolute density using the estimated at-sea population size. However, an important consideration with these absolute density estimates is that uncertainty in the scalars is not propagated through to the confidence intervals around the mean, which only reflect uncertainty in the habitat preference relationships.

Distribution Estimates for SACs

Using the spatial prediction approach described above, distribution estimates can be made emanating from specific haulout cells, allowing users to apportion at-sea abundance to specific areas, such as designated sites. To investigate the at-sea distribution of seals that haul-out in SACs, at-sea density estimates (mean and associated lower and upper 95% confidence intervals) were generated, for both species, for haulout cells within each of the SACs in the UK and Ireland for which the species is a primary or qualifying feature for designation using the associated regional habitat preference model. As above, estimates were normalised to represent the percentage of the at-sea population for that SAC present in each grid cell (i.e. relative density), thus cells in the mean distribution map sum to 100%, representing at-sea distribution of all individuals hauling-out in the SAC during the main foraging season. To demonstrate how these estimates may be used in an applied sense to apportion at-sea seal density to an SAC, grey seal estimates for both the Isle of May SAC and the Berwickshire and North Northumberland Coast SAC were converted to absolute density using the most recent counts (SAC totals) and population scalars (Russell et al., 2015; Russell and Carter, 2021) (**Supplementary Material S7.4**). The number of seals

estimated to be present within a windfarm footprint (Neart na Gaoithe; currently under construction 15 km off the east coast of mainland Scotland) was estimated for (a) the UK and Ireland population, (b) seals hauling-out at Isle of May SAC, and (c) seals hauling-out at the Berwickshire and North Northumberland Coast SAC. Cell values in the absolute density layers were weighted by multiplying the number of seals by the proportion of the cell that overlapped the windfarm polygon (i.e., a cell with an estimated ten seals present, but with only a tenth of its area overlapping the polygon would be counted as one seal). Area-based (i.e., windfarm footprint) 95% confidence intervals were estimated by adapting the posterior simulation process (see **Supplementary Material S7.3**).

Seasonal Abundance and Movements of Grey Seals in SACs

Grey seals aggregate in large numbers to breed, and SACs are often designated for this species based on breeding numbers, but there may be temporal variation in abundance at these sites. To investigate the relative importance of these sites for grey seals in both the breeding and foraging seasons, the most recent available counts (2019) during the breeding season (pup production estimates; SCOS (2021)) for frequently monitored sites (Scotland and eastern England) were compared to counts of grey seals hauled-out during the harbour seal moult surveys in August (representing the main foraging season for grey seals). Counts for SACs were calculated as percentage of the area-wide totals (i.e., including monitored sites outside of SACs). To update the knowledge base on seasonal movements of grey seals presented by Russell et al. (2013), tracking data from females tagged in this study were examined for evidence of breeding. This analysis focussed on females that were tagged in and/or likely bred in SACs. Following the protocol developed by Russell et al. (2013), a female was assumed to have bred if it was recorded as hauled-out for the majority of an 18-day period during the breeding season and spent <10% of this time diving. Breeding locations were then compared to tagging locations (individuals were tagged during the summer foraging season) to examine seasonal variation in SAC use.

RESULTS

Regional Habitat Preference

Habitat preference modelling revealed regional and inter-specific differences in environmental drivers of distribution. Below we outline some key results with the covariates retained in each regional model shown in **Table 1**, but full results and associated plots of modelled relationships from each region are given in **Supplementary Material S8** (grey seals) and **S9** (harbour seals).

For grey seals, distance to haulout site was the primary driver of distribution in all regions, with predicted density declining with increasing distance. In addition to distance to haulout, the following covariates were retained in the models: substrate type (Regions 1, 2, 3, 4, 6, 7, 8), water depth (Regions 2, 4, 5, 6, 8, 10), stratification (Regions 2, 3, 4, 6, 8), mean winter SST lagged 1 yr (Regions 1, 5, 6, 7, 10), Δ stratification (Regions 1, 5), shelf edge (Regions 5, 10) and

TABLE 1 | Covariates retained in the best ranked model according to model selection for each species in each region.

Region	Grey seals	Harbour seals
1: Southeast England	s(Distance) (41.2%) s(Δ Stratification) (5.3%) Substrate (0.7%)	s(Distance) (23.2%) s(SST) (2.3%) s(Δ Stratification) (0.6%) s(Rugosity) (0.6%) s(Depth) (0.5%) s(Distance) (15.2%) s(SST) (2.5%) s(Depth) (1.3%)
2: East Coast	s(Distance) (28.2%) s(Depth) (2.9%) Substrate (0.9%) s(Stratification) (0.7%)	s(Distance) (6%) s(Depth) (0.2%) s(Δ Stratification) (0.1%) s(Distance) (75.3%) s(SST) (0.5%)
3: Moray Firth	s(Distance) (71.7%) s(Stratification) (6.9%) Substrate (1.9%)	s(Distance) (56.2%) s(Depth) (1.5%) Substrate (0.1%) s(Distance) (84.3%) Substrate (0.6%) s(Δ Stratification) (0.1%)
4: North Coast & Northern Isles	s(Distance) (34.1%) s(Stratification) (2.8%) s(Depth) (1.2%) Substrate (0.9%)	s(Distance) (75.5%) s(Depth) (1.5%) s(Rugosity) (0.6%) NA
5: Western Isles	s(Distance) (41.8%) s(SST) (10.2%)s(Depth):Shelf (4.9%) s(Δ Stratification) (0.2%)	s(Distance) (15.4%) s(Depth) (1.9%) s(Distance) (98.7%)
6: West Scotland & Ireland North	s(Distance) (46.6%) s(SST) (4.2%) s(Depth) (0.3%) s(Stratification) (0.5%) s(Rugosity) (0.2%) Substrate (0.2%)	
7: Irish Sea North	s(Distance) (68.2%) Substrate (1.1%) s(SST) (0.1%)	
8: Celtic Sea & Irish Sea South	s(Distance) (39.4%) s(Stratification) (1.9%) s(Depth) (1.2%) Substrate (0.3%)	
9: English Channel	NA	
10: West Ireland	s(Distance) (42.7%) s(Depth) (1.9%)s(SST):Shelf (0.6%)	

Smoothed terms are shown in brackets. “:” denotes an interaction. Percentage deviance explained is shown for each covariate. Model plots shown in **Supplementary Material S8** for grey seals and **S9** for harbour seals reveal the shape and magnitude of covariate effects.

rugosity (Region 6) (**Table 1**). The best model for grey seals in Region 1 (Southeast England) according to model selection criteria revealed a positive influence of Δ stratification, with seals preferentially selecting habitat in areas with high frontal intensity (**Figure S8.1**). Mean winter SST (lagged 1 year) was also retained in the model, and preference peaked at values between 6–8°C. The model also revealed an effect of substrate type, with sandy mud having a negative effect on preference. Grey seals in Region 4 (North Coast and Northern Isles) demonstrated a more coastal distribution than in other regions, having a negative association with areas >100 km from the haulout (**Figure S8.4**). The best model for grey seals in Region 5 (Western Isles) revealed a positive association with shelf edge; areas at the shelf edge had a stronger influence on habitat selection than areas on-shelf (proportionate to their availability), although confidence intervals overlapped (**Figure S8.5**). Indeed, nine (60%) of the tagged individuals in this region performed repeated trips to the shelf edge. A similar relationship with shelf was found for grey seals in Region 10 (West Ireland; **Figure S8.9**).

As with grey seals, distance to haulout site was also the primary driver of distribution for harbour seals in all regions. The following

covariates were also retained in the models for harbour seals: Δ stratification (Regions 1, 3, 6), mean winter SST lagged 1 yr (Regions 1, 2, 4), substrate type (Regions 5, 6) and rugosity (Regions 1, 7) (**Table 1**). The best model for harbour seals in Region 1 revealed a similar but stronger relationship to that of grey seals for mean winter SST, with preference peaking at values between 5–7°C. However, in contrast to grey seals the best model also revealed a negative influence of frontal intensity (**Figure S9.1**). Water depth was also an important driver of distribution for harbour seals, with predicted density declining with increasing depth in Regions 1, 2, 3, 5, 7 and 9. A negative effect of distance to haulout >130 km was predicted for harbour seals in Region 1, but other regional models revealed a much more coastal distribution, with a stronger negative effect for lower values of distance to haulout. For example, in Regions 2 (East Coast; **Figure S9.2**) and 4 (**Figure S9.4**), the best model revealed a strong negative association with areas >50 km from the haulout. In Regions 5 and 10 where grey seals showed positive association with the shelf edge, harbour seals had a tight coastal distribution; the best model for Region 5 revealed a strong negative association with both distance to haulout and depth

(Figure S9.5), and the best model for Region 10 revealed a strong negative association with distance for areas >20 km from the haulout (Figure S9.9).

UK and Ireland Predicted Distributions

Figures 4, 5 show the mean and associated cell-wise 95% confidence intervals of the at-sea distribution of grey and harbour seals hauling-out in the UK and Ireland according to the combined predictions from the best model for each region. Large areas of relatively high at-sea density are apparent for grey seals adjacent to centres of abundance in Orkney, Northeast England, Southeast England and the Western Isles (Figure 4). The maps also reveal hotspots of grey seal density offshore from Southeast Scotland and Northeast England, along the southern fringes of the Dogger Bank, and at the shelf edge west of Scotland (Figure 4). High at-sea density areas are revealed for harbour seals adjacent to relatively large centres of abundance in Shetland, The Wash (Southeast England), and West Scotland (Figure 5).

Distribution Estimates for SACs

At-sea distribution estimates for grey seals hauling-out in SACs (Supplementary Material S10.1) revealed that hotspots of

density occur offshore, often >150 km from the SAC itself. This is particularly apparent for SACs in regions where seals travel further offshore, for example the Humber Estuary SAC in Southeast England, and the Monach Islands SAC in the Western Isles (Figure 6). In general, at-sea distribution estimates of harbour seals (Supplementary Material S10.2) were much more tightly concentrated in waters surrounding the SAC, with hotspots of density extending outwards to ~50 km from the SAC boundaries.

Seasonal Grey Seal Abundance in SACs

SACs represent 42.8% of pup production in Scotland and eastern England, and host 30.4% of individuals during the foraging season, with all but one SAC (Humber Estuary) having a higher proportion of pup production than summer count (Table 2). Some SACs host large breeding numbers but only a small number in the foraging season (e.g. Isle of May: 2.9% of the pup production but only 0.1% of the summer haulout count).

Analysis of absolute density emanating from both the Isle of May and the Berwickshire and North Northumberland Coast SACs revealed large differences in the number of animals estimated to be within the footprint of the Neart na

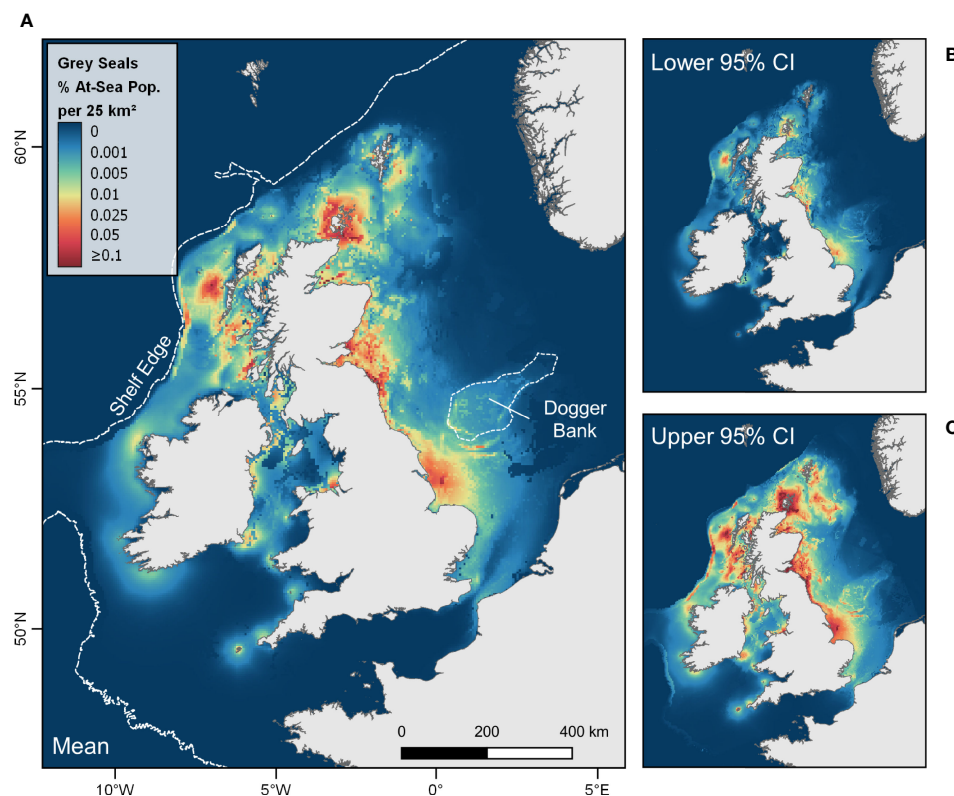


FIGURE 4 | At-sea distribution (relative density) of grey seals from haulouts in the UK and Ireland. Maps show (A) mean with associated cell-wise (B) lower and (C) upper 95% confidence intervals of the percentage of the at-sea population (i.e. excluding hauled-out animals) estimated to be present in each 5 km x 5 km grid cell at any one time.

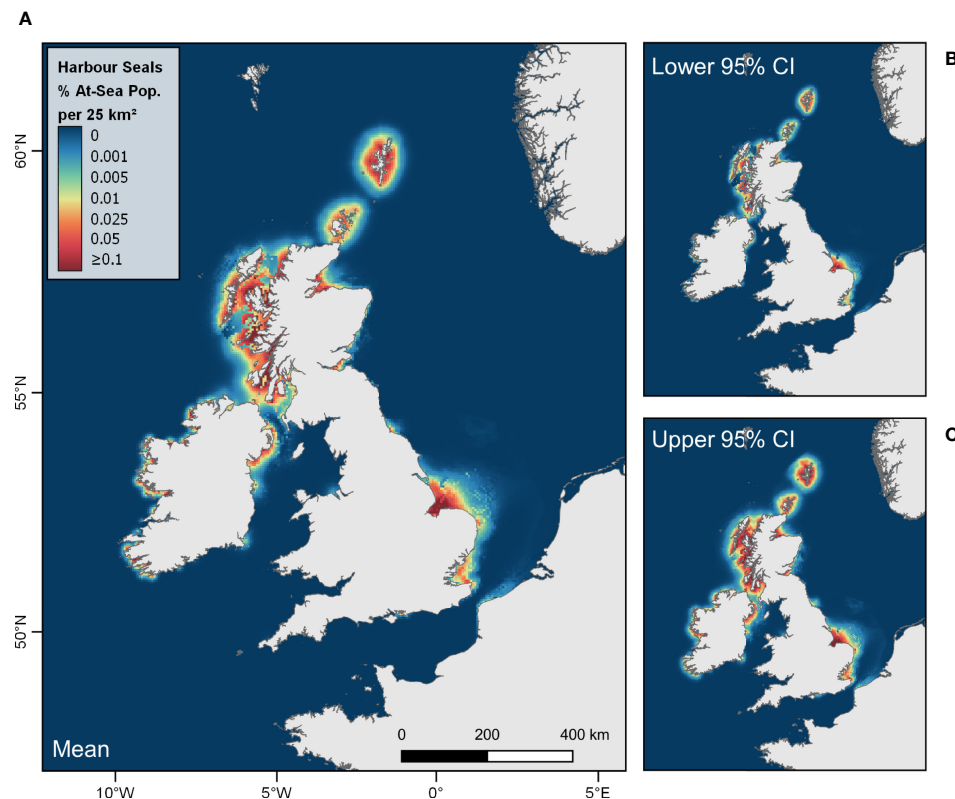


FIGURE 5 | At-sea distribution (relative density) of harbour seals from haulouts in the UK and Ireland. Maps show **(A)** mean with associated cell-wise **(B)** lower and **(C)** upper 95% confidence intervals of the percentage of the at-sea population (i.e. excluding hauled-out animals) estimated to be present in each 5 km x 5 km grid cell at any one time.

Gaoithe windfarm at any one time. Of the 148 (81-204 95% CIs) seals estimated to be within the footprint, 68.2% (101: 48-116 95% CIs) can be apportioned to the Berwickshire and North Northumberland Coast SAC (~50 km from the windfarm), and 1.4% (2: 1-2 95% CIs) can be apportioned to the Isle of May SAC (~15 km from the windfarm) (**Figure 7**).

Seasonal Movements of Grey Seals in SACs

Of the 69 grey seal females tagged in this study, 12 transmitted data through to the breeding season, showed evidence of breeding activity and were tagged in and/or likely pupped in SACs. Of the 12, ten were tagged and likely pupped in an SAC, one was tagged in an SAC but appeared to pup outside of an SAC, and one was tagged outside of an SAC but appeared to pup in one. Half of the ten females that were tagged and likely pupped in SACs appeared to pup in a different SAC to the one in which they were tagged. Three of these movements constituted a transition between different Seal Monitoring Units (SMUs) (**Table 3**). For two of the females that had different pupping and tagging sites, the tags continued to transmit after breeding and the tracks revealed the seals returning to the tagging site (**Figure 8**).

DISCUSSION

Seal Habitat Preference and Overall Distributions

This study presents the first habitat-based at-sea distribution estimates for the entire UK and Ireland populations of grey and harbour seals. Critically, region-specific habitat preference models were used to allow for spatial variation in the species-environment relationship around the coast. UK and Ireland-wide predicted distributions revealed large areas of relatively high at-sea density of grey seals adjacent to large haulout clusters in Southeast England, Northeast England, Orkney and the Western Isles (**Figure 4**). Hotspots of density were also predicted offshore along the continental shelf edge west of Scotland, off the east coast of Scotland and off the east coast of England extending out to the southern fringes of the Dogger Bank in the central North Sea (**Figure 4**). The regional habitat preference model for grey seals in Southeast England revealed a positive association with areas of strong heterogeneity in water column stratification values (**Figure S8.1**), analogous to areas of high frontal intensity. The Flamborough tidal mixing front is a persistent frontal system that occurs from late spring to early autumn off the east coast of England, extending offshore from

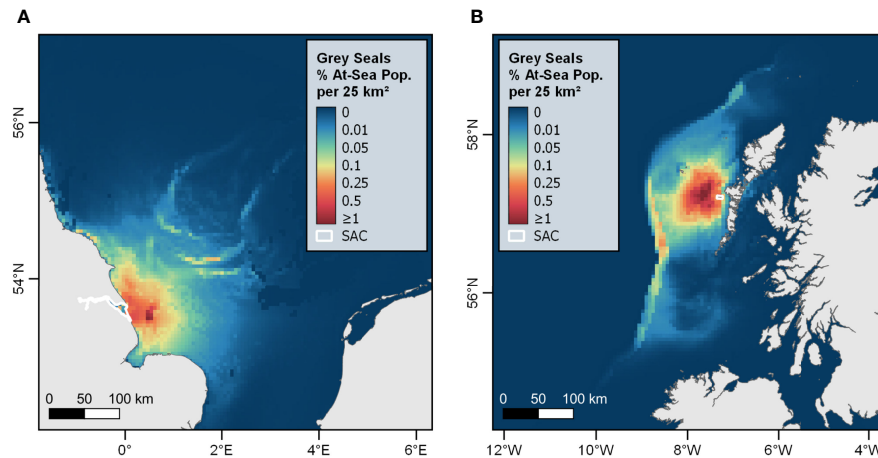


FIGURE 6 | Mean at-sea distribution estimates for grey seals hauling-out in the (A) Humber Estuary SAC, and (B) Monach Islands SAC reveal high concentrations of individuals >200 km from the SAC. Colour scale shows relative density (% SAC at-sea population) per 5 km x 5 km grid cell.

Flamborough Head and encircling the Dogger Bank (Hill et al., 1993). Our results suggest that this feature is an important driver of distribution for grey seals hauling-out in Southeast England. This finding supports the results of Wyles et al. (2022) who showed that the fringes of the Dogger Bank represent an important foraging area for grey seals hauling-out in Southeast England. Being primarily a bottom feature with weak surface signature (Hill et al., 1993), this frontal system may be particularly attractive to grey seals, which predominantly target benthic and demersal prey (Gosch et al., 2019; Wilson and Hammond, 2019). Tidal mixing fronts can alter the density and behaviour of prey and thus may represent a temporally and spatially predictable area of high foraging success for predators (Cox et al., 2018). Similar tidally driven processes may occur at the continental shelf break, where upwellings from deeper water may provide predictable foraging opportunities (Cox et al., 2018). While persistent surface fronts, detectable with satellite imagery, have been shown to correlate with the foraging behaviour of seabirds (Scales et al., 2014; Grecian et al., 2018), our results demonstrate the importance of also considering vertical water column structure as a potential predictor of habitat use for aquatic predators.

Harbour seal distribution was predominantly driven by a negative association with increasing distance from haulout and water depth. As such, predicted density is more tightly concentrated in coastal and inshore waters compared to grey seals, but with fine-scale structuring of density around the coast (Figure 5). The exception to this is in Southeast England, where the negative associations with distance and depth were weaker. High at-sea density areas of seals hauling-out in this region extended further offshore than elsewhere around the coast (Figure 5). In general, the influence of dynamic covariates (SST, stratification and Δ stratification) was variable among the regions. We found relatively high densities of grey seals predicted in coastal waters (Figure 4) in areas where harbour seal populations have suffered the most rapid declines: including Orkney and the east coast of Scotland which have exhibited declines of over 80% between 2000 and 2016 (Thompson et al., 2019). Competition with grey seals for prey resources is one of several putative drivers of regional harbour seal declines (Thompson et al., 2019). Although comparing inter-specific differences in habitat associations and space use is an important step in quantifying the potential for competition, inference of inter-specific competition for prey resources is

TABLE 2 | Latest pup production estimates and August counts for grey seals within frequently monitored SACs in Scotland and eastern England.

SAC	Region	Pup production estimate (2019)	Latest august count (year)
Treshnish Isles	West Scotland	1,131 (1.8%)	160 (0.4%) (2018)
Monach Islands	Western Isles	12,511 (19.5%)	2,701 (7.1%) (2017)
North Rona	Western Isles	286 (0.4%)	175 (0.5%) (2014)
Faray & Holm of Faray	N. Coast & Orkney	2,186 (3.4%)	228 (0.6%) (2019)
Isle of May	East Scotland	1,885 (2.9%)	40 (0.1%) (2016)
Berwickshire & North	East Scotland/Northeast England	7,322 (11.4%)	4,322 (11.4%)
Northumberland Coast*		[FI: 2,823 (4.4%), FC: 4,449 (6.9%)]	[FI: 4,251 (11.2%) (2020), FC: 71 (0.2%) (2018)]
Humber Estuary	Southeast England	2,187 (3.4%)	3,897 (10.3%) (2021)

Percentages indicate the contribution to the total counts for Scotland and eastern England. SMU refers to Seal Monitoring Units used in seal conservation. *Berwickshire and North Northumberland Coast SAC comprises two discrete colonies, Farn Islands (FI) in the Northeast England SMU and Fast Castle (FC) in the East Scotland SMU. These sites are surveyed independently, thus the combined total is shown with component values in square brackets. The boundary of the SAC transects the Fast Castle colony but here we have included all pup production within the total for the SAC.

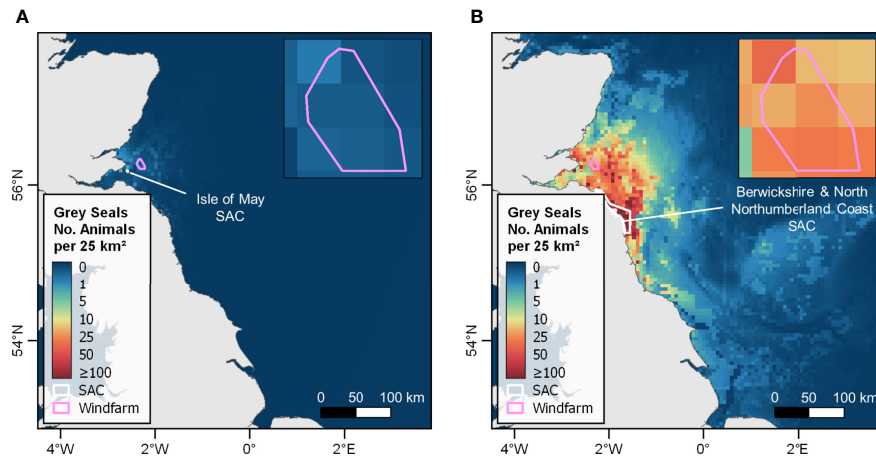


FIGURE 7 | Mean at-sea distribution estimates for grey seals hauling out in (A) the Isle of May SAC, and (B) the Berwickshire and North Northumberland Coast SAC. Estimates are scaled to absolute density (i.e. number of seals) based on most recent August counts, demonstrating that some SACs designated based on breeding numbers (e.g. the Isle of May) do not host large numbers of seals during the main foraging season. Inset maps show the number of seals apportioned to each SAC estimated to be within the footprint of the Neart na Gaoithe windfarm. Windfarm polygon source: EMODnet Human Activities dataset (<https://www.emodnet-humanactivities.eu/>; accessed 07/10/2021).

limited by a number of factors. For example, high levels of overlap in distribution may equally be indicative of exploitative competition, or sufficient prey resources to support both species. Similarly, low levels of overlap may result from competitive exclusion or spatial partitioning of foraging resources between the species. Moreover, it is impossible to disentangle spatial variation in prey preference or prey distribution from competition without examining changes in foraging habitat preference and distribution through time. This study considered overall habitat preference (i.e. not discriminating by behaviour) in order to capture the overall distribution of seals, since all forms of habitat use are of relevance for marine spatial planning. A priority for future work is to identify foraging behaviour using robust statistical models (such as hidden Markov models; Carter et al., 2016), which will facilitate a

comprehensive study of foraging habitat preference and may provide more insight regarding the dynamics of competition between the two species.

Technical Considerations

The habitat preference approach used here provides some key improvements over previous large scale distribution estimates for grey and harbour seals (i.e. usage maps (Matthiopoulos et al., 2004; Jones et al., 2015)). For example, where no tracked seal visited a specific cluster of haulout sites, predictions emanating from the haulout sites were based on null usage; a simple study-wide relationship between distance from haulout site and observed usage (Jones et al., 2013; Russell et al., 2017). In our approach, such predictions are based on a region-specific species-environment relationship, which includes distance to haulout

TABLE 3 | Seasonal movements of 12 breeding female grey seals. Seal Monitoring Unit for each site is shown in brackets.

		Pupping Site					
		Monach Islands SAC (Western Isles)	Non-SAC (N. Coast & Orkney)	Fast Castle, Berwickshire & N. Northumb. SAC (East Scotland)	Humber Estuary SAC (Southeast England)	Ramsey Island SAC (Wales)	Duvillaun Islands SAC (Rep. Ireland)
Tagging Site	Monach Islands SAC (Western Isles)	3	1				
	Non-SAC (West Scotland)	1					
	Humber Estuary SAC (Southeast England)			1	2		
	Lleyn Peninsula & The Sarna SAC (Wales)					3	
	Blasket Islands SAC (Rep. Ireland)						1

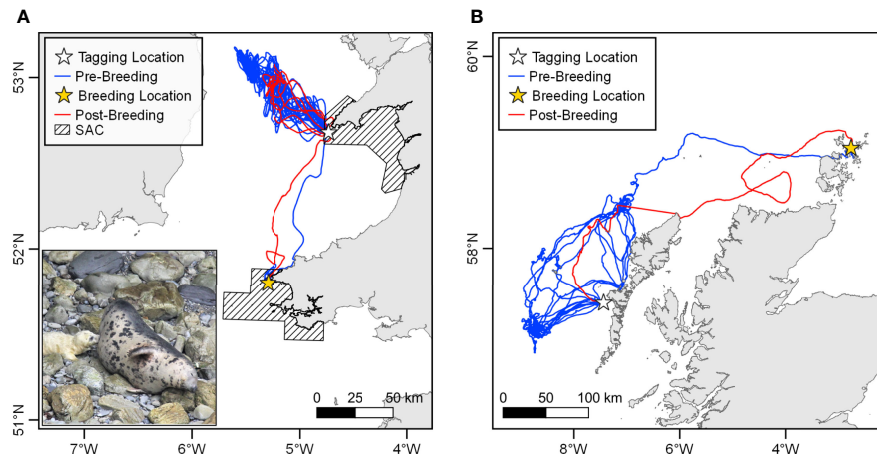


FIGURE 8 | Examples of grey seal breeding migrations. **(A)** A female seal tagged on Bardsey Island in the Llyn Peninsula and the Sarnau SAC foraged throughout the summer northwest of Bardsey, using Bardsey as a haulout site, before breeding on Ramsey Island in the Pembrokeshire Marine SAC in the Autumn. The seal returned to Bardsey after breeding. Inset photo shows the tagged seal nursing a pup on Ramsey (courtesy of RSPB Ramsey Island). **(B)** A female seal tagged in the Monach Islands SAC spent the summer foraging to the west of the Western Isles, hauling-out in the Monach Islands, before migrating to Orkney for breeding in Autumn. The seal returned to the Monach Islands SAC after breeding.

and any other covariates deemed to be good predictors of habitat preference by the model selection process. As such, areas of suitable habitat not visited by the tagged seals may still be detected, whereas they may be overlooked or underrepresented in the usage maps. Nevertheless, in data-rich areas (e.g. harbour seals in Southeast England), distribution patterns resulting from the track smoothing approach may be favourable to habitat-based predictions since they are able to describe features of the distribution which may not be captured by modelled habitat preference relationships averaged across individuals and dependent on relatively simple descriptors of habitat. Future work should seek to combine these two modelling frameworks to maximise robustness and ecological insights; previous work has been restricted to a small, discrete spatial extent (Jones et al., 2017). The usage maps have been an important resource for management applications, and they have also been used in ecological studies (Sadykova et al., 2017; Sadykova et al., 2020). For example, Sadykova et al. (2017) inferred habitat preference relationships for grey and harbour seals from the usage map distribution estimates presented by Jones et al. (2013). However, such inferred relationships, and resulting ecological conclusions, may be subject to distortion due to the reliance on null usage and the assumption that habitat preference does not vary among regions. Moving forwards, the maps presented here offer an updated resource for marine spatial planning, with increased potential for ecological insights on both regional and population-wide scales.

While the distribution estimates presented here represent a valuable resource for both ecology and management, as with any predicted species distribution, there are considerations which should be acknowledged depending on their application. Below we outline four important such considerations. (i) As with the “usage maps” (Jones et al., 2013; Jones et al., 2015; Russell et al., 2017), the upper and lower 95% confidence intervals presented in

this study are generated on a cell-wise basis, meaning that they should not be summed across an area (e.g., windfarm footprint), as doing so would lead to inflated uncertainty estimates. Specific area-based confidence intervals can be generated on a case-by-case basis, as demonstrated in the Neart na Gaoithe windfarm example presented here. (ii) The latest count for each haulout cell was used to weight the distribution estimates, and these are taken from different days, and in some cases different years around the coast (Figure A6.1 in Supplementary Material). There may be spatial as well as day-to-day variation in the proportion of the population hauled-out during the surveys, and such variation is not considered here. (iii) For some applications, such as identifying areas of ecosystem-level importance, it should be noted that the estimates presented here represent the at-sea distribution of seals hauling-out in the UK and Ireland and are not inclusive of seals from haulouts in continental Europe. (iv) There are additional considerations when using absolute density estimates, and thus relative density estimates should be used where possible (e.g. for comparison of density between areas). Uncertainty in total abundance (population size) for the study area could not be propagated. Furthermore, the proportion of time spent hauled out, and thus the at-sea population size, varies across the focal months (Russell et al., 2015) but was assumed constant (averaged) to generate maps of absolute abundance.

SAC-Specific Distribution Estimates

The distribution estimates presented here provide an opportunity to link changes in abundance detected at land-based monitoring sites with areas at sea where such changes are likely to be mediated. The ability to draw such links is particularly pertinent for SACs, which provide monitored conservation areas with management efforts focussed on maintenance of (or recovery to) Favourable Conservation

Status (FCS). By extension, knowledge of the at-sea distribution of individuals hauling out in an SAC is critical to predicting and managing the potential impact of offshore activities on the integrity of the SAC. Furthermore, in instances of declining SAC abundance, particularly for SACs no longer in FCS, these maps give guidance on where such change may be mediated. The results show that, unless the SAC encapsulates the majority of the abundance within a region (e.g. Monach Islands SAC), UK and Ireland-wide distribution maps may not be representative of SAC-specific distributions. For example, the Firth of Tay and Eden Estuary SAC has seen a steep decline in harbour seal abundance over the last two decades (Thompson et al., 2019). As such, overall distribution patterns in this area are largely driven by individuals hauling-out elsewhere within the region, and hotspots of density are not representative of the distribution of individuals using the SAC (**Figure S10.2**). Thus, the locations of processes occurring at sea most likely to impact the SAC population cannot be easily identified using the UK and Ireland-wide maps. However, an important consideration is connectivity between haul out sites; unlike true central place foragers (e.g. breeding seabirds) which always return to the same site between foraging trips, seal foraging trips often start and end at different haulout sites. Indeed, only 35% of grey seal trips and 44% of harbour seal trips analysed here started and ended at the same 5 km x 5 km grid cell. These differences in central place strategies mean that seals may utilise multiple designated and non-designated sites throughout the foraging season. Inter-regional movements within the foraging season are more limited (Russell et al., 2013) particularly for harbour seals (Carroll et al., 2020), thus we advise that stakeholders use the SAC-specific maps in conjunction with the overall prediction for the area to identify both primary and potentially secondary (through use of multiple haulouts) areas of linkage with SACs.

In addition to the management implications of movements within the foraging season (discussed above), there are particular complexities for grey seals associated with the relationship between breeding and foraging distributions on land. Grey seals are classic capital breeders and aggregate in large numbers during the breeding season (Bonner, 1972). SACs are generally designated based on breeding numbers, and population monitoring is focussed on trends in pup production (Russell et al., 2019). However, grey seal use of sites on land varies between the foraging and breeding season on two spatial scales. Indeed, breeding sites do not always represent a central place for foraging (**Table 2**). For example, the Isle of May SAC contributes 2.9% of pup production for Scotland and eastern England with >1,800 pups born annually (almost a quarter of the total pups born in SACs in this area), but hosts just 0.1% of seals hauled-out in this area during the foraging season (most recent count = 40) (**Table 2**). In such cases, hotspots of density in the area are unlikely to be attributable to individuals hauling-out at the SAC despite the large reported population size (based on breeding numbers). Our analysis reveals that only 1.4% (n=2) of seals estimated to be present within the footprint of the Neart na Gaoithe windfarm at any one time can be apportioned to individuals hauling-out in the Isle of May SAC (~15 km away),

while the majority (68.2%; 101) can be apportioned to the Farne Islands within the Berwickshire and North Northumberland Coast SAC ~75 km away (**Figure 7**). Any decline in the Isle of May breeding population would therefore not be easily attributed to processes occurring at sea, since the non-breeding distribution of these seals is largely unknown.

Grey seals also exhibit seasonal redistribution at broader spatial scales. Our analysis reveals that, of the 12 females that transmitted data through to the breeding season and were tagged in and/or likely bred in SACs, six (50%) bred in different SACs to where they were tagged, with four (33%) breeding at colonies in different Seal Monitoring Units (SMUs) (**Table 3**). Although these results come from a relatively small sample size, they support the findings of Russell et al. (2013) that 21–58% of breeding females use different regions for breeding and foraging. This highlights the level of uncertainty associated with linking abundance trends observed on grey seal breeding colonies to processes occurring at offshore foraging areas. Partial migration, where a population is comprised of migratory and resident individuals, is a widespread phenomenon in the animal kingdom (Chapman et al., 2011), but has not been widely identified in seals. Evidence from other terrestrial-breeding marine predators has demonstrated that migratory strategy may influence fitness; Grist et al. (2017) showed that breeding success was higher for non-migrating than migrating pairs of European shags (*Phalacrocorax aristotelis*) breeding on the Isle of May. In grey seals, the drivers of this behaviour are likely related to an inclination to natal philopatry and fidelity to breeding sites following recruitment (Pomeroy et al., 2000). Indeed, the rate of increase in pup production in Southeast England over recent decades lagged behind the rate of increase in seals counted during the foraging season (Russell et al., 2019) likely due to seals foraging in the south, where trends in abundance indicate conditions are favourable compared to further north where a proportion returned to breed. Further work is required to determine the implications of partial migration in grey seals for breeding success, population dynamics and conservation management.

CONCLUSION

This study presents the most up-to-date and comprehensive at-sea distribution maps for grey and harbour seals hauling-out in the UK and Ireland. These results represent a step forward in our understanding of predator distributions at sea and provide a valuable resource for marine spatial planning and conservation efforts. Furthermore, we reveal that overall hotspots of density at sea are not necessarily attributable to nearby designated sites, and present SAC-specific estimates of distribution. For both sets of resources we provide a comprehensive list of technical considerations to ensure that they are used with acknowledgement of their limitations. We demonstrate a disconnect between monitored sites where impacts are likely to be detected (i.e., SACs) and areas where impacts are likely to occur (i.e., at sea). For harbour seals, this problem can be largely overcome

using the SAC-specific distribution estimates. However, for grey seals we show that SACs designated based on breeding numbers cannot be reliably linked to areas where individuals may be exposed to threats at sea due to local redistribution outside of the breeding season and partial migration. The work presented here has focussed on the distribution of seals aged one and above. Grey and harbour seal pups exhibit different movement patterns to experienced individuals, and habitat preference may also vary throughout early life (Blanchet et al., 2016; Carter et al., 2020). Further work should therefore focus on generating distribution estimates for pups.

More generally, our study highlights the importance of considering regional variation in habitat preference. Regional habitat preference models have been shown to be favourable to global models for marine predator populations occupying different sides of an ocean basin (Torres et al., 2015; Mannocci et al., 2020), or discrete regions within shelf seas (Huon et al., 2021). However, few studies have combined predictions from different regional habitat preference models to generate large scale distribution estimates. Our results demonstrate that, although tracking data from a small number of patchily distributed locations can be used to provide species distribution estimates across a region, habitat associations can vary within a population between contiguous regions on a relatively fine spatial scale. Seals exhibited different habitat preference to those hauling-out in adjacent regions despite almost complete overlap in the accessible habitat available (**Figure S11.1**). We therefore show that differences in habitat associations can occur on a spatial scale that is smaller than the species' scale of movement, demonstrating the importance of tracking individuals from throughout the study area when using tracking data to predict species distributions. In addition, our results highlight the considerations in designating and managing land-based protected sites for mobile marine predators, particularly those which are not strict central place foragers, aggregate to breed and/or exhibit partial migration. To maximise the effectiveness of such management, there is an urgent need for ecologists and policy makers to assess the links between sites and scales at which monitoring can be conducted and at-sea areas where impacts may occur.

DATA AVAILABILITY STATEMENT

The datasets generated in this study are available from the University of St Andrews data repository: <https://doi.org/10.17630/f2a9cc5a-4fac-4740-937e-ed79fc907ebc>.

ETHICS STATEMENT

The study was reviewed and approved by the University of St Andrews Animal Welfare and Ethics Committee and the University College Cork Animal Ethics Committee (required since 2011). All UK capture, handling and other licenced procedures were carried out under UK Home Office project

licence PF84B63DE (and previous iterations: 60/2589, 60/3303, 60/4009 and 70/7806) under the Animals (Scientific Procedures) Act 1986. The capture of seals was conducted under licence from Marine Scotland (Scotland), the Marine Management Organisation (England) and Natural Resources Wales (Wales). In Ireland the work was conducted under licence from the National Parks and Wildlife Service, with additional licences from the Irish Health Products Regulatory Authority. Appropriate site-specific approvals were obtained, with any associated mitigation measures observed for designated sites, including ethics approval from the Royal Society for Protection of Birds (RSPB) for work on Ramsey Island (EAC2018-01). SMRU aerial surveys of haulout sites have been approved by the University of St Andrews Animal Welfare and Ethics Committee (SEC21032).

AUTHOR CONTRIBUTIONS

DJFR led conception and management of the study. MIDC performed the analysis and wrote the manuscript, with support from DJFR. Data and/or technical expertise were provided by DJFR, BJM, CDD, CDM, DLM, JM, DT, GDH, LB, MAC, MJ, PMT and WJG. SEWM led telemetry data collection.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.875869/full#supplementary-material>

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Design of an Optimal Testbed for Acoustic Tags: Test Case for Marine Megafauna

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Underwater acoustic technologies are a key component for exploring the behavior of marine fauna such as sea turtles, sharks, and seals. The animals are marked with acoustic devices (tags) that periodically emit signals encoding the device's ID along with sensor data such as depth, temperature, or the dominant acceleration axis - data that is collected by a network of deployed receivers. In this work, we aim to optimize the locations of receivers for best tracking of acoustically tagged marine fauna, and provide a test case with tags suitable for megafauna tracking. The outcomes of such tracking allows the evaluation of the animals' motion patterns, their hours of activity, and their social interactions. In particular, we focus on how to determine the receivers' deployment positions to maximize the coverage area in which the tagged animals can be tracked. For example, an overly-condensed deployment may not allow accurate tracking, whereas a sparse one, may lead to a small coverage area due to too few detections. We formalize the question of where to best deploy the receivers as a non-convex constraint optimization problem that takes into account the local environment and the specifications of the tags, and offer a sub-optimal, low-complexity solution that can be applied to large testbeds. Numerical investigation for three stimulated sea environments shows that our proposed method is able to increase the localization coverage area by 30%, and results from a test case experiment demonstrate similar performance in a real sea environment. We share the implementation of our work to help researchers set up their own acoustic observatory.

Keywords: acoustic marine testbed, acoustic tags, underwater acoustic tracking, anchor deployment, acoustic telemetry

INTRODUCTION

Underwater acoustic tracking is a key enabling technology for exploring long-term behavior of marine fauna (Kraus et al., 2018). Acoustic telemetry of fish developed in the mid 1950s by the U.S. Bureau of Commercial Fisheries (BCF), enabling the identification and localization of the individual fish without the need to recapture it (Hockersmith and Beeman, 2012). Tracking of decapod crustaceans with acoustic telemetry devices evolved since the 1970s and as of today 60% of published studies are based on acoustic telemetry (Florko et al., 2021), mostly using acoustic tags. Although tracking of fauna can be performed by passive and active system, e.g., (Diamant et al., 2019), the data obtained from acoustic tagging is far more informative. As a result, acoustic tagging

is used in multitude of research projects such as the ocean tracking network (OTN) (<https://oceantrackingnetwork.org/>). For marine megafauna, acoustic tags have been used for understanding the behavioral and social interactions of animals like sharks, sea turtles, and seals (Berejikian et al., 2016; Lea et al., 2016). Anchored receivers are deployed in known locations within the explored area to decode and measure the time of arrival (ToA) of the tags' emissions for, usually offline, tracking of the tagged animals. The long-term durability of the tags and receivers that can operate for many months and years allows operation over a long period of time for the statistical evaluation of the activity of the tagged animals. Examples of tagged sharks (Lea et al., 2016) and turtles (Thums et al., 2013) revealed valuable information about the animals' local motion patterns, their hours of activity, and their social interactions.

The detection of the animal's tag emissions using a single receiver is sufficient for collecting indications of presence/absence of an animal in an area of interest (Jackson, 2011; Gazit et al., 2013). However, in the case of fixed receivers, receptions of a tag's emissions by at least three receivers is required to localize the animal in a two-dimensional (2D) plane with no ambiguities. Such localization involves time synchronizing the receivers and fusing their ToA data collection in a time difference of arrival (TDoA) localization framework (Alexandri et al., 2018). In this context, a key for obtaining a large coverage area for tracking the tags is the positioning of the anchored receivers. Specifically, on one hand, overly-close deployment would decrease the localization accuracy due to small angular difference between the tag to be localized and each of the receivers. On the other hand, an overly-wide deployment would yield a small coverage area due to the limited transmission range of the emitting tag. This problem is further exacerbated when the bathymetry of the explored area is complex and the propagation loss for the tag-receiver link depends on the varying water column temperature and depth change of the seabed. As a result, not only the relative distance between the receiver should be considered, but also the receivers' geographic position (Huveneers et al., 2016).

When designing a testbed for the acoustic tracking of tagged marine fauna, the anchors are commonly spaced according to the declared detection range (Thelma Biotel, 2021), and are spread geographically to best cover an *area of interest*, I . Deployment strategies include a line of receivers to detect tagged individuals passage through a river or along a coastline (Kraus et al., 2018), or an array of evenly-spread receivers (Kessel et al., 2014; Thelma Biotel, 2021). A common practice (CP) for positioning the receivers is to cover the area of interest using equilateral triangles (Shiu et al., 2010), whose edges are set to half of the detection range. This practice stems from the fact that, under a simplified scenario of a cylindrical propagation loss, a close-to-optimal solution is obtained (see analysis in the **Appendix**). However, in the practical case where the seabed is complex and the detection range is not iso-symmetric, a more rigorous way to determine the anchors' deployment location is required. Two examples of the under-utilization of the deployment setup using CP are a testbed setup to track acoustically tagged slipper

lobsters, *Scyllarides latus*, at the Achziv Marine Nature Reserve in northern Israel (Alexandri et al., 2018), and a testbed aimed to explore the motion of tagged sandbar sharks, *Carcharhinus plumbeus*, close to the "Orot Rabin" Power and Desalination Station in Hadera, Israel (32°28'N; 34°52'E) (Alexandri et al., 2019). In the former, four receivers were anchored in a triangle according to the CP approach over a rocky seabed, and 19 lobsters were tagged and tracked for a period of 8 months. Out of more than 45,000 detected tags' emissions, only 252 (0.5%) were received by 3 or 4 receivers. In a second testbed, 20 tagged sharks were tracked for a period of 87 days by a set of 4 receivers deployed on a shallow sandy seabed according to CP. Out of a total of 42,589 detected tags' emissions, only 180 (0.4%) emissions were received by 3 receivers to enable localization. A summary of the poor results due to under-utilization of CP deployment setup is presented **Table 1**.

The problem of how to position receiving nodes resembles the "Art gallery problem" (Rajagopal et al., 2016), whose goal is to find the minimal set of guards such that every point in a floor plan is covered by at least one guard. In the case of 2D localization, three receivers represent a guard. While this type of optimization problem is proven to be NP-Hard (nondeterministic polynomial time hard) (Lee and Lin, 1986), i.e., the complexity of search increases with the problem size in such a way that a solution would compare with the brute-force approach of trying out the entire state-space, some work-arounds are possible. For indoor localization, information about the floor plan is utilized to reconcile position ambiguities formed by the localization of a node by only two receivers (Rajagopal et al., 2016). The proposed method disqualifies potential positions located outside the floor or behind barriers/walls that block the signals. To manage spatial-dependent propagation loss in indoor localization, templates of the reception pattern are used (Mnasri et al., 2015) as well as modeled calculations (Rajagopal et al., 2016). However, the solution for underwater localization is somewhat different. First, while the sea includes barriers that can be used to resolve localization ambiguities, these mostly apply in near shore locations. Furthermore, while some solutions relied on the structure of the seabed for localization, e.g., in Dubrovinskaya et al. (2017), localization accuracy is low if the structure is not diverse.

In this paper, we propose a systematic method to determine the deployment setup of a marine fauna tracking testbed considering the acoustic specifications of the tags, the number of receivers, and the environmental properties. As a test case, we consider 16 mm tags that are suitable for tagging megafauna. Relying on prior knowledge of the bathymetric and bathythermal conditions in the explored area, we formalize a constraint optimization problem that accounts for the spatially dependent propagation loss, and yields the best deployment locations to maximize the coverage area. In our analysis, we consider the user's area-of-interest, I , and evaluate the coverage quality by the geometrical dilution of precision (GDOP) (Sharp et al., 2009). Since I may be non-convex, the optimal solution is often NP-hard, i.e. to solve the decision problem of "where to position the

TABLE 1 | Records of successful tag detections from Achziv Marine Nature Reserve tracking 19 slipper lobsters for a period of 8 month, and from “Orot Rabin” Power and Desalination Station testbed tracking 20 sandbar sharks for a period of 87 days.

Testbed	Achziv	“Orot Rabin”
Number of received emissions by single receiver	45,000	42,589
Number of received emissions by three or more receivers	252	180
Percentage of received emissions by three or more receivers [%]	0.5	0.4

Only 0.4% to 0.5% of received tags' emissions were received by 3 or more receivers. Results demonstrate the under-utilization of CP deployment setup.

receivers?” requires unreasonable long time such that even for a modest I the solution becomes too hard to evaluate. For these cases, we offer a sub-optimal implementation based on a genetic algorithm (GA). We refer to our approach as the *Propagation-Dependent Anchor Deployment* (PDAD) scheme. For simple setups, we show that PDAD achieves the optimal solution, as verified by a brute force search. For more complex setups, we compare the coverage area yielded by PDAD to that of CP.

Our contribution is twofold:

1. A novel systematic approach and optimization formalization for how to set up the location of anchored receivers in an underwater testbed.
2. A method to merge the GDOP metric with bathymetric information to quantify detection ranges.

We explore the performance of our method in numerical simulations and in a sea experiment. The former demonstrates the obtained deployment strategy for three different seabed environments and explores the sensitivity of the results to the system's parameters, as well as the degree of sub-optimality of the proposed solution. The latter demonstrates the merit of using the proposed approach in a real sea environment as a test case for tracking megafauna. Compared to the CP strategy, the results show an increase of roughly 30% in the size of the covered area as obtained by PDAD.

MATERIALS AND METHODS

In this section, we describe our system model and formulate our solution. We use the following notations: coordinates are marked by a macron sign, e.g. I sets are marked by bold letters, e.g., D_i . **Table 2** summarizes the paper's main variables and notations.

Study Area

Our setup includes N receivers deployed to cover a given area-of-interest \mathcal{I} . Our goal is to determine the optimal location and deployment depth for the receivers, such that a tagged animal that passes through \mathcal{I} is well-localized within area \mathcal{I} and possibly beyond it. For each tag's emission, the detecting receiver measures the local arrival time, such that, assuming all N receivers are time-synchronized, localization is performed by TDoA cf. (Alexandri et al., 2018).

We assume prior knowledge to evaluate the propagation loss between any pair of positions within and beyond \mathcal{I} . In particular, we require information about the bathymetry within the

explored area and the expected bathythermal profile of the water. This information is used to run a propagation loss model such as ray-tracing, normal modes, or parabolic equation (Bahrami et al., 2016; Gul et al., 2017). We admit that, since the bathythermal profile is time varying and depends on seasons, the sound velocity profile (SVP) cannot be accurately known for the entire deployment time period. Yet, a track of the bathythermal profile may reveal temporal trends in the sound speed, allowing the evaluation of a *nominal SVP*. Alternatively, the user may perform periodic measurements of the bathythermal and change the locations of the receivers if needed.

Detection Range

Let P_{SL} be the source power level of the tag to-be-localized. Let P_{NL} be the ambient noise level, assumed constant in the explored area, and let $p_{TL}(\bar{r}_i, \bar{p})$ the power transmission loss between a source node at position $\bar{p} = (x, y, z)$ and the i th receiver at position $\bar{r}_i = (x_i, y_i, z_i)$, $i = 1, 2, \dots, N$. We calculate $p_{TL}(\bar{r}_i, \bar{p})$ and P_{NL} by acoustic channel modeling, i.e., modeling the acoustic attenuation by considering the environmental conditions, the ambient noise, and the emitted frequency, e.g., (Gul et al., 2017), and from the Wenz curves for acoustic ambient noise in the ocean (National Research Council, 2003), showing the average ambient noise spectra for different levels of shipping traffic, and sea state conditions. Specifically, analyzing a huge set of acoustic measurements of ambient noise, Wenz was able to provide an empirical curve for the ambient noise level and to show that it is frequency and environment dependent. Then, comparing the received level

$$P_{SNR} = \frac{P_{SL} \times p_{TL}(\bar{r}_i, \bar{p})}{P_{NL}} \quad (1)$$

to a detection threshold, P_{DT} , we measure whether location \bar{r}_i is suitable for detecting a source located at \bar{p} . That is, if $P_{SNR} \geq P_{DT}$ a receiver positioned at \bar{r}_i will detect a tag emitting at \bar{p}

Localization Quality

A common metric to measure the achievable localization accuracy for the planned receivers' deployment is the GDOP. This is a unitless metric that ranks the deployment setup by considering both the measurement precision and the geometry between the source and receivers to account for the effect of the geometry setup on localization (Kaplan and Hegarty, 2005). As localization quality improves, the GDOP decreases. Classification of GDOP values are outlined in **Table 6**. For example, if all receivers are colinear, the achievable localization

TABLE 2 | Main variables and notations - Coordinates' variables are marked by a macron sign, e.g., \bar{p} .

Variables	Descriptions
α	User-defined GDOP threshold for localization quality
β	Number of required receivers for localization
i	Index of a receiver and its associated detection area
j	Receivers set index whose detection areas intersect
\bar{r}_i	Position of receiver number i
\bar{p}_i	Position of an emitting source
D_i	Detection area of the i^{th} receiver as defined by (4)
λ_j	Set of receivers whose detection areas intersect as defined in (5)
Λ	A group containing sets λ_j
L_j	Localization area resulting from the intersection of β detection areas. Defined in (6)
μ_j	Set of all positions of the source, \bar{p} , in the localization area, L_j , in which $\text{GDOP}(\bar{p}, L_j) \leq \alpha$. Defined in (7)
C	Coverage area, a union of all J usable areas
\mathcal{I}	Area-of-interest, the area to be covered by the optimized deployment
GDOP	Geometrical dilution of precision
η	Ratio between the area covered by deployment according to PDAD to deployment according to CP
θ	Ratio between the coverage and the usable areas
P_{SL}, P_{TL}	Source level power and transmission loss respectively
P_{NL}, P_{SNR}	Noise level power and received signal to noise respectively
$\xi_{i,r}$	Throughput of the tags - receivers link

Sets are marked by bold letters, e.g., D_i .

quality is poor. Given a set $\lambda = \{\bar{r}_1, \bar{r}, \dots, \bar{r}_N\}$ of N receivers stationed at locations, $\{\bar{r}_1, \bar{r}, \dots, \bar{r}_N\}$ the GDOP is defined as the ratio between the accuracy of a position fix to the variance of the measurements (Sharp et al., 2009). Formally, denote the visibility matrix (Yarlagadda et al., 2000; Kaplan and Hegarty, 2005)

$$H(\bar{p}, \lambda) = \begin{bmatrix} a_{x1} & a_{y1} & a_{z1} & 1 \\ a_{x2} & a_{y2} & a_{z2} & 1 \\ a_{x3} & a_{y3} & a_{z3} & 1 \\ \vdots & \vdots & \vdots & \vdots \\ a_{xN} & a_{yN} & a_{zN} & 1 \end{bmatrix} \quad (2)$$

whose elements are the unit vectors pointing from a potential position of the source, $\bar{p} = [p_x, p_y, p_z]$, to the location of the i^{th} receiver, $\bar{r} = [r_x, r_y, r_z]$, such that, $a_{xi} = (p_x - r_x) / R_i$, $a_{yi} = (p_y - r_y) / R_i$ and, $a_{zi} = (p_z - r_z) / R_i$ where, $R_i = \sqrt{(p_x - r_x)^2 + (p_y - r_y)^2 + (p_z - r_z)^2}$ all in Cartesian coordinates. The $\text{GDOP}(\bar{p}, \lambda)$ equals, $\sqrt{g_{11}^2 + g_{22}^2 + g_{33}^2 + g_{44}^2}$, where

$$(H^T H)^{-1} = \begin{bmatrix} g_{11} & g_{12} & g_{13} & g_{14} \\ g_{21} & g_{22} & g_{23} & g_{24} \\ g_{31} & g_{32} & g_{33} & g_{34} \\ g_{41} & g_{42} & g_{43} & g_{44} \end{bmatrix}. \quad (3)$$

Problem Statement

To formulate the receivers' deployment problem, four sets of variables are required. Recall that the source node is detected when $P_{DT}(\bar{r}_i, \bar{p}) \leq P_{SL} \times P_{TL} / P_{NL}$. We define the *detection area*, D_i , as the set of all possible positions of the source such that a receiver located at \bar{r}_i will detect the source's transmissions. Formally,

$$\bar{p} \in D_i | P_{DT}(\bar{r}_i, \bar{p}) \leq \frac{P_{SL} \times P_{TL}(\bar{r}_i, \bar{p})}{P_{NL}} \quad (4)$$

The resolution of set D_i is determined by the resolution of the bathymetric information. An example of a detection area for four receivers is shown in **Figure 1A**. Note that the detection area obtained is not necessarily convex. Let $\Lambda\beta$ be a group containing sets λ_j , $j=1, \dots, J$, where λ_j is the j^{th} set of at least β receivers whose detection areas intersect such that

$$\lambda_j \in \Lambda(\beta) | \bigcap_{i \in \lambda_j} D_i \neq \emptyset, |\lambda_j| \geq \beta. \quad (5)$$

For example, $\beta = 3$ for 2D localization¹, and $\beta = 4$ for 3D localization. As shown in **Figure 1A**, for $\beta = 3$, there are two sets of 3 receivers, $\{r_1, r_2, r_3\} \in \lambda_1$, $\{r_1, r_3, r_4\} \in \lambda_2$. The group containing all the sets is $\{\lambda_1, \lambda_2\} \in \Lambda(\beta)$.

For a given λ_j , we define a *localization area*, $L_j(\lambda_j, \beta)$, as an area resulting from the intersection of at least β detection areas. Formally,

$$L(\lambda_j, \beta) = \bigcap_{i \in \lambda_j} D_i | \lambda_j \in \Lambda(\beta). \quad (6)$$

Denote a *usable area*, $U_j(\lambda_j, \beta)$, as the set of all positions of the node to be localized, \bar{p} , in the localization area $L(\lambda_j, \beta)$ for which "good" localization is attainable. Specifically, the usable area is an area for which, $\text{GDOP}(\bar{p}, L_j(\lambda_j, \beta)) \leq \alpha$ where α is a scalar value determined by e.g., **Table 6**. Formally,

$$\bar{p} \in U_j(\lambda_j, \beta) | \text{GDOP}(\bar{p}, L_j(\lambda_j, \beta)) \leq \alpha, \bar{p} \in L_j(\lambda_j, \beta). \quad (7)$$

Our fourth set is the *coverage area*, $C(\beta)$, denoted as the union of all usable areas,

$$C(\beta) = \bigcup_j U_j(\lambda_j, \beta). \quad (8)$$

We formulate the task of receiver deployment as an optimization problem whose solution is locations, \bar{r}_i , $i = 1, \dots, N$, which maximize the size of the coverage area $\|C\|$:

$$\begin{aligned} & \text{argmax}_{r_1, r_2, \dots, r_N} \|C(\beta)\| \\ & \text{st. } \|C(\beta) \cap I\| \geq \rho \|I\|. \end{aligned} \quad (9)$$

Since most applications require the coverage of a given area of interest, I , we constrain the solution such that the resulting convergence area covers at least ρ percent of I . This constraint also allows for the discrimination between a "must-be-covered" area and a "nice-to-have" coverage area. An example of such a

¹note that when the source is mobile $\beta = 2$ will also support 2D localization as shown in (Alexandri et al., 2018).

consideration is presented in (Pickholtz et al., 2018) for the monitoring of acoustically-tagged herbivorous fish, *Siganus rivulatus*, close to the shore area. In this case, the movements of the herbivorous fish close to the shallow fringing coral reefs are of interest (the “must-be-covered” area), along with information from other areas along the shore (the “nice-to-have” area).

The PDAD Approach

Optimal Formalization

We formulate the problem statement in (9) as a mixed constraint optimization problem. In accordance with (9), let I , D , LU and C be 3D matrices representing the area-of-interest, the detection area, localization area, usable area, and the coverage area, respectively. The matrices' rows, columns, and depths represent the quantized x , y , z grid in Cartesian coordinates, with lower-case letters representing the matrix entries with a resolution set by the bathymetry information (e.g., every 5m). For example, entry is the entry of $i^{K \times L \times M}$. The capability to detect a source located in position $\bar{p}(x = k, y = l, z = m)$ by the i^{th} receiver located in position \bar{r}_i is defined by the binary operator

$$d_{k,l,m}(\bar{r}_i) = \begin{cases} 1 & \text{if } P_{DT}(\bar{p}(k, l, m), \bar{r}_i) \leq \frac{P_{SL} \times P_{TL}}{P_{NL}} \\ 0 & \text{otherwise} \end{cases} \quad (10)$$

Then, a source located in position \bar{p} can be localized if it is detected by at least β receivers. The elements of $L(\lambda_j, \beta)$ are formalized by the binary operator

$$l_{k,l,m}(\lambda_j) = \begin{cases} 1 & \sum_{i=1}^N d_{k,l,m}(\bar{r}_i) \geq \beta, \bar{r} \in \lambda_j \\ 0 & \text{otherwise} \end{cases}, \quad (11)$$

where each λ_j is a subset of, $\wedge(\beta)$ containing at least β receivers. Here, $\wedge(\beta)$ is the complete set of \bar{r}_i receivers $i = 1, \dots, N$. Note that the maximum number of such λ_j sets is $J = \sum_{p=\beta}^N \binom{N}{p}$.

Recall that the usable area U_j is the mapping of all locations \bar{p} inside $L(\lambda_j, \beta)$ whose GDOP is smaller than a given threshold α . In the matrix representation,

$$u_{k,l,m}(\lambda_j, (\beta)) = \begin{cases} 1 & \text{GDOP}(L_j(\lambda_j, \beta)) \leq \alpha \\ 0 & \text{otherwise} \end{cases}. \quad (12)$$

Similarly, the coverage area matrix, defined as the union of all the different usable areas $j = 1 \dots J$, is formalized by the binary operator

$$c_{k,l,m}(\beta) = \begin{cases} 1 & \text{if } u_{k,l,m}(\Lambda, (\beta)) = 1 \\ 0 & \text{otherwise} \end{cases}. \quad (13)$$

The intersection of $C(\beta)$ and I in the constraint of (9) can thus be expressed by

$$\|C(\beta) \cap I\| = \sum_k \sum_l \sum_m c_{k,l,m}(\beta) i_{k,l,m}. \quad (14)$$

Note that $d_{k,l,m}$, $l_{k,l,m}$, $c_{k,l,m}$ are all a function of locations $\bar{r}_i, \dots, \bar{r}_N$ which in turn can take any value within C and whose determination is the goal of this work. The deployment is obtained by solving

$$\Lambda = \operatorname{argmax}_{\bar{r}_1, \dots, \bar{r}_N} \sum_k \sum_l \sum_m c_{k,l,m} \quad (15a)$$

$$\text{s.t.} \quad \sum_k \sum_l \sum_m c_{k,l,m} i_{k,l,m} \geq \rho \sum_k \sum_l \sum_m i_{k,l,m} \quad (15b)$$

Algorithmic Solution

A closed-form solution of (15) for the simple case of three receivers deployed over a flat seabed with isotropic propagation loss is presented in the **Appendix**. We note that, in the general case, problem (15) is non-convex. This is because, as illustrated in **Figure 1**, even when the detection area of each receiver is convex (a circle or an ellipsoid) - and thus so is the localization area - the coverage area may be constructed from a number of non-continuous usable areas. Furthermore, as demonstrated in **Figures 1A, B**, even for a convex localization area, the usable area itself may be non-convex. Hence, (15) is a constrained non-convex optimization problem, which can be solved by procedures such as branch and bound (B&B) (Clausen, 1999) with a polynomial complexity on average (Zhang and Korf, 1992; Shabi et al., 2017), or by randomized approaches such as simulated annealing (Blum et al., 2021). Here, we propose to use GA, which is suitable for complex deployments, i.e., a larger number of receivers and diversified bathymetric and bathothermal conditions. We chose GA since it is suitable for overcoming local minima in problems involving a non-convex objective function (Mnasri et al., 2015). The fitness function is multi-objective, seeking to maximize the coverage area inside I and to minimize a penalty function for coverage outside I .

Evolutionary algorithms (EA) have probabilistic convergence time (Ankenbrandt, 1991). The average convergence time is defined as the number of generations it takes to reach convergence (Rylander, 2001). To that end, the complexity depends on the individual's and population's representation, the implementation of mutation, crossover and selection processes, and the fitness function (Corus et al., 2017). Given the above, the complexity is on the order of, where g is the number of generations, p is the population size, and i is the size of the individuals. We implemented PDAD using Python's “DEAP” evolutionary computation framework package and used it both for the simulation and the sea experiment.

Numerical Investigation Setup

To analyze PDAD performance, we consider three environments with different attributes:

1. A theoretical, simple environment: a flat seabed with an isotropic SVP, termed SVP_{ISO}. This type of environment may be considered when the environmental conditions are unknown.
2. A moderate spatially diverse area: an area of $6000 \times 6000 \text{ m}^2$ shallow water area close to the “Orot Rabin” Power and Desalination Station in Hadera, Israel ($32^\circ 28' \text{N}$; $34^\circ 52' \text{E}$; an

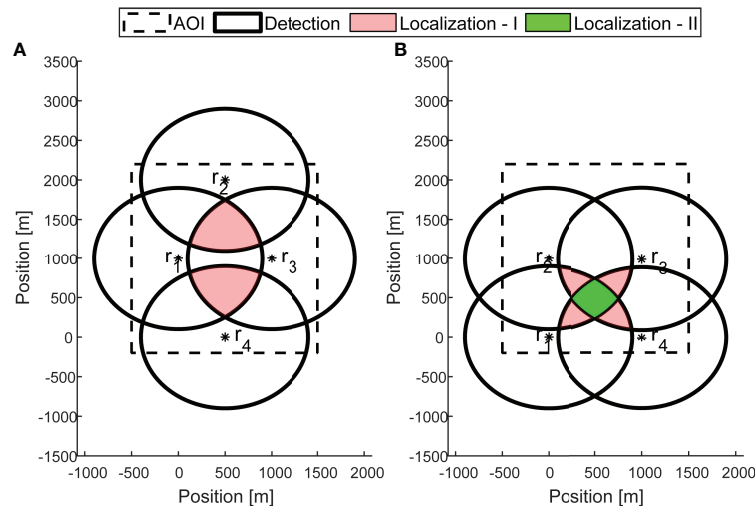


FIGURE 1 | An example showing the deployment of $N = 4$ receivers $\bar{r}_1, \bar{r}_2, \bar{r}_3, \bar{r}_4$, with corresponding detection areas marked by black contour lines. For the case of $\beta = 3$, in deployment setup (A), although $J = 5$, there are two localization areas, $L(\lambda_1), L(\lambda_2)$, marked by the light red shading. The two sets of at least 3 receivers are $\lambda_1 = \{\bar{r}_1, \bar{r}_2, \bar{r}_3\}$ and $\lambda_2 = \{\bar{r}_1, \bar{r}_3, \bar{r}_4\}$. The coverage area, C , is the union of $L(\lambda_1), L(\lambda_2)$. In the deployment setup (B), the light red areas form “Localization area - I”, which merges localization areas $L(\lambda_1), L(\lambda_2), L(\lambda_3), L(\lambda_4)$ for which $\beta = 3$ detection areas overlap. The light green areas form “Localization area - II”, for which $\beta = 4$ detection areas overlap. For both deployment setups, the resulting localization area is non-convex.

area we also explored in our sea experiment. Within this area, the selected I area is a $2000 \times 2000 \text{ m}^2$ rectangle with a water depth ranging from 0 to 25 meters. The entire area was divided into a grid of 60×60 , yielding a sample resolution of 100 m. Here, the receivers are anchored at a depth of 0.5 m above the seabed, and the mobile transmitter moves at a depth of 3 m. The bathymetry of this area is shown in **Figure 2A**.

3. An extremely diverse seabed: a coastal area north of San Diego between 32.65°N to 32.755°N and -117.265° to -117.265° W and -117.35 to -117.35° W (Divins and Metzger, 2021). Out of

this $5000 \times 4000 \text{ m}^2$ area, we picked I to be a square of $3000 \times 3000 \text{ m}^2$, which was divided into grid cells of a 100 m resolution. For this environment, the simulated receivers are anchored at a depth of 2 m above the seabed, while the mobile node maintains its depth at 10 m. **Figure 3A** shows the bathymetry of the considered area, and its SVP is shown in **Figure 3B**. The diversity of the considered area is demonstrated in **Figures 3C, D**, showing significant differences between the effective detection area for two different grid positions.

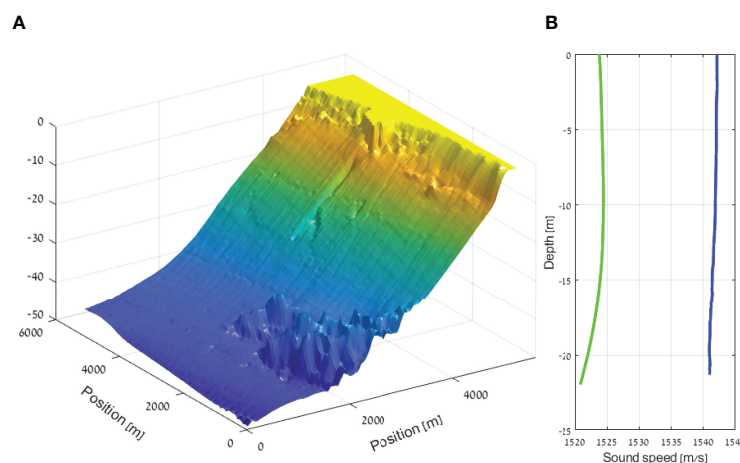


FIGURE 2 | (A) Bathymetry, (B) eastern Mediterranean winter SV, SVP_H (blue) measured sea experiment SVP_M (green) of the area near “Orot Rabin” Power and Desalination Station in Hadera, Israel.

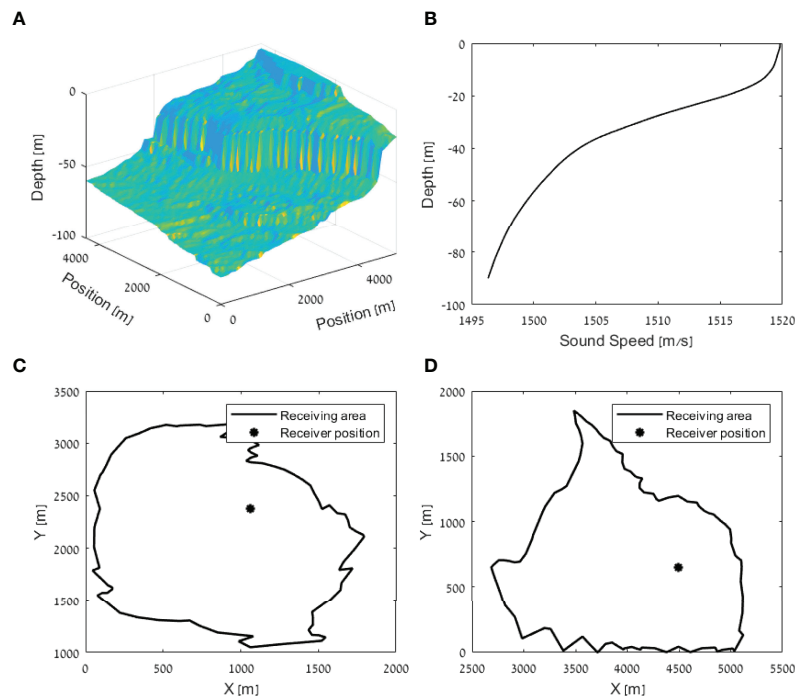


FIGURE 3 | Environmental condition of shallow water close to San Diego Bay. **(A)** Bathymetry and **(B)** the sound velocity profile. The impact on the expected detection area of a single receiver is shown in **(C)** for a receiver positioned at (1000, 2400, -10) and in **(D)** for a receiver positioned at (4500, 750, -10).

We consider the specification of an actual acoustic tag manufactured by Thelma-Biotel Inc., Trondheim, Norway (Alexandri et al., 2018). These acoustic tags are used globally in applications to monitor fauna in marine environments and to track migration patterns (Lennox et al., 2021; Reubens et al., 2021). The mobile node is an acoustic tag (model: ID-HP16) emitting 69kHz single-tone signals of intensity 158dB re 1μPa @ 1m. A range test we performed showed that the detection distance is 1000m in shallow water with a sandy bottom (Alexandri et al., 2019).

To measure the GDOP in each deployment setup, the spatial-dependent propagation loss must be accounted for. We consider two ways to attain the propagation loss. The first, assigned only in the case of a flat seabed with an isotropic SVP, applies a transmission loss model of

$$TL = 10\log(R) + \alpha R/1000, \quad (16)$$

with R being the transmission range and α the absorption parameter. The result is a transmission power loss of 48dB, where $\alpha = 18$ dB/km for 69 kHz (Urick, 1983). For complex environments, we consider the Bellhop ray-tracing propagation model (Porter, 2011). In both cases, the detection area is calculated by setting a limit on the signal-to-noise ratio to be above 10 dB.

For each of the above three areas, two types of deployment setups were compared. The first is based on the CP method of positioning the receivers at the vertices of equilateral triangles

partially covering the inner area of I . The distance between the receivers is set to half of the tags' specified detection range, namely 500 m. The second deployment setup is based on positioning the receivers according to the PDAD. Each individual is a set of the receivers' coordinates x and y . For the GA sub-optimal solution, the initial population size is based on a single individual positioned at the center of I with the rest of the individuals positioned around the center position. The effectiveness of the two methods is compared in terms of the size of the resulting coverage area for each deployment strategy. To this end, we chose the coverage area to be such that for each point inside I , $DOP \leq 5$.

In our simulations, we used an AMD Ryzen™ Threadripper™ 3990X CPU with 128 threads and measured processing time of about 100 msec per thread per each possible deployment setup. To evaluate the complexity of the proposed deployment scheme, we note that the size of a search space to position N receivers in a given area divided into a rectangular grid of $x \times y$ is $(xy)^N$. For example, for a grid size of 100×100 and $N = 3$, the search space size is 10^{12} . Hence, with the full utilization of our server, a complete search of the search space will last more than 24 years. This is because of the complexity of a solution in which brute-force searches the considered area is $O((xy)^N)$. In our case, using the PDAD approach, the best solution for the flat bottom isotropic propagation environment was achieved in the range of 500 to 2700 GA's generations for the different available number of receivers. Using a 64 core, 128GB memory computer, the processing time was 2:30 hours for 3 receivers deployment and 28 hours for 10 receivers deployment.

Sea Experiment Setup

The sea experiment aimed to demonstrate the applicability of our simulation results, and to explore the benefit of the proposed PDAD strategy in the realistic case of a low-resolution possibly-mismatched bathymetry map. The experiment took place in November 2021 close to the “Orot Rabin” Power and Desalination Station in Hadera, Israel ($32^{\circ}28'N$; $34^{\circ}52'E$), in an area of interest of $1200 \times 1400 \text{ m}^2$, at the southeastern part of the same area used in one of our numerical analysis cases (see the bathymetry map in **Figure 2**). We used acoustic equipment from Thelma Biotel AS., Trondheim, Norway - specifically, 7 acoustic tags and the standard receivers that decode these emissions. The experiment involved four kayaks, each was towing a small buoy 2 m behind its stern. The tags were attached roughly 2 m below the buoy, and maintained their depth using a balancing weight attached below the tags. For groundtruthing, each kayak carried a GPS receiver that logged its location throughout the trial. Two clusters of four receivers each were anchored at a depth of 1 meter above the seabed in the explored area. One cluster was positioned according to the CP approach, and the other according to the results of a PDAD calculation using a given bathymetry map of the area and an SVP measured prior to the experiment. The measured SVP, SVP_M , is shown in **Figure 2B**.

In addition to comparing the size of the usable area for CP and PDAD, a second performance metric explored the throughput of the tags - receivers link, defined as $\xi_{i,r}$. Here, the throughput is defined by the ratio between the number of receptions to the total number of emissions. Specifically, two cases are considered. 1) $\xi_{2,r}$ is the ratio between the number of received emissions by one or two receivers and the total number of emissions, and 2) $\xi_{3,r}$ is the ratio between the number of received emissions by three or four receivers and the total number of emissions throughout the experiment. The former reflects on the detection properties of the deployed setup, while the later on the localization quality. The throughput metric accounts for possible uneven time spent by the kayaks in the CP or PDAD setups. To avoid bias, we normalized the throughput by the tags' distances to the center of each area. Specifically, for each cluster of four receivers, the geometric center of the area was calculated. Then, the throughput was calculated and normalized by the tag's range from the cluster centroid.

Figure 8 shows the receivers' locations in the explored area. The position of the CP's receivers are marked by aqua-colored squares, and the positions of the PDAD's receivers are marked by red-colored diamonds. In a previous work (Alexandri et al., 2019), a range test showed that in the considered environment, the detection range of a similar tag and receiver pair is roughly 1,000 m. Thus, for CP, the distance between the receivers was set to 500m. We note that both CP and PDAD shared receiver number 2.

The experiment lasted for 240 min. During that time, each tag emitted a signal in a fixed interval every 30 to 45 sec, for a total of 2,730 emissions. Out of these, 406 emissions were detected by at least one receiver and 280 emissions were detected by at least three receivers of the CP or PDAD clusters. In order to ensure

that the four kayaks cover the complete area of interest, their route, provided in **Figure 8**, was planned to reach beyond the anticipated detection range of the tags. As a result, we report low tag detection rate. For each detected emission, the receivers measured the ToA by their internal clock. The receivers were time-synchronized prior and after the experiment. This involved both synching the receivers' clock to a reference clock by attaching a specific acoustic tag to one of the receivers, and using its emissions to time-synchronize the others (see details in (Alexandri et al., 2018)). Tag emissions were sorted and aggregated to the CP and PDAD clusters. If received by either three or four receivers, the emissions were considered to be inside the usable area that allows localization. To comment on the receiving conditions we also recorded the ambient noise level, as measured by each receiver.

RESULTS

In this section, we report results from the numerical investigation of our deployment method and from the designated sea experiment. For the simulations, we used the size of the area which achieves good localization, i.e., $GDOP \leq 5$, and explored the results against the brute-force solution and compared to CP. We also investigated the sensitivity to the system's parameters - in particular, the number of receivers, the size of C for different GDOP values, and to different SVPs. For reproducibility, we shared our implementation code in the **Supplementary Material**.

Simulation Results

We start by analyzing the results of the theoretical environment. **Figure 4** shows the size of C ($\beta=3$) for the case of three receivers as a function of the distance between the receivers, l , normalized by their receiving range, R . The maximum coverage area for $GDOP=5$ is attained when the distance between the receivers is about half of the receiving range. For cases of higher GDOP values, i.e. the localization accuracy in some parts of C is of lower quality, a larger coverage area can be attained. For example, for $GDOP=8$, the optimal distance between the receivers is about 40% of the receiving range and $C=1.85R^2$. For a lower GDOP, when localization accuracy is of high priority, a smaller coverage area is attainable. For example for $GDOP=2$ the maximal attainable coverage area is $C=1.14R^2$ for $l=0.66$. This result may serve as a guideline for deployments in non-spatially diverse areas. The analytical derivation of the attainable coverage area for the theoretical environment is outlined in the **Appendix** and in **Figure 10**. In **Figure 5**, we compare the achieved coverage area between CP and PDAD for different numbers of receivers, ranging from 3 to 13. We observe that the coverage area gained by using PDAD over CP increases with the number of receivers. This is attributed to the increase in the number of degrees of freedom for the receivers' placement.

For the moderate spatially diverse area, in **Table 3**, we compare the results for two SVPs: a simple fixed profile of 1520 m/s, SVP_{ISO} , and an eastern Mediterranean winter SVP, as shown in **Figure 2B** (Salon et al., 2003), termed SVP_H . The

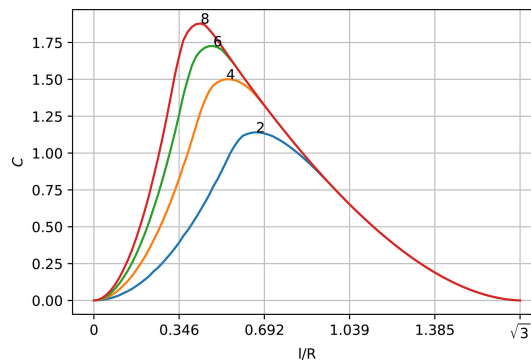


FIGURE 4 | Effect of distance between the receivers, I/R , normalized to the maximum receiving range, R , on covered receiving area, C , and attained positioning quality for 3 equilateral receivers' deployment in isotropic propagation loss. As the quality of positioning increases (the GDOP is smaller), the attained covered area C decreases.

first two columns of **Table 3** summarizes the ratio between the size of the coverage area as obtained by PDAD and CP, for the moderate diverse bathymetry in Hadera

$$\eta = C_{\text{PDAD}}/C_{\text{CP}} \quad (17)$$

The results are presented in **Table 3** for the different number of receivers, and for $\text{GDOP} \leq 5$. We observe that, using PDAD, for both SVPs the attainable covered area is larger than that of CP. An interesting result presented in **Figure 6** shows that for the deployment of 5 receivers in isotropic conditions - in contrast to CP where all of the receivers are placed inside I - the PDAD solution suggests that 3 out of the 5 receivers be placed outside I . This deployment yields an increase of 67% in the localized area. Finally, from the results in **Table 3**, we observe the difference of the gain obtained for the two different SVPs. A much higher gain in using PDAD is shown when the SVP is complex. This is because a diverse SVP impacts the propagation loss, rendering the channel to be spatial dependent.

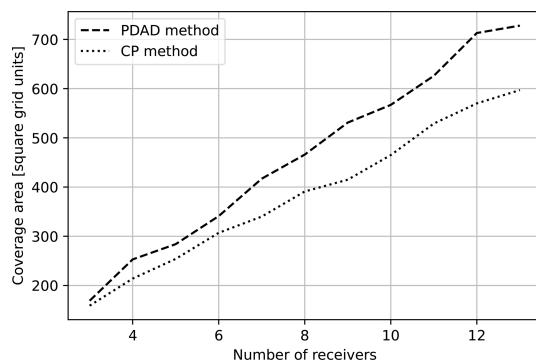


FIGURE 5 | Area covered by deployment setup based on CP method, i.e., positioning the receivers at the vertices of equilateral triangles vs. deployment based on the proposed PDAD method, i.e., optimization of receivers locations based on the surrounding environmental conditions.

TABLE 3 | η - from (17) for deployment of 3, 5 and 10 receivers at the Hadera power station and in San Diego.

	Hadera	Hadera	San Diego	San Diego
	SVP _H	SVP _{ISO}	SVP _S	SVP _{ISO}
# of receivers	η	η	η	η
3	7.3	2.8	1.6	2.33
5	7.1	2.8	1.9	2
10	3.5	2.02	2.3	1.74

The results are shown for Hadera's SVP_H and a theoretical isotropic SVP_{ISO}, and for San Diego's SVP_S and theoretical isotropic SVP_{ISO} for $\text{GDOP} \leq 5$.

The third and fourth columns of **Table 3** show the values of η from (17) for the third explored environment with the highly diverse bathymetry (the San Diego area) for its SVP_S and a theoretical isotropic SVP_{ISO}. We observe that the size of the coverage area obtained by PDAD is also significantly larger than that of CP in the case of complex bathymetry. We note that the marginal added coverage area for the SVP in San Diego increases with the number of receivers but an opposite trend is shown for the Hadera area. This is due to the higher diversity of the San Diego seabed and due to the deployment strategy. The former is attributed to bathymetry complexity. That is, when the bathymetry is highly complex, e.g., the one from San Diego, adding receivers helps cover shadow zones and their proper deployment location becomes more important. In less complex environments, e.g., the one from Hadera, adding receivers helps CP cover more area for localization and the gain in using PDAD decreases. We observe that the performance gain in the Hadera area increases for the more complex SVP, but the performance gain in the San Diego area is higher for the isotropic SVP. We explain this by the randomness of the CP method. In particular, in the center of the area of interest, CP may or may not achieve good performance. Still, since PDAD seeks to maximize the convergence area, performance gain is still above 1 in all cases.

Next, we explore the ratio between the coverage and the usable areas,

$$\theta = C/U \quad (18)$$

for two values of localization qualities, GDOP=5 and GDOP=12. Results for the moderate and complex environments are shown in **Table 4** for 3, 5, and 10 receivers. As expected, the results show that for the complex environment, sacrificing the positioning quality, e.g., GDOP=12, may increase the coverage area compared to that of the moderate environment. We argue that this is because of the diverse bathymetry, which impacts the propagation loss, and thereby the channel's spatial diversity.

The impact of the geometrical relations between 3 receivers on the usable area, μ , and on the coverage area, $C(\beta)$, is demonstrated in **Figure 7** for $\beta = 3$ and $\beta = 4$. The green, blue, and red circles are the detection areas of the green, blue, and red receivers positioned at the corresponding colored markers, respectively. Comparing **Figures 7A, B**, we observe that, in the latter, the receivers are located closer to each other and the size of the usable area, μ , highlighted in gray, is larger. However, the resulting coverage area, C , highlighted in light blue, for $\alpha = 5$, is smaller in **Figure 7D**. This is due to the small distance between the receivers, which yields a smaller angle between pairs of receivers and the node to be localized, thereby leading to poor localization.

Experiment Results

As our first performance metric, we explore the size of the usable area for CP and PDAD. **Figure 8** shows the position of tags received by at least three receivers for each deployment strategy. For the sake of comparison, we also show the planned usable area and the minimum convex hull for each method. We observe that the size of the usable area obtained by PDAD is 30% larger than that produced by CP. We also observe that, in the case of CP, three of the receivers are positioned outside the usable area. This is because CP does not account for the area's specific propagation conditions. Finally, we note that compared to the planned usable area of the CP and PDAD - marked by solid blue and green lines, respectively - the actual usable areas span to the east further than expected. This is attributed to the acoustic propagation conditions on the day of the experiment, which were likely better than those at the time of the tag's range testing.

As a second performance metric, we explored the throughput of the tags - receivers link. The results presented in **Figure 9** show that the performance benefit of PDAD over CP in terms of the throughput increases with the above range. This implies that tags

farther away from the receivers can still be localized by the PDAD cluster; thus, the usable PDAD area is effectively larger than that of CP. The figure also shows the throughput performance for less than three detecting receivers. While this setup does not allow localization without ambiguity, such detection indications can still provide valuable positioning information and is thus of interest (Baktoft et al., 2017). We note that, for emissions received by three or four receivers, the PDAD's throughput is higher than that of CP by at least 80%. However, for emissions received by one or two receivers the CP throughput is sometimes higher than that of PDAD. This is because the PDAD locations are planned for localization by at least three receivers. Still, the difference is not greater than 25%, implying that the benefit of gaining larger coverage by PDAD is not highly diminished by the reduction of valuable positioning information.

In **Table 5**, we report the 10th, 50th and 90th percentiles of the noise measurements as obtained by each receiver. We note the relatively small noise level difference between the 10th and 90th percentiles and conclude that the detection conditions during the experiment did not vary much. From **Table 5**, we further note that two receivers of the PDAD cluster, namely receivers # 557 and # 558, experienced higher noise level since their position was close to the shoreline. Still, regardless the higher noise level, the PDAD outperformed CP. Finally, we observe from **Figure 8** that, for PDAD, the tag's detections are consistently along the kayak routes, whereas, for CP, the detections appear more sporadically along these tracks. This is an indication of the better stability in detection that the PDAD setup can obtain.

DISCUSSION

We start our discussion by surveying some relevant solutions to the deployment problem. The optimal receiver deployment problem is shown to be NP-Hard with similarities to the k-vertex problem (Tekdas and Isler, 2010; Garcia-Diaz et al., 2019). For a given graph $G(V, E)$ and for parameters k, l , this problem seeks to discover whether G contains k vertices that cover at least one edge. Considering the high complexity required to solve the deployment problem optimally, some heuristic solutions are proposed. Much like our sub-optimal GA-based solution for PDAD, these include GA to determine the best locations for the receiving nodes (Díez-González et al., 2019a; Díez-González et al., 2019b), and (Díez-Gonzalez et al., 2020) by iteratively improving the position of the receivers along a given grid, while maintaining constraints in the form of clock drifts and the existence of obstacles. Due to its diversification and intensification in the search within the space of solutions, GA can also avoid falling into local minima (Mnasri et al., 2015) for diverse propagation loss conditions (Díez-González et al., 2019a). Another approach is to compute a Pareto front with a diversified local search for the optimal placement of nodes (Roa et al., 2007). Here, the deployment plan is examined under two local criteria: reception availability and quality of positioning. A different approach is simulated annealing, where a set of n nodes to be localized are randomly selected and the positions of the anchor nodes are stochastically optimized to

TABLE 4 | Ratio between the coverage and the usable area, θ for the deployment of 3, 5 and 10 receivers for San Diego and the Hadera power station areas, for GDOP = 5 and GDOP = 12.

Environment	San Diego		Hadera	
# of receivers	θ		θ	
for GDOP	5	12	5	12
3	0.75	0.94	1.0	1.0
5	1.0	1.0	0.87	1.0
10	0.84	1.0	0.99	0.99

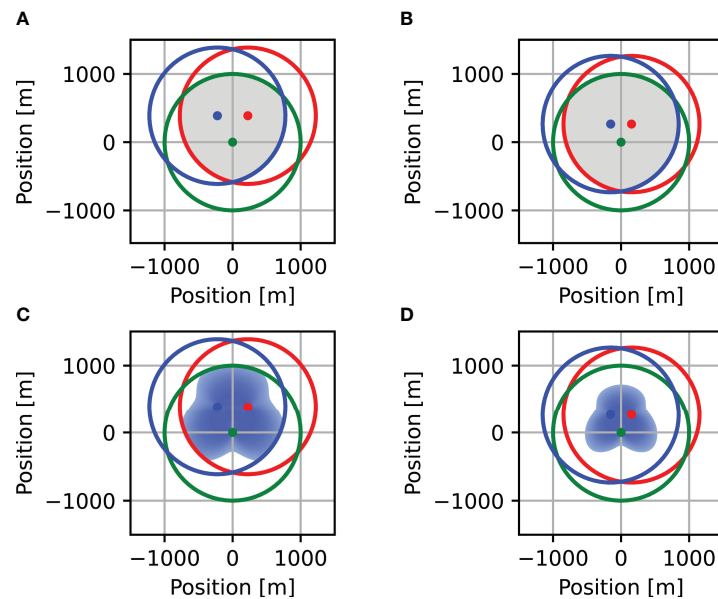


FIGURE 7 | Effect of distance between the receivers on the usable area and the coverage area with attained positioning quality. In setup 1, plots **(A, C)**, the receivers are placed 450m away from each other creating a usable area of $S \approx 1.782 \text{ km}^2$ and the coverage area is $C \approx 1.544 \text{ km}^2$ occupying 86% of the usable area. In setup 2, plots **(B, D)**, the receivers are placed 300m away from each other creating a usable area of $S \approx 2.1472 \text{ km}^2$. For this setup, the receivers are closer to each other than in Setup 1, and the coverage area is $C \approx 0.791 \text{ km}^2$, occupying only 37% of the usable area. The usable area in plots **(A, B)** is highlighted in gray. The coverage area, plots **(C, D)** for $\text{GDOP} \leq 5$ is highlighted in light blue.

increase the accuracy of the localization estimation (Niewiadomska-Szynkiewicz and Marks, 2009). Other heuristics are particle swarm optimization (Wang et al., 2007) and Tabu search methodologies (Laguna et al., 2009). The firefly algorithm (Tuba et al., 2018) is used to initialize anchors' positions at the corners of the explored area, and then move them trying to increase the angle between anchors and the node to be localized, while the relative distance between the anchors and the node to be localized is decreased.

The above works obtain good results for terrestrial networks. Yet, some of the underlying assumptions may be too hard for the underwater acoustic environment. Specifically, it is assumed that the propagation loss does not change with space; that the node to be localized is either bounded inside a polygon whose anchors are its

vertices or that some information about its route is known; and that a receiver can be added upon demand to increase the quality of the covered area. In our considered case, due to the spatially-dependent bathymetry, the propagation loss is often a complex location-dependent function, and the optimum coverage solution dictates positioning of receivers in non-overlapping areas.

Using the GDOP to Measure Localization

We would like to comment about our usage of the GDOP [cf. Sharp et al. (2009)] as a utility metric. We use the GDOP to assess the expected accuracy of the localization by the receivers' deployment setup. Other common metrics are the Cramér-Rao lower bound (CRLB), which expresses a lower bound on the variance of unbiased estimators, and which is widely used as a positioning performance estimator in wireless networks (Miao et al., 2007). Alternatively, the root mean square error (RMSE) of the location estimates or the cumulative distribution probability of the location errors can both be used as a localization quality of measures (Sharp et al., 2009). However, it is useful to decouple the statistical error component of the positional error from the geometric factors of the deployment setup. We find this representation in the GDOP metric. The GDOP quantifies how errors in the ToA measurements translate into the covariance components of the estimated position, and represents the influence of the standard deviation of the measurement errors onto the solution. The GDOP values can be categorized to measure the localization quality. One such option is presented in **Table 6** as proposed in (Dutt et al., 2009).

TABLE 5 | 10 Minutes average noise measured by the receivers.

Cluster	Receiver #	Percentile		
		0.1	0.5	0.9
CP	417	8.4	9	9
CP	418	11	14	15
CP	1765	7.8	10	10.6
CP	1766	8.4	11	12
CP & PDAD	721	7.8	11	13
CP & PDAD	1153	7.4	9	9.6
PDAD	557	18	23	29.6
PDAD	558	23	26	28
PDAD	1154	8	9	10
PDAD	1155	9	11	13

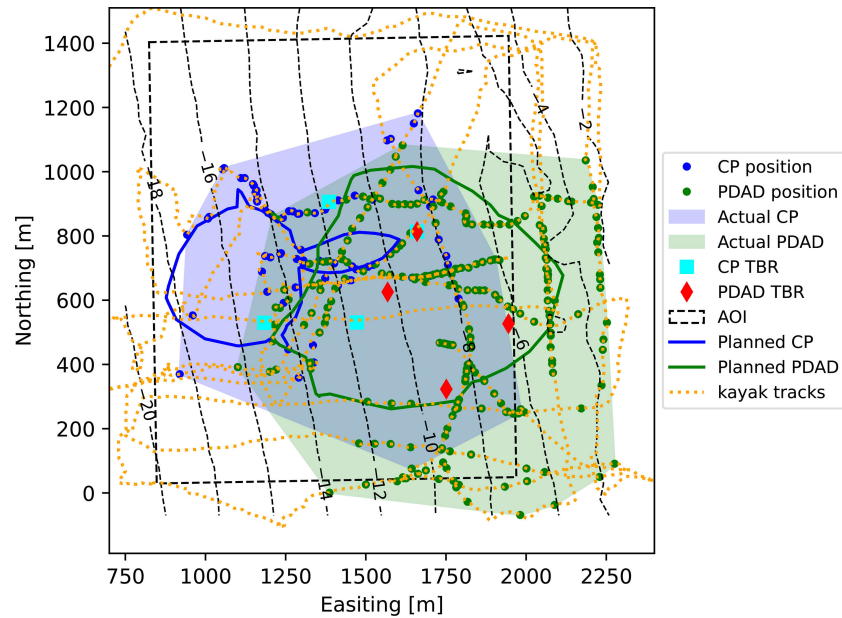


FIGURE 8 | Positioning of tags and coverage areas for CP and PDAD methods. Light blue and green-filled areas are the minimum convex hull encompassing all points of CP and PDAD, respectively. Solid lines are the planned usable areas. Triangles are the receivers' positions. Blue and green dots are emissions received by at least three receivers of the CP and PDAD sets, respectively.

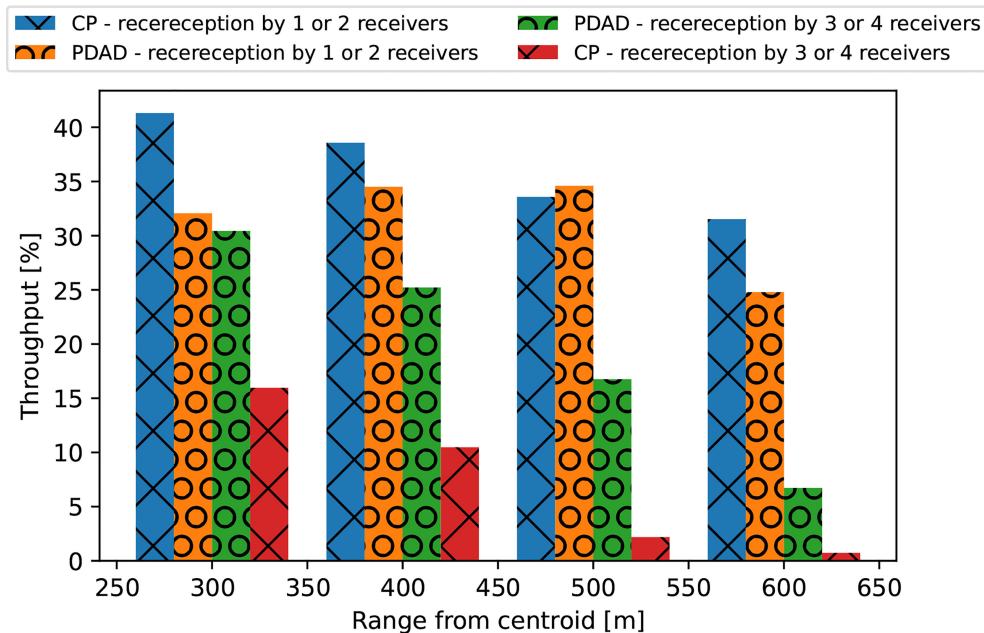


FIGURE 9 | $\xi_{2,r}$ ratio between emissions received by one or two receivers and the total number of acoustic emissions (CP - blue, PDAD - orange), and $\xi_{3,r}$ - ratio between localized tags to the total number of acoustic emissions (CP - red, PDAD - green). For the PDAD method, the throughput of localized emissions is better than the CP as the range increases, i.e., more emissions are localized at larger ranges for the PDAD method, leading to a larger usable area.

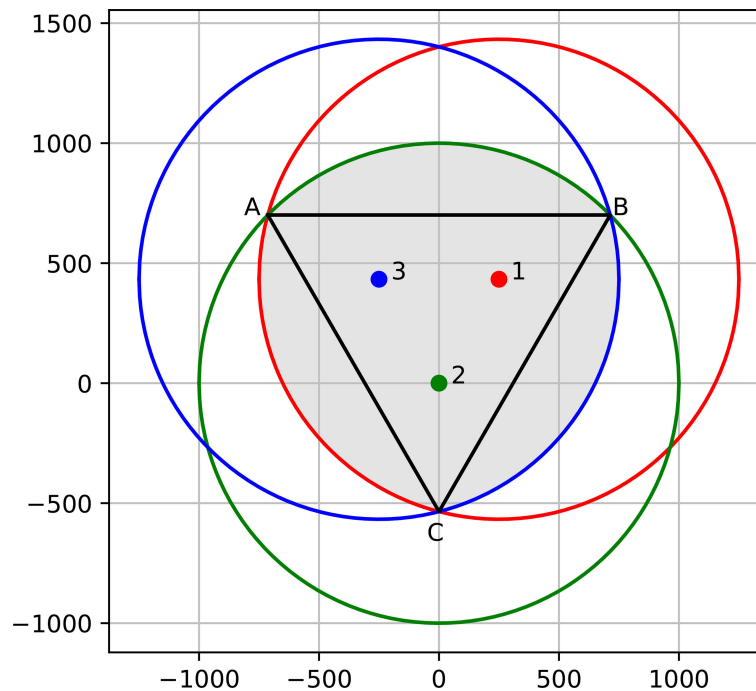


FIGURE 10 | The receivers' position are marked by numbers; the intersections between the contour of the receiving ranges are marked by letters. The shaded area is the usable receiving area S . The distance between the 3 receivers is $0 \leq x \leq R$.

TABLE 6 | GDOP Ratings.

GDOP Value (a)	Ratings
1	Ideal
2-4	Excellent
4-6	Good
6-8	Moderate
8-20	Fair
≥ 20	Poor

Discussion of Results

We next make some comments about our results. As demonstrated in our sea experiment, optimized placement of the receivers can gain extra coverage area of about 30%. This is attributed to the high dependency of the underwater acoustic propagation on environmental conditions, such as temperature profile and the bathymetric map. This dependency is demonstrated in **Figure 3**, showing the different shapes of detection areas in different positions of a tag in the area of interest. This is because the propagation loss and thus the detection rate depends not only on its range from the receiver. Consequentially, there may be cases of *blind spots*, where, albeit short range, the tag's emissions are not properly detected. While such a diversity may also be present in terrestrial or aerial testbeds, it is highly dominant in the underwater acoustic environment with spatial variations on the order of a few tens of meters. Hence, while our method can be applied also for other domains, it is mostly attractive for underwater testbeds. As a test case, we analyzed and tested our method with large acoustic

tags, suitable for megafauna. However our method may suit smaller tags with weaker SL. Hence, by using our method, the 30% increase in the explored area holds much more impact for the task of tracking the locations of marine fauna and megafauna.

CONCLUSIONS

This study focused on developing a systematic framework for planning the deployment of underwater receivers for the task of localizing acoustically-tagged marine fauna, with test case for tracking of megafauna such as sharks, sea turtles, and seals. We formalized the deployment position as a constraint optimization problem that takes into account the environmental conditions, the desired localization quality, and a given area-of-interest that should be covered with high priority. For a flat bottom bathymetry and isothermal conditions, we showed that the common practice can achieve optimal coverage area. For the case of complex bathymetry where the complexity is too high to directly solve the problem, we offered a sub-optimal solution based on a genetic algorithm that is able to efficiently solve the problem for large areas of a few square kms and for a large number of receivers. We explored the benefits of our proposed approach in terms of the size of the coverage area and the throughput of the tags' emissions. The performance is evaluated in numerical simulations and verified in a field experiment, using large tags suitable for tracking megafauna as a test case. The results show that the performance of our proposed deployment -

in terms of the coverage area - is superior to that of the common practice. Future work will further investigate how the setup can better account for the expected seasonal changes of the SVP and verify the applicability of our method to a smaller scale testbeds, i.e. smaller tags.

DATA AVAILABILITY STATEMENT

The datasets and supplementary material presented in this study can be found here: https://figshare.com/articles/dataset/Tags_emissions/17942534 (for the database - sea experiment) and <https://github.com/kerentalmon/Receiver-Deployment> (for the software).

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AUTHOR CONTRIBUTIONS

TA conceived and led the study. TA and RD conducted the field work. TA analyzed the data. Both authors interpreted the findings, wrote the manuscript, and RD approved the final version.

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APPENDIX

An interesting case to explore is the deployment of 3 receivers on a flat seabed with isotropic propagation loss and with no constraint on the area of interest. The question explored is: What is the best receivers setup to attain the maximal covered area C . The expected answer is an equilateral triangle setup (Fewell, 2006; Shiu et al., 2010). Yet, the proof is not trivial.

Let R be the receiving radius of a receiver of all 3 receivers, and let l be the range between the 3 receivers deployed in an equilateral setup. Without the loss of generality, let the position of one of the receivers be at $x_2, y_2 = (0, 0)$. Consider the setup $x_1, y_1 = (0.5l, 0.5\sqrt{3}l)$, $x_3, y_3 = (-0.5l, 0.5\sqrt{3}l)$. For $l = 0$, the 3 receivers are placed in the same location and $S = \pi R^2$. We derive the area of S for any $0 \leq l \leq \sqrt{3}R$. **Figure 10** illustrates this setup.

Referring to **Figure 10**, the total usable area $S = S_T + 3S_S$, where S_T denotes the area of triangle ABC and S_S denotes the segments area between the cords AB, BC, CA. The intersection points of the two circles $(x - a_1)^2 + (y - b_1)^2 = R_1^2$ and $(x - a_2)^2 + (y - b_2)^2 = R_2^2$ are

$$\begin{aligned} x_{1,2} &= \frac{a_1 + a_2}{2} + \frac{(a_2 - a_1)(R_1^2 - R_2^2)}{2 * l^2} \pm 2 \frac{b_1 - b_2}{l^2} d \\ y_{1,2} &= \frac{b_1 + b_2}{2} + \frac{(b_2 - b_1)(R_1^2 - R_2^2)}{2 * l^2} \mp 2 \frac{a_1 - a_2}{l^2} d \end{aligned} \quad (19)$$

where

$$d = 0.25 \sqrt{(l + R_1 + R_2)(l + R_1 - R_2)(l - R_1 + R_2)(-l + R_1 + R_2)} \quad (20)$$

For the case at hand, $R_1 = R_2 = R$ such that the distance between any two intersection points creating triangle ABC is $D = 0.5(\sqrt{3(4R^2 - l^2)} - l)$. Thus,

$$\begin{aligned} S_T &= 0.25\sqrt{3}D^2(28) \\ S_S &= R^2 \sin^{-1} \left(\frac{D}{2R} \right) - 0.25D\sqrt{4R^2 - D^2} \\ S &= S_T + 3S_S \end{aligned} \quad (21)$$

Figure 4 shows the coverage area for the distance between the receivers of $0 \leq l \leq \sqrt{3}R$ for a number of GDOP values.



Predicting Seabird Foraging Habitat for Conservation Planning in Atlantic Canada: Integrating Telemetry and Survey Data Across Thousands of Colonies

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Conservation of mobile organisms is difficult in the absence of detailed information about movement and habitat use. While the miniaturization of tracking devices has eased the collection of such information, it remains logistically and financially difficult to track a wide range of species across a large geographic scale. Predictive distribution models can be used to fill this gap by integrating both telemetry and census data to construct distribution maps and inform conservation goals and planning. We used tracking data from 520 individuals of 14 seabird species in Atlantic Canada to first compare foraging range and distance to shorelines among species across colonies, and then developed tree-based machine-learning models to predict foraging distributions for more than 5000 breeding sites distributed along more than 5000 km of shoreline. Despite large variability in foraging ranges among species, tracking data revealed clusters of species using similar foraging habitats (e.g., nearshore vs. offshore foragers), and within species, foraging range was highly colony-specific. Even with this variability, distance from the nesting colony was an important predictor of distribution for nearly all species, while distance from coastlines and bathymetry (slope and ruggedness) were additional important predictors for some

species. Overall, we demonstrated the utility of tree-based machine-learning approach when modeling tracking data to predict distributions at un-sampled colonies. Although tracking and colony data have some shortcomings (e.g., fewer data for some species), where results need to be interpreted with care in some cases, applying methods for modeling breeding season distributions of seabirds allows for broader-scale conservation assessment. The modeled distributions can be used in decisions about planning for offshore recreation and commercial activities and to inform conservation planning at regional scales.

Keywords: tracking, seabirds, machine-learning, conservation planning, North Atlantic

INTRODUCTION

There is considerable interest in using seabirds to identify ecologically important marine areas (Hooker and Gerber, 2004; Lascelles et al., 2016; Krüger et al., 2017; Hindell et al., 2020). Seabird marine distributions, both around colonies and offshore, may be key information sources for designating Marine Protected Areas (MPAs) (Hyrenback et al., 2000; Ronconi et al., 2012; Davies et al., 2021) or proposing other conservation measures (Arcos et al., 2012; O'Brien et al., 2012; Sonntag et al., 2012; Augé et al., 2018). Globally, seabirds are threatened by a broad range of anthropogenic activities at sea (Cury et al., 2011; Zydels et al., 2013; Lieske et al., 2019) which necessitates marine conservation planning to mitigate threats. Moreover, seabirds are considered important indicators of marine ecosystem processes (Piatt et al., 2007), and because they are readily observable and tracked, they may serve as sentinels for broad-scale marine conservation planning for other marine top predators (Hazen et al., 2019; Hindell et al., 2020).

Fundamentally, setting priorities for marine area conservation is a spatial allocation decision-making process, and is more likely to succeed when information about biological resources can be combined with an assessment of threats and risks of interacting with those threats (Le Corre et al., 2012; Montevecchi et al., 2012; Lieske et al., 2020). For instance, cumulative risks can be assessed by overlaying multiple spatial layers (Halpern et al., 2008; Ban et al., 2010) to better understand spatial patterns of offshore marine anthropogenic threats. Understanding the foraging areas of certain seabird species can highlight areas of importance to a species and where individuals might be particularly vulnerable during the breeding season (Thaxter et al., 2012; Soanes et al., 2016; Wakefield et al., 2017; Cleasby et al., 2020). Such information forms the base upon which considerations for marine conservation can be layered to provide direct protection of seabirds from threats or indirect protection through conservation of their prey base and habitats.

Seabird foraging areas may be quantified in many ways, the simplest being the delineation of foraging ranges as maximum distributions around breeding colonies (Thaxter et al., 2012; Oppel et al., 2018). A maximum radius approach, however, does not consider underlying habitat associations and is further complicated by significant within and among individual, species, colony, and annual variation (Thaxter et al., 2012; Soanes et al.,

2016; Camprasse et al., 2017). Model-based approaches offer a way to relate foraging distributions to important constraints, such as interactions between distance to a colony and underlying habitat requirements, and allow better estimation of geographic areas where a species is most likely to be present (Soanes et al., 2016; Wakefield et al., 2017; Baylis et al., 2019). Furthermore, because it is logistically and financially intractable to obtain tracking information from all species across all of their breeding sites, a modelling approach that incorporates data on species-specific and colony-based foraging areas for sampled colonies provides a way to extrapolate distributions to other colonies that have no tracking data, thereby addressing critical information gaps (Grecian et al., 2012; Gaston et al., 2013; Wakefield et al., 2017; Hindell et al., 2020). Although foraging ranges may be applied as a preliminary tool to investigate important marine areas for breeding seabirds (Thaxter et al., 2012), such foraging radii extrapolation can be further improved with consideration of colony population sizes (Grecian et al., 2012; Jovani et al., 2016) and density dependent effects (Wakefield et al., 2017), indicating the predicted abundance of birds within a particular foraging radius.

While attending the colony, seabirds are central place foragers, and thus are geographically constrained (Orians and Pearson, 1979). This means that their feeding areas and foraging decisions are constrained by how far they can fly from a colony before having to return to incubate eggs or feed chicks. Seabird distribution during the nesting period is limited by a complex set of interacting factors including time and energetic constraints associated with flight and commuting distance (Houston and McNamara, 1985), competition with conspecifics (Elliott et al., 2009; Wakefield et al., 2013), availability of prey within foraging ranges (Birt et al., 1987; Burke and Montevecchi, 2009), as well as both dynamic and static marine habitat variables affecting prey distribution, such as oceanographic fronts and bathymetry (Weimerskirch, 2007; Bost et al., 2009; Soanes et al., 2016). Taken together, these constraints can determine and control the realized foraging ranges of breeding seabirds (Gaston et al., 2013).

We used tracking data and a machine-learning approach to model distributions of seabirds around colonies as a function of distance from colony sites, coastlines, and shelf breaks, as well as associations with seafloor characteristics such as depth, slope, and ruggedness. Constructing this model based on static environmental variables ensured that central place foraging

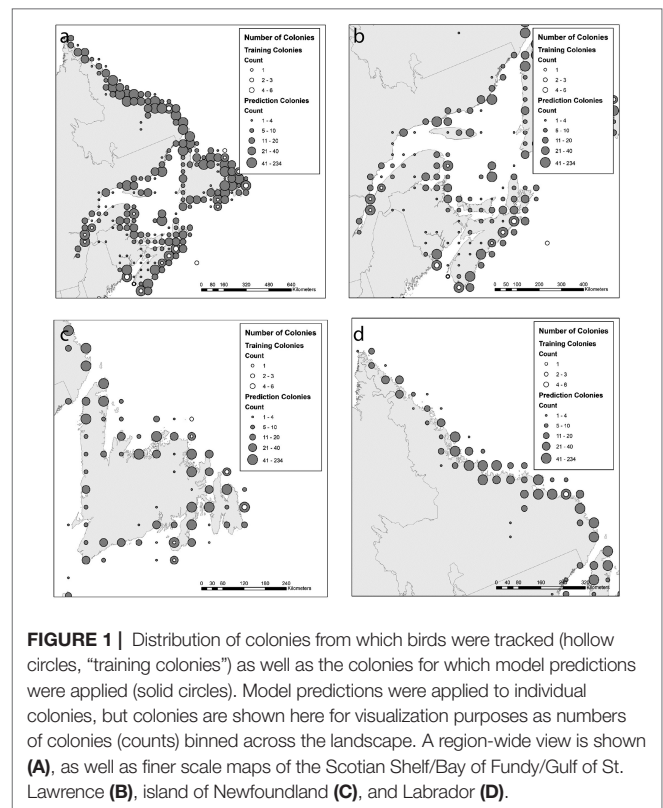
constraints could be captured (e.g. Wakefield et al., 2017) while still maintaining sufficient generalizability for predictions to be applicable to other colonies. Machine-learning techniques such as Boosted Regression Trees (BRT) make no assumptions about the functional forms of relationships with the predictors, are flexible in handling missing data, and can easily capture complex, non-linear interactions (De'ath and Fabricius, 2000; Lieske et al., 2018) such as those that may underlie seabird foraging distributions. Similarly, Hindell et al. (2020) used BRT to model multi-species tracking data to develop broad-scale, predictive maps for marine conservation planning in the Southern Ocean.

Using tracking data compiled from 2005 to 2016, we investigated foraging ranges of 14 of the 21 marine bird species that regularly breed in Atlantic Canada, representing different families, modes of foraging, and positions in marine food webs: pursuit-diving piscivores (5 species), a plunge-diving piscivore (1), surface-feeding piscivores and scavengers (6), surface-feeding planktivore (1), and a benthic foraging seaduck (1). Our objectives were to 1) describe marine bird foraging ranges as a function of several environmental covariates, 2) examine inter- and intraspecific variability in foraging ranges, comparing against available literature, and 3) develop a predictive modeling approach to make region-wide species distribution models for breeding seabirds in Atlantic Canada. The latter objective used BRT model-derived predictions combined with information on colony size from a comprehensive colony database of more than 3500 sites surveyed between 1996 and 2016. Our goal was to better describe and predict the marine distribution of a suite of species around breeding colonies, thereby creating the first layer of information for identifying important marine areas, and laying an enhanced groundwork for assessing risks and setting conservation priorities in Atlantic Canada (Lieske et al., 2020).

METHODS

Study Area and Species

This study focused on seabirds and one seaduck species (hereafter “seabird” unless specifically referring to seaducks) tracked in Atlantic Canada (Figure 1) including Newfoundland and Labrador (NL), Nova Scotia (NS), New Brunswick (NB), Prince Edward Island (PEI), and Quebec (QC). Major eco-regions in this area include the Bay of Fundy (NB/NS), Scotian Shelf (NS), Laurentian Channel (NS/NL), Gulf of Saint Lawrence (NB/PEI/NS/NL/QC), Grand Banks (NL), and Labrador Shelf (NL). Seabird colony data (site locations and census numbers) were obtained from all provinces (see below). Tracking data were obtained from government and academic researchers from studies in all provinces except Prince Edward Island (no known studies in this province). We studied 14 seabird species in Atlantic Canada representing five foraging guilds (Table 1, see also Table S1 for sample sizes and study years). Study species encompassed most breeding seabird species from this region, for which tracking data were available: common eider (*Somateria mollissima dresseri*), Leach's storm-petrel (*Hydrobates leucorhous*), northern gannet (*Morus bassanus*), great black-backed gull (*Larus marinus*), herring gulls (*L. smithsonianus*), black-legged kittiwake (*Rissa tridactyla*),



common tern (*Sterna hirundo*), Arctic tern (*S. paradisaea*), roseate tern (*S. dougallii*), razorbill (*Alca torda*), Atlantic puffin (*Fratercula arctica*), common murre (*Uria aalge*), thick-billed murre (*U. lomvia*), and black guillemot (*Cepphus grylle*).

Colony Data

A comprehensive seabird colony database from Environment and Climate Change Canada (Atlantic Colonial Waterbird Database, Banque informatisée des oiseaux de mer au Québec; <http://donnees.ec.gc.ca/data/species/assess/atlantic-colonies-density-analysis/>) contained more than 8,000 colony records (species-colony combinations) for five Canadian provinces (Figure 1), most of which were accompanied by estimates of population size, dating back to the 1960s. In Quebec, our analysis included only colonies from the Gulf of St. Lawrence, thus excluding colonies from the northern Arctic coastlines. From this, we extracted the largest known colony size for each site and species in the last 20 years (1996 to 2016), resulting in 3556 unique sites (colony locations) and 5318 species-colony combinations. As a precautionary approach, by selecting the largest known population size per species at each site within that period, we account for variation in survey timing, survey methods, cyclical natures of some populations, and declining colonies that might recover – this is meant to capture the recent potential for seabird distributions in a given area and to ensure consistency across sites. By including colony data from the most recent 20 years, data represented both current and past colony locations and helped identify not only the important colonies, but the range

TABLE 1 | Study species names, abbreviations, foraging guilds, and tag types.

Common Name	Scientific Name	Abbreviation	Foraging guild	Tag types
common eider	<i>Somateria mollissima</i>	COEI	benthic-foraging diver	PTT
roseate tern	<i>Sterna dougallii</i>	ROST	surface-feeding piscivore/scavenger	VHF,GPS
common tern	<i>Sterna hirundo</i>	COTE	surface-feeding piscivore/scavenger	VHF
arctic tern	<i>Sterna paradisaea</i>	ARTE	surface-feeding piscivore/scavenger	VHF
great black-backed gull	<i>Larus marinus</i>	GBBG	surface-feeding piscivore/scavenger	PTT,GPS
herring gull	<i>Larus smithsonianus</i>	HERG	surface-feeding piscivore/scavenger	GPS
black-legged kittiwake	<i>Rissa tridactyla</i>	BLKI	surface-feeding piscivore/scavenger	GPS
black guillemot	<i>Cepphus grylle</i>	BLGU	pursuit-diving piscivore	GPS
razorbill	<i>Alca torda</i>	RAZO	pursuit-diving piscivore	GPS
Atlantic puffin	<i>Fratercula arctica</i>	ATPU	pursuit-diving piscivore	GPS
thick-billed murre	<i>Uria lomvia</i>	TBMU	pursuit-diving piscivore	GPS
common murre	<i>Uria aalge</i>	COMU	pursuit-diving piscivore	GPS
northern gannet	<i>Morus bassanus</i>	NOGA	plunge-diving piscivore	GPS
Leach's storm-petrel	<i>Hydrobates leucorhous</i>	LESP	surface-feeding planktivore	GLS

Tag types used on species included Platform Terminal Transmitters (PTT), Very High Frequency radio tags (VHF), Global Positioning System (GPS), and Geolocation Light Sensing (GLS).

of possibilities (i.e., if some colonies had disappeared). This selection also ensured that remote, less frequently visited colony sites were not excluded from the analysis.

Tracking Data

Tracking data were obtained from 520 tag deployments between 2005–2016 at 23 sites, providing 43 independent datasets (species-site combinations; **Table 2** and **Figure 1**). At the time, this included all known telemetry studies using devices enabling geographic positions of breeding seabirds in Atlantic Canada, plus additional data from common eiders from two colonies in

Maine, USA, and from Leach's storm-petrel from one colony in France (Saint Pierre and Miquelon). These included unpublished data (Black, 2006; Symons, 2018; and other unpublished sources) as well as reassessment of previously published data on terns (Rock et al., 2007a; Rock et al., 2007b; Pratte et al., 2021), gulls (Maynard & Ronconi, 2018; Anderson et al., 2019; Shlepr et al., 2021), alcids (Regular et al., 2013; Pratte et al., 2017; Gulka et al., 2019), northern gannet (Garthe et al., 2007; Garthe et al., 2011; Montevecchi et al., 2012), Leach's storm-petrel (Pollet et al., 2014; Hedd et al., 2018), and common eider (Mallory et al., 2020).

Species were tracked with different tag types (**Table 1** and **Table S1, Supplementary Material**), each of which have differences

TABLE 2 | Study species and sites where tracking devices were deployed (see **Table 3** for tracking effort).

Country, Province/State	Colony name	Latitude	Longitude	Study species	References
Canada, Newfoundland & Labrador	Gannet Islands	53.9429	-56.5115	ATPU, COMU, RAZO, TBMU	a
	Funk	49.7565	-53.1855	COMU, NOGA	b,c,d
	Cabot	49.1709	-53.3587	COMU	e
	Baccalieu	48.1198	-52.7986	LESP, NOGA	c,d,f
	Gull	47.2629	-52.7730	ATPU, BLKI, COMU, HERG, LESP	f,g,h
	Middle Lawn	46.8700	-55.6200	LESP	f
Canada, Quebec	Bonaventure	48.4913	-64.1471	NOGA	b
	Bicquette	48.4126	-68.8861	RAZO	
	Gros Pot	47.8722	-69.6894	RAZO	
	Gros Pelerin	47.7487	-69.6903	RAZO	
France, Saint Pierre and Miquelon	Grand Colombier	46.8220	-56.1660	LESP	
Canada, Nova Scotia	Country	45.1005	-61.5419	ARTE, BLGU, COTE, LESP, ROST	f,i,j,k
	Bird	44.8681	-62.2783	COEI, LESP	f,l
	West Brother	44.8238	-62.3609	COEI	l
	Devil's	44.5811	-63.4603	GBBG	m
	Brier	44.2528	-66.3582	HERG	h,n
	Sable	43.9402	-60.0094	GBBG, HERG	h
	North Brother	43.6368	-65.8234	ROST	q
	Bon Portage	43.4620	-65.7460	LESP	f,k
	Kent	44.5784	-66.7567	BLGU, HERG, LESP	f,h,n
	Machias Seal	44.5014	-67.1017	ARTE, ATPU, COTE, RAZO	o,p
Canada, New Brunswick					
USA, Maine	Metinic	43.8880	-69.1260	COEI	l
	Flag	43.7517	-69.8911	COEI	l

We refer to these as "training sites" with respect to predictive modeling described in the body of the text. Sites are listed from north to south within provinces and states. References are provided where methods and/or tracking data have been previously described for some species or sites. See **Table 1** for species names and abbreviations. ^aPratte et al., 2017; ^bGarthe et al., 2007; ^cGarthe et al., 2011; ^dMontevecchi et al., 2012; ^eGulka et al., 2019; ^fHedd et al., 2018; ^gRegular et al., 2013; ^hAnderson et al., 2019; ⁱRock et al., 2007a; ^jRock et al., 2007b; ^kPollet et al., 2014; ^lMallory et al., 2020; ^mMaynard and Ronconi, 2018; ⁿShlepr et al., 2021; ^oBlack, 2006; ^pSymons, 2018; ^qPratte et al., 2021.

in accuracy and location frequency. Though location data frequency (i.e. number of locations per day) varied considerably among species and tag types, the predictive modeling analyses (see below) were done at the site/colony level; therefore we were able to maintain the maximum amount of data at each site, but ensured that there was consistent processing among individuals within species-site combinations. The following data quality considerations were applied. Ten species were tracked with GPS tags with expected positional accuracy of < 15 m. Great black-backed gulls (Sable Island) and common eiders (all sites) were tracked with Platform Terminal Transmitters (PTTs) and we used the highest accuracy location classes of 2 and 3 (expected accuracy <1000 m and <500 m, respectively; Nicholls et al., 2007). Herring gulls on Sable Island were tracked with GPS-PTT which collected GPS locations at regular intervals of 1 to 2 h, and Argos (PTT) locations every 4 days when tags transmit data to satellites. For these GPS-PTT data we applied Bayesian state-space models to estimate locations at regular (1-h) intervals, giving higher weighting to GPS locations and higher accuracy PTT locations (Jonsen et al., 2005), thus providing estimated locations likely as accurate as most of the GPS data. Bayesian models treated GPS locations as “fixed” locations, used a hierarchical first-difference correlated random walk (hDCRW), was run in batches on groups of 4 birds, and modeled with Markov chain Monte Carlo method with 10,000 iterations (thinned every 10th record) after a burn-in of 40,000 iterations. Geolocation-Sensing (GLS) tags were used to track Leach’s storm-petrels at all sites (see Pollet et al., 2014; Hedd et al., 2018 for details and data processing). GLS tags have an estimated error of approximately 180 ± 114 (SD) km (Phillips et al., 2004), and given that foraging ranges vary from 500–1500 km for this species, this error still provides a reasonably accurate estimation of at-sea distribution (Hedd et al., 2018). VHF data were obtained from studies of common and Arctic terns (Black, 2006; Rock et al., 2007a) which rely on aerial surveys to obtain location estimates, thus providing limited, but the only, tracking data available for these species. Roseate terns were tracked by VHF tags at Country Island (Rock et al., 2007b) and GPS at North Brother Island (Pratte et al., 2021).

All tags were deployed on breeding adults. Most species were tracked only during the breeding season, except common eiders, herring gulls, and great black-backed gulls, from which we used a breeding-season subset of the year-round tracks. We retained common eider locations from 0–60 days after the estimated hatch date for each colony, when females attend young in crèches as they disperse from nest sites (Goudie et al., 2000). Within this period, we also excluded locations > 30 km from nest sites to account for presumed unsuccessful breeders, which began early migrations (Goudie et al., 2000). For both herring and great black-backed gulls, we included locations during incubation and early chick-rearing, up to 30 days before and after average hatch dates for each colony. For gulls, we also excluded data for presumed unsuccessful breeders that left colonies prematurely, prior to 30 days post-hatch.

To concentrate on locations associated with foraging activity, including transits to foraging areas, we excluded locations associated with colony attendance and focused the analysis on breeding season at-sea distribution for all study species. This

was also necessary to make data comparable among species and study sites because not all tag types recorded locations when individuals were at a colony. The proportion of locations obtained for each colony was highly variable depending on tag type, tag programming, and species behaviour. To standardize within species among colonies, and omit “colony attendance”, we used the following criteria. For burrow-nesting Leach’s storm-petrels tracked with GLS, we omitted locations within 50 km of the colony (7% of the data), because these devices had low accuracy in location estimates (see above). For herring and great black-backed gulls which may forage on land and in the intertidal areas of their nesting colonies, we omitted locations within 200 m of nest sites (data associated with localized activities including incubation, chick provisioning, and roosting; 55–59% of the data), but retained locations which occurred on land in other parts of their colonies/islands.

For all other species, a polygon was traced around the colony perimeter using the polygon tool in GoogleEarth, exported as kml files and imported into program R where they were converted to standard internal representations (e.g. `SpatialPolygons[DataFrame]`) using `readOGR` function of package ‘`rgdal`’ (Bivand et al., 2013). These polygons were drawn in consideration of raw tracking data plotted in GoogleEarth to identify and encompass associated roosting sites on colonies or adjacent rocky outcrops (which may not have appeared in the shoreline layer, below). We measured distance of points to the polygons (on the WGS84 ellipsoid) using `dist2Line` function in package ‘`geosphere`’ (Hijmans, 2014) and determined if points were “on land” using the `gContains` function of package ‘`rgeos`’ (Bivand and Rundel, 2013). We then excluded all points “on land” and at-sea within 20 m of the colony edge (selected as an expected buffer against the accuracy of the shoreline perimeter and the location error of the GPS data). This buffer excluded the following data for each species: common eider (4%), northern gannet (1%), razorbill (37%), Atlantic puffin (5%), common murre (20%), thick-billed murre (48%), black guillemot (26%), roseate tern (73%), and black-legged kittiwake (25%). No locations were excluded from the VHF data collected for tern species, as these were not tracked in the colonies.

Data Quality

Given the wide range of species in this study and associated variability in tracking technology as well as sample sizes, we provide a qualitative assessment of data reliability used to assess foraging ranges and as inputs to predictive distribution models (below). This assessment is not incorporated into modeled results, but is provided to facilitate interpretation and understand the likely reliability of the results.

For each study species, we scored quality and quantity of tracking data, and the completeness and accuracy of colony data, on a scale of 1 (low) to 3 (high): the sum of the scores represent the overall reliability of the model inputs on a scale of 4 (minimum) to 12 (maximum). Quality of tracking data is based on device type: VHF and GLS (code 1), PTT (2), and GPS (3). Quantity of tracking data is based on a combination of the number of individuals, number of sites, and number

of bird locations. Examples of low (1) scores include low numbers of location data (terns, common eider), tracking of few individuals (black guillemots) and/or few colonies (black-legged kittiwakes). In contrast, examples of high (3) quantity of data include high sampling intensity (common murre) and/or tracking of many individuals across multiple sites (herring gull, razorbill, Leach's storm-petrel). Colony data are scored based on their completeness (likelihood that all colony locations are represented in the database) and expected accuracy with respect to population estimates (which may vary by the census method and/or availability of recent estimates). For example, low scores are associated with species that are infrequently censused or difficult to census at colonies (e.g. black guillemot, common eider), and high scores are associated with species that are frequently censused, easy to observe, and accurately counted (e.g. northern gannet, common murre).

While it was beyond the scope of this paper to assess effects of tags on the behaviour and reproduction of each study species, it should always be considered that attaching devices to birds may disrupt their normal behaviours and movements. Species like gulls, terns, and storm-petrels seem to experience slight or no effects of tagging (Pollet et al., 2014; Thaxter et al., 2016; Seward et al., 2021), yet other species groups, such as the auks, may be more prone to negative effects of logger attachment (Paredes et al., 2005; Symons and Diamond, 2019) and, thus, tracking data may be less representative of true foraging behaviours.

Foraging Ranges

Distance from a colony and distance to coastline were used to describe and compare foraging ranges and habitats among species. For each location we measured distance to individuals' colonies using the *distance* function of package 'argosfilter' (Freitas, 2012). For the study area coastline, we used version 1.0 of the CanCoast shoreline database compiled from the Canadian National Topographic Database, Geobase, and Landsat 7/SPOT imagery (Smith et al., 2013). Distance to nearest coastline was measured for each location using the *dist2Line* function. For gulls, which may use inland terrestrial habitat, we further quantified "on land" locations using the *gContains* function with a polygon of the entire coastal area, and inland locations were transformed to negative values so that distances from coastline measurements ranged from positive (marine) to negative (terrestrial) values, relative to the coast (value of zero).

For each species-site combination, we determined the *maximum range* (distance from colony) of all individuals, as is frequently reported in literature on foraging ranges (Thaxter et al., 2012; Soanes et al., 2016), and the *maximum distance to nearest coastline*. Because these metrics are sensitive to outlier individual birds or trips, we additionally report the 99th percentile distances for each species-site combination, which better represents the typical maximum for a given site. Furthermore, we report the *mean maximums* among individuals for each species-site, thus characterizing typical ranges within populations. Finally, to illustrate how densities of birds may differ with respect to distance from coastlines, we summarize distance to shore of all

locations pooled into distance bins: inland (gulls only), 0-1, 1-10, 10-100, and >100 km from coastline.

Predictive Species Distribution Models

Pre-Processing

To support the calculation of species-specific, colony-centered distribution models (see *Statistical modelling*), analysis grids were constructed for each tracked individual, centered on the breeding colony of the bird. Because of differences in sampling effort between colonies, resulting from disparities in the performance of different tracking devices as well as the fact that some colonies had more tracked individuals than others, the density of positions (per grid cell) was converted to relative density ($RD_{i,k}$):

$$RD_{i,k} = \frac{count_{i,k}}{\sum_i^N count_{i,k}} \quad (1)$$

where i = a particular grid cell location, k = a particular tracked bird, and N = the total number of grid cells in the surface. As a final pre-processing step, grids from each tracked individual were combined (concatenated) to form a single RD grid prior to habitat modelling (see *Statistical modelling*).

The maximum extent of each grid was empirically defined as the mean of the maximum observed foraging distances across the training colonies. The analysis grids for most species were 2-km resolution, except for the herring gull (5-km), northern gannet (5-km), and Leach's storm-petrel (12-km) where a combination of very large foraging distances and computing performance warranted greater spatial aggregation.

Predictor Variables

Prior to statistical modelling, six variables were generated for each grid cell, though different combinations were used for different groups of species (**Table 3**). Bathymetry (BATH), both marine (bathymetry) as well as terrestrial (elevation), was estimated for all species using the 30-arc second resolution ETOPO 2v2 grid, from which slope (SLOPE) and ocean floor/terrain ruggedness (RUGGED) were derived at the same spatial resolution.

The remaining three variables were planimetric in nature and defined at a resolution of 2- x 2-km. Distance to coast (COASTDIST), where the reference coastline was delineated using the CanCoast 1.0 vector coastline database, was calculated for each species/species group as the shortest straight-line (Euclidean) distance. Distance to colony (COLONYDIST) was defined for all species, but in two different ways depending upon the group. For gulls, which travel over land, simple Euclidean distance to the colony center was employed. For all other (i.e., non-gull) species, distance to colony center was defined using the minimum distance by sea, calculated using the *Path Distance* procedure of ESRI (2015). This procedure allowed for the specification of surface travel weights and, in this case, terrestrial grid cells were defined as having a very high cost weight of 999,999, with water having a value of 1. Distance to shelf break (SHELFDIST), a variable used only in the model for the Leach's

TABLE 3 | Environmental predictor variables used to construct colony-centered species distribution models.

Abbreviation	Variable	Unit	Resolution	Source
COASTDIST	Euclidean distance to coast	m	2 x 2 km	Euclidean distance to coast, with vector coastline based on CanCoast 1.0 ¹
COLONYDIST	Distance to colony center	m	2 x 2 km	Alternately defined: (1) For gulls: defined by the Euclidean distance, calculated using <i>Spatial Analyst, Euclidean Distance Tool</i> ² ; (2) For non-gulls: defined by the minimum distance by sea, calculated using the <i>Spatial Analyst Path Distance tool</i> ² with terrestrial grid cells defined using a very high cost weight (999,999)
BATH	Marine bathymetry and terrestrial elevation	m	30-arc seconds	ETOPO 2v2 ³
SLOPE	Slope	Deg.	30-arc seconds	Derived from ELEV using <i>Benthic Terrain Modeller</i> ⁴
RUGGED	Ocean floor/terrain ruggedness	Index ranging from 0 to 1	30-arc seconds	Derived from ELEV using <i>Benthic Terrain Modeller</i> ⁴ , defined using a 3x3 neighbourhood
SHELFDIST	Euclidean distance to shelf break	m	2 x 2 km	Euclidean distance to shelf break (defined as the 1200-m isobath)

¹Smith CD, Manson GK, Couture NJ, James TL, Lemmen DS, Forbes DL, Fraser P, Frobel D, Jenner KA, Lynds TL, Szlavko B, Taylor RB, Whalen D. 2013. CanCoast: A National-scale framework for characterising Canada's marine coast. URL: <http://coimatlantic.ca/coastgis2013/docs/proceedings.pdf>.

²Environmental Systems Research Institute. 2017. ArcGIS, version 10.5. Redlands, California.

³National Geophysical Data Center. 2006. 2-minute Gridded Global Relief Data (ETOPO2) v2. URL: <http://www.ngdc.noaa.gov/mgg/fliers/06mgg01.html>.

⁴Benthic Terrain Modeller. 2016. Benthic Terrain Modeler (BTM), version 3.0 <http://www.arcgis.com/home/item.html?id=b0d0be66fd33440d97e8c83d220e7926>.

storm-petrel, was calculated as the Euclidean distance to the 1200-m isobath.

Statistical Modelling

The procedure for construction of statistical models is outlined in **Figure 2**, and employed BRT (see Friedman, 2001). The BRT algorithm has been described as a “slow learning” technique where predictions are constructed additively, sequentially, and incrementally (Elith et al., 2008; James et al., 2013). Data were not bootstrap-sampled nor was the response variable directly modelled; rather the attention of the model-fitting procedure is focused on the residual or unexplained variation (James et al., 2013). The BRT algorithm was implemented using the *gbm* R package of Ridgeway (2012), with tuning parameters defined as follows: learning rate of 0.01, 2000 trees per iteration, and a tree (interaction) depth of 3. Given the specification of the BRT

interaction depth parameter ($k=3$), importance values reflect complicated three-way interactions between predictor variables.

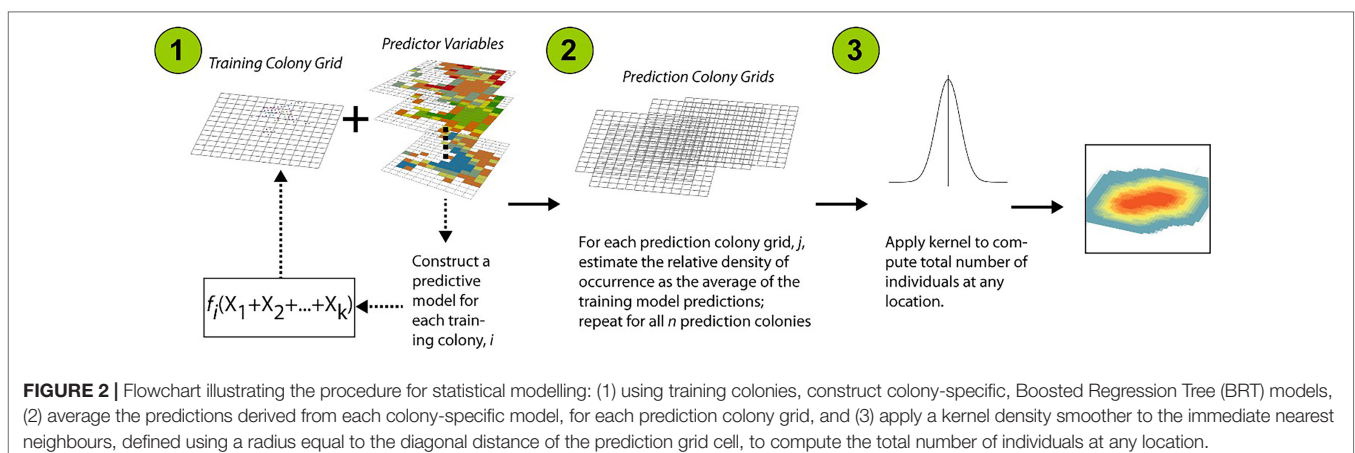
BRT models were constructed for each training colony using one of two possible combinations of predictor variables to estimate \widehat{RD} :

$$\widehat{RD} \sim f(\text{COASTDIST}, \text{COLONYDIST}, \text{BATH}, \text{SLOPE}, \text{RUGGED}) \quad (2)$$

for all species except Leach's storm-petrel, which was modelled as:

$$\widehat{RD} \sim f(\text{COASTDIST}, \text{COLONYDIST}, \text{BATH}, \text{SLOPE}, \text{RUGGED}, \text{SHELFDIST}) \quad (3)$$

Predicted \widehat{RD} values (\widehat{RD}), derived from each of the colony-specific training models, were combined by averaging, and re-scaled from 0 to 1 to yield an estimated probability of grid cell usage (P):



$$\check{P}_i = \frac{\widehat{RD}_i}{\sum_i^N \widehat{RD}_i} \quad (3)$$

The estimated number of individuals per grid cell, per colony ($\check{E}_{i,j}$), was estimated as the product of the colony size, C , times the probability of grid cell usage by individuals from that colony, \check{P} :

$$\check{E}_{ij} = \check{P}_i * C_j \quad (4)$$

for grid cell location i , and colony j .

Total number of individuals, per grid cell, per colony, were combined together as spatially overlapping points, and a kernel density moving window applied (using a nearest-neighbour distance equivalent to $1.41 * \text{grid cell resolution}$) to estimate the total number of individuals present at that location (see **Figure 2**). The resulting prediction surface represented the final estimate of the number of individuals, from all colonies, at any given location.

Prediction error was assessed using a 10-fold cross-validation procedure, with 70% of randomly-chosen analysis grid cells selected for model training, and 30% withheld for error assessment. Error was measured using mean mean-square prediction error (Mean MSE) calculated over the ten iterations.

RESULTS

Tracking data from 520 individuals yielded 9,291 bird-tracking days, and 390,461 locations after filtering out locations for

colony attendance (**Table S1** and **Supplementary Material**). Tracking effort among species varied widely due to the types of tags used and number of years tracked. Northern gannets and gulls, tracked by data-rich GPS and PTT across multiple sites and years, comprised 41% and 38% of the locations, respectively. The remainder of the data includes other species tracked by GPS (~19%), Leach's storm-petrels tracked by GLS (~1%), common eiders tracked by PTT (0.3%) and terns tracked by VHF (0.04%). The quality and the quantity of the tracking data likely influence reliability of empirical results (e.g., measured foraging ranges). The relative quality of tracking and colony data used in this study highlight some important differences among species or species groups (**Table 4**). Alcids (except black guillemots), herring gulls, and the northern gannets had the highest quality owing to the availability of tracking data from multiple sites and well-censused colonies. Terns (except roseate tern), common eiders, and black guillemots had the lowest quality scores, typically due to limited availability of tracking data. Nonetheless, we expect the predictive distribution models to be more robust to variations in data density, because tracking positions were counted and represented as relative densities within analysis grids (see Discussion regarding additional considerations of reliability). Still, predictions are not possible when colony locations are not known; therefore, incomplete colony data (e.g. black guillemot, common eider, black-legged kittiwake) may lead to the largest source of error with respect to predictive distribution models.

Foraging Ranges

Foraging ranges spanned more than 1,000 km for Leach's storm-petrel to less than 20 km for coastal species such as common eider, black guillemot, and terns (**Table 5** and **Figure 3**). In general, species that travel farther from colony sites also travel farther from coastline, yet this is not always the case (**Figure 3**). Comparisons of distance from colony and distance to coast

TABLE 4 | Qualitative assessment of the data used as inputs to the predictive distribution models.

	Tracking data		Colony data		Sum
	Quality	Quantity	Completeness	Accuracy	
common murre	3	3	3	3	12
northern gannet	3	3	3	3	12
Atlantic puffin	3	2	3	3	11
herring gull	3	3	3	2	11
razorbill	3	3	3	2	11
thick-billed murre	3	2	3	3	11
roseate tern	2	2	3	3	10
great black-backed gull	2	2	3	2	9
Leach's storm-petrel	2	3	2	2	9
black-legged kittiwake	3	1	2	2	8
arctic tern	1	1	3	2	7
common tern	1	1	3	2	7
black guillemot	3	1	1	1	6
common eider	2	1	2	1	6

1, low; 2, moderate; 3, high.

Species are ordered by sum of scores, from highest to lowest quality of input data. For each type of data and species we score the data reliability as low, 1, moderate, 2, and high, 3; the sum of the scores represent overall reliability of the model inputs on a scale of 4 (minimum) to 12 (maximum). Quality of tracking data is based on device type (see methods). Quantity of tracking data is based on a combination of the number of individuals, number of sites, and number of bird locations. Colony data are scored based on their completeness (likelihood that all colony locations are represented in the database) and accuracy (which may vary by the census method and/or availability of recent estimates).

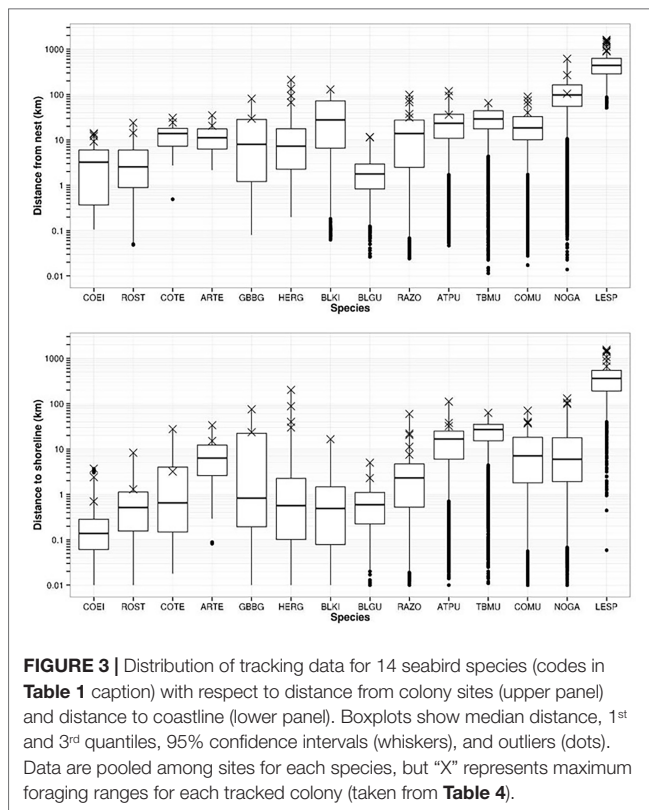
TABLE 5 | Summary of breeding season foraging ranges of 14 species from 23 colonies.

Species	Site	All individuals			Averaged among individuals			Percentage of locations at distance to shore intervals (excluding colony attendance)				
		Foraging range	Dist. to shore	Foraging range	Dist. to shore	Foraging range	Dist. to shore	inland	0-1 km	1-10 km	10-100 km	>100 km
		Birds (n)	Maximum (99th perc.)	Maximum (99th perc.)	Mean max. (sd)	Mean max. (sd)	Mean max. (sd)					
COEI	Bird	9	12.1 (10.1)	3.7 (1.3)	6.8 (3)	1.2 (1)	n/a	96.9	3.1	0.0	0.0	
COEI	West Brother	3	14 (14)	0.7 (0.7)	9.4 (6.5)	0.6 (0.2)	n/a	100.0	0.0	0.0	0.0	
COEI	Metinic	4	13.2 (13)	0.7 (0.6)	12.5 (1)	0.5 (0.2)	n/a	100.0	0.0	0.0	0.0	
COEI	Flag	4	9.2 (8.4)	2.4 (1.5)	5.7 (3.5)	1.2 (0.9)	n/a	97.7	2.3	0.0	0.0	
ROST	Country	8	23.9 (20.6)	1.3 (1.1)	9.8 (6.6)	0.5 (0.4)	n/a	96.4	3.6	0.0	0.0	
ROST	North Brother	7	14.2 (14.2)	8.3 (6.2)	11.4 (1.8)	6.6 (1.3)	n/a	71.2	28.8	0.0	0.0	
COTE	Country	14	24.2 (24)	3.2 (2.9)	12.6 (6.8)	1 (1)	n/a	82.9	17.1	0.0	0.0	
COTE	Machias Seal	14	30.8 (30.3)	27.6 (26.5)	20.9 (5.5)	13.1 (8.5)	n/a	22.2	37.0	40.7	0.0	
ARTE	Country	13	20.6 (19.1)	15.1 (14)	10.3 (5.8)	4 (4.5)	n/a	26.7	66.7	6.7	0.0	
ARTE	Machias Seal	12	34.9 (34.7)	33.5 (32)	21.4 (10.7)	16.9 (9.2)	n/a	7.1	42.9	50.0	0.0	
GBBG	Devil's	3	29.5 (24.8)	23.5 (14.7)	22.1 (11.9)	9.1 (12.5)	55.4	40.1	2.4	2.2	0.0	
GBBG	Sable	9	81 (67.3)	75.4 (61.4)	30.4 (27.5)	22.5 (26.5)	57.8	18.3	5.9	17.9	0.0	
HERG	Gull	8	93.9 (67.5)	39.9 (3)	60 (16.9)	18.1 (15)	77.1	19.6	3.1	0.2	0.0	
HERG	Kent	13	134.3 (74.1)	88 (21.7)	64.4 (40.5)	27.6 (24.5)	47.7	34.4	14.9	3.0	0.0	
HERG	Brier	16	67.3 (56.9)	29.9 (6.3)	44.7 (8.8)	10.2 (6.4)	67.4	17.5	15.0	0.1	0.0	
HERG	Sable	8	211.5 (114.2)	201.9 (104.3)	109 (51.5)	99 (50.9)	58.7	15.8	7.8	16.6	1.2	
BLKI	Gull	8	129.9 (128.2)	16.5 (10)	77.6 (52.6)	9.6 (6.7)	n/a	68.4	30.6	1.0	0.0	
BLGU	Country	5	11.4 (7.6)	2.3 (2.1)	6.5 (3)	1.9 (0.3)	n/a	77.9	22.1	0.0	0.0	
BLGU	Kent	2	11.6 (10.2)	5 (5)	9.2 (3.4)	4.9 (0.2)	n/a	51.6	48.4	0.0	0.0	
RAZO	Gannet	6	67.3 (66.8)	59.4 (59.3)	41.3 (21.1)	15.4 (21.6)	n/a	41.9	49.2	8.9	0.0	
RAZO	Bicquette	11	37.5 (29.5)	22 (18.7)	24.6 (9)	16.8 (4.6)	n/a	30.4	45.1	24.5	0.0	
RAZO	Gros Pot	3	31.1 (30.1)	7.5 (6.5)	21.1 (8.7)	6.2 (1.3)	n/a	73.4	26.6	0.0	0.0	
RAZO	Gros Pelerin	20	99.3 (79.2)	11.2 (9.7)	58.3 (18.5)	8.7 (2.3)	n/a	27.9	71.6	0.5	0.0	
RAZO	Machias Seal	12	77.9 (74)	20.4 (20)	48.9 (20.9)	12.1 (6.5)	n/a	33.2	48.5	18.3	0.0	
ATPU	Gannet	3	35.9 (35.6)	32 (29.5)	32.2 (3.7)	28.6 (3.2)	n/a	13.9	23.9	62.1	0.0	
ATPU	Gull	11	118.7 (79.8)	111.2 (63.2)	59.4 (26)	48.8 (26.7)	n/a	9.1	25.2	65.3	0.4	
ATPU	Machias Seal	12	93.9 (89.2)	37.7 (31.7)	45.7 (23)	24.6 (11.3)	n/a	2.1	40.5	57.4	0.0	
TBMU	Gannet	9	65.1 (64)	63 (61.6)	41.2 (17.3)	39.1 (17)	n/a	11.5	9.5	79.0	0.0	
COMU	Gannet	6	73.9 (73.8)	36.8 (36.3)	38.3 (21.5)	17.2 (11.5)	n/a	34.3	44.7	21.1	0.0	
COMU	Funk	9	62 (60.4)	37.6 (35.8)	45.9 (10.7)	29.9 (4.8)	n/a	5.6	27.4	67.1	0.0	
COMU	Cabot	6	39.9 (38.4)	39.9 (38.4)	31.1 (6.9)	18 (11.7)	n/a	29.0	64.7	6.3	0.0	
COMU	Gull	10	90.1 (89.8)	70.2 (69.5)	27.5 (23.5)	18.4 (20.8)	n/a	30.4	48.3	21.3	0.0	
NOGA	Funk	26	268 (245)	130 (66)	111 (77)	47 (30)	n/a	16.7	40.6	42.6	0.1	
NOGA	Bonaventure	46	616 (336)	105 (88)	229 (118)	66 (32)	n/a	14.2	49.0	36.6	0.2	
NOGA	Baccalieu	6	104 (91)	98 (86)	60 (28)	33 (36)	n/a	11.1	65.2	23.7	0.0	
LESP	Baccalieu	19	892 (825)	880 (806)	714 (116)	686 (123)	n/a	0.0	0.4	4.2	95.4	
LESP	Gull	23	1394 (1181)	1376 (1160)	845 (198)	827 (195)	n/a	0.0	0.2	3.3	96.5	
LESP	Middle Lawn	19	1619 (1465)	1554 (1368)	1029 (295)	904 (303)	n/a	0.0	0.5	3.7	95.8	
LESP	Grand Colombier	2	1272 (1266)	1062 (1052)	1200 (102)	1016 (65)	n/a	0.0	0.0	3.7	96.3	
LESP	Country	16	1459 (1255)	1460 (1003)	1083 (206)	743 (265)	n/a	0.0	0.0	6.0	94.0	
LESP	Bird	10	1131 (1110)	1064 (1007)	994 (163)	860 (154)	n/a	0.0	0.3	3.7	96.0	
LESP	Kent	32	939 (812)	663 (509)	592 (190)	330 (135)	n/a	0.3	2.6	24.3	72.7	
LESP	Bon Portage	43	1542 (1175)	1400 (983)	755 (271)	671 (234)	n/a	0.1	0.3	4.4	95.3	

Foraging range is measured as the maximum distance (km) from colonies and the maximum distance to coastline, for all individuals pooled (maximum) and averaged among individuals (mean maximum). 99th percentiles of all locations provide more typical maximum foraging ranges by eliminating outlier foraging trips (see Methods). Percentage of locations at distance to coastline intervals illustrate how birds are distributed within the maximum ranges presented (see also **Figure 2**). See **Tables 1, 2**, and **S1** for species names, island locations, and years of study. n/a = not applicable.

(**Figure 3**) suggest clusters of species groups including short-range and nearshore (common eider, roseate tern, and gulls), medium range (razorbill, common murre, Arctic and common terns), long-range and nearshore (northern gannet and black-legged kittiwake), and long-range and offshore (Atlantic puffin and thick-billed murre). Leach's storm-petrel foraged extremely far from colonies, nearly always far offshore, at an order of magnitude greater than all other species.

Distance from colony and/or distance to coastline differed among colonies for each species (**Table 5**). Colony-specific differences in foraging ranges are likely a result of local habitats or greater distance of colonies from mainland coastlines (e.g., Machias Seal Island and Funk Island). Colony-specific differences in foraging ranges and distance to coastline were also evident from density plots of raw tracking data, and highlight strong variability in foraging ranges that are well below "mean

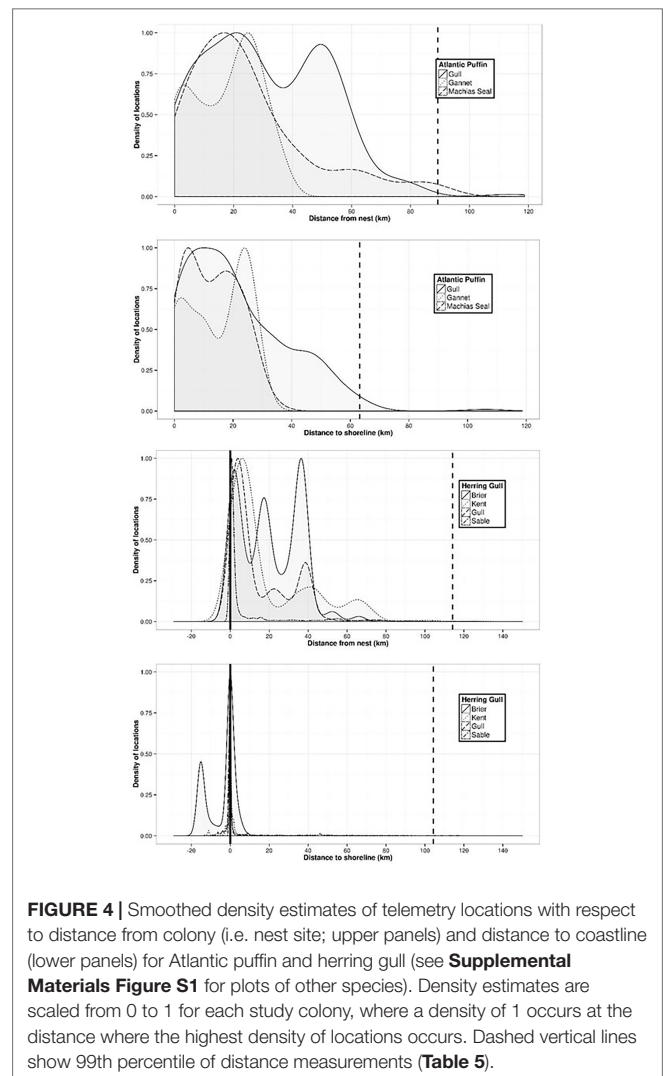


maximum” levels (**Figure 4**, with additional species presented in supplementary material **Figure S1**). For example, although maximum foraging ranges for Atlantic puffin may be ~ 100 km at some sites, peak densities in tracked locations occur near 5, 20, and 50 km from colonies, and nearly always within 40 km of land (**Figure 4**). Similarly, herring gulls tracked from four colonies had considerable variability in peak densities from colonies (ranging from 40–60 km maximum distance depending on colony), but strong convergence on coastal areas.

We compared our results to those from a literature review (Thaxter et al., 2012, and also Masden 2012; Shoji et al., 2015) which reported on the same species, primarily from studies in the eastern North Atlantic (**Table 6**). Overall, maximum and mean maximum foraging ranges were quite similar for most species, though large differences were observed with common eider (maximum range of 14 km vs. 80 km previously reported), herring gull (mean maximum ranges 2.1 times larger in the current study), and Leach’s storm-petrel (mean maximum approx. 14 times larger than reported by Thaxter et al., 2012), owing mostly to limited or poor data available when the original review was conducted.

Predictive Species Distribution Models

The relative importance of each predictor variable varied by species, though some predictors were common to most (**Table 7**). Distance to colony (COLONYDIST) was the first or second most influential predictor for 12 of the 13 species, whereas distance from coastlines (COASTDIST) was the first or second most



influential predictor for six species. Other influential predictors were seafloor slope (SLOPE) for two species (common eider, razorbill) and terrain/seafloor ruggedness (RUGGED) for two species (roseate tern and great black-backed gull). Bathymetry (BATH) was the second most influential predictor for three species groups: terns, black-legged kittiwake, and Leach’s storm-petrel (**Table 7**).

Prediction error, assessed for the averaged BRT predictions, showed that errors tended to be higher for the terns, which were at least partially tracked using VHF receivers, as well as common eider and black guillemot, which had lowest numbers of tracked individuals.

Maps derived from the predictive models varied considerably by species (**Figures 5** and **S2**). Common murre, which we describe as a medium range species, had distributional halos several orders of magnitude larger than those of the black guillemots, and at the regional scale were primarily concentrated near the very large colony of Funk Island, Newfoundland, in contrast to the smaller colonies in southern New Brunswick

TABLE 6 | Summary of species-specific breeding season foraging ranges (km), comparing results of the current study against a comprehensive literature review (Thaxter et al., 2012).

Species	Thaxter et al., 2012				Method	Confidence in assessment	This study				Difference (proportion)	
	Max.	Mean max.	SD	n			Max.	Mean max.	SD	n	Max.	Mean max.
common eider	80	80	na	1	All data	Poor	14	12.1	2.1	4	0.2	0.2
roseate tern	30	16.6	11.6	6	Survey	Low	24	19.1	6.9	2	0.8	1.1
common tern	30	15.2	11.2	6	Direct	Moderate	31	27.5	4.7	2	1.0	1.8
arctic tern	30	24.2	6.3	4	Direct	Moderate	35	27.8	10.1	2	1.2	1.1
great black-backed gull	Not reported						81	55.3	36.4	2	n/a	n/a
herring gull	92	61.1	44	2	Direct	Moderate	212	126.8	62.9	4	2.3	2.1
black-legged kittiwake	120	60	23.3	6	Direct	Highest	130	129.9	na	1	1.1	2.2
black guillemot*	7.6	4.7	4.1	2	Direct		12	11.5	0.1	2	1.5	2.4
razorbill	95	48.5	35	4	Direct+indirect	Moderate	99	62.6	28.4	5	1.0	1.3
Atlantic puffin	200	105.4	46	9	Indirect	Low	119	82.8	42.5	3	0.6	0.8
common murre	135	84.2	50.1	5	Direct	Highest	90	66.5	21.1	4	0.7	0.8
thick-billed murre	Not reported						65	65.1	na	1	n/a	n/a
northern gannet	590	229	124	7	Direct	Highest	616	330	261	3	1.0	1.4
Leach's storm-petrel	120	92	28	3	All data	Poor	1619	1282	272	8	13.5	14.0

Max represents greatest foraging range among all study sites, mean max \pm standard deviation (SD) represents the average maximum across multiple study sites (n = number of studies). Difference is calculated as proportion relative to this study: max. current study/max. n/a = not applicable, previous study.

*values calculated from Masden (2012) and Shoji et al. (2015), no data from Thaxter et al. (2012).

and Nova Scotia (**Figure 5A**). Herring gull, which had similar 99th percentiles for foraging distances as common murre, were present at many more colonies (1,207 vs. 65) including some inland colonies (e.g. Lake Melville, Labrador) (**Figure 5B**). The presence of this species at numerous colonies, combined with a propensity to forage in coastal and terrestrial zones (**Figure 5B**), made herring gulls ubiquitous throughout Atlantic Canada. However, regional hotspots were observed in the St. Lawrence estuary, the northern Gulf of St. Lawrence, the Gaspé Peninsula and northeastern New Brunswick, eastern Newfoundland, and the Bay of Fundy. As a short-range species, black guillemot were notably discrete in their occurrence, owing to their small foraging ranges, and concentrated at colonies primarily along the Labrador coastline in the northern portion of the study area (**Figure 5C**). Important concentrations of this species also occurred off the Gaspé Peninsula, Anticosti Island, and the Magdalen Islands. More localized and isolated breeding colonies occurred in the Grand Manan Archipelago and off the southwest coast of Nova

Scotia. As a species that over the past 20 years is only known to have occurred at eight different colony sites, the northern gannet was particularly concentrated around the large colonies of Bonaventure and Bird Rock in the Gulf of St. Lawrence, and Cape St. Mary's, Newfoundland (**Figure 5D**). Distribution maps of the other species are provided in the supplemental materials (**Figure S2**).

DISCUSSION

Using tracking data and a predictive Boosted Regression Tree method, we were able to describe foraging distributions for the majority of seabirds and colonies in Atlantic Canada. Tracking data from 520 birds illustrated variability in foraging ranges among species and sites, but provided a robust dataset for modeling predictive distributions around colonies. Foraging ranges and distance to shoreline helped describe species

TABLE 7 | Relative influence (%) of environmental predictor variables (see **Table 3**), based on a BRT predictive model trained using all individuals pooled, and an interaction depth (k) equal to three.

Species	COLONYDIST	COASTDIST	BATH	RUGGED	SLOPE	SHELFDIST	Mean MSE
common eider	18.8	23.9	7.9	7.3	42.1	n/a	200.5
roseate tern	27.0	24.5	3.5	30.2	14.8	n/a	92.7
tern spp.	29.4	23.3	26.5	8.6	12.2	n/a	98.0
great black-backed gull	22.7	22.4	12.7	29.7	12.5	n/a	10.9
herring gull	60.1	20.3	12.8	3.9	2.9	n/a	44.5
black-legged kittiwake	38.6	1.9	32.6	19.0	7.9	n/a	0.4
black guillemot	48.0	33.7	8.7	5.1	4.6	n/a	123.0
razorbill	20.4	4.8	3.7	13.6	57.5	n/a	7.7
Atlantic puffin	40.1	34.7	3.6	19.1	2.5	n/a	2.0
common murre	26.5	3.7	20.3	24.2	25.3	n/a	3.6
thick-billed murre	18.5	55.2	8.6	1.7	15.9	n/a	3.3
northern gannet	39.3	25.5	17.6	12.0	2.6	n/a	0.9
Leach's storm-petrel	48.9	13.2	18.2	2.4	10.0	7.2	0.2

Values in bold indicated the predictor variables with the highest and second highest relative influence for each species. Mean mean-square prediction error (MSE) of relative density (RD) values ($\times 10^{-5}$) last column. SHELFDIST was only included in the models for Leach's Storm-petrel (see Methods). n/a = not applicable.

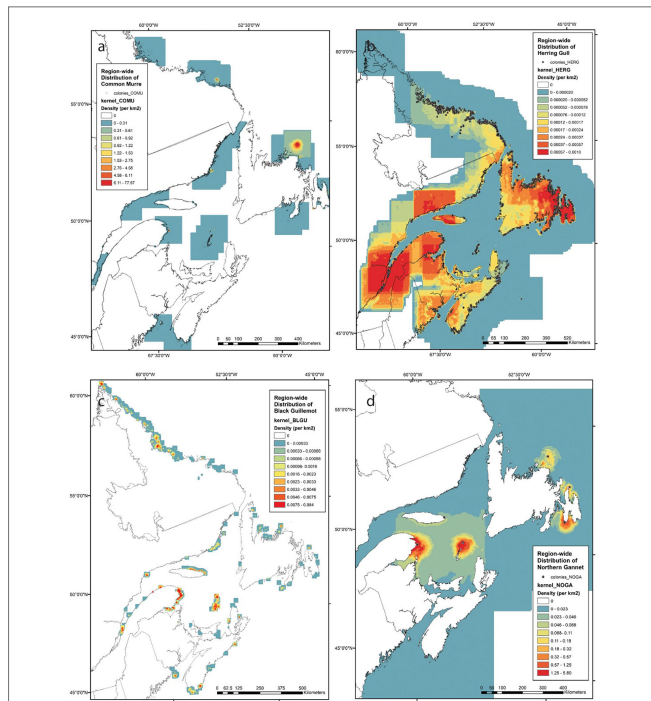


FIGURE 5 | Predictive models of the region-wide distribution of seabird abundance around breeding colonies for **(A)** common murre (COMU), **(B)** herring gull (HERG), **(C)** black guillemot (BLGU), and **(D)** northern gannet (NOGA). See **Supplemental Materials (Figure S2)** for maps of other species. Boosted Regression Trees (BRT) were used to model the relative density of tracking locations for each species separately. BRT models were then used to predict abundance distribution, using maximum colony size (based on census data gathered between 1996 and 2016) for each colony, and a kernel smoother applied to estimate abundance distribution region-wide.

distributions by guilds and highlight that space use is more nuanced than just “maximum foraging range” (Thaxter et al., 2012). Using predictive density surface modelling, we were able to map the spatial “footprint” of breeding seabirds among more than 5000 colonies distributed along more than 5000 km of shoreline, which enhances our toolkit and opportunities for conservation planning at a landscape scale, rather than the site-by-site approach typically viewed from individual tracking datasets.

Foraging Ranges

Foraging ranges have been proposed as a tool for preliminary assessment to help identify important areas for seabird conservation (BirdLife International, 2010; Thaxter et al., 2012; Oppel et al., 2018). Taken together, summary statistics (**Table 3**) and density plots (**Figures 4** and **S1**) in this study suggest that use of absolute maximum foraging ranges for sites may dramatically over-estimate typical foraging ranges for any given species. This is consistent with Soanes et al. (2016) who recommended using mean values of all previously reported maxima, informed further by bathymetric data. Alternatively, our approach using predictive density surface modeling provides a realistic presentation of

breeding seabird distribution which weights foraging ranges (up to a maximum) along with habitat constraints (such as distance to shorelines) in combination with colony sizes.

Not surprisingly, we observed large variability in foraging ranges of this diverse group of species. Nonetheless, the comparisons presented here provide useful metrics for conservation planning around seabird colonies in marine areas of Atlantic Canada. Moreover, similarities in ranges among species identify groupings that may simplify conservation planning, for example, when MPA boundaries or other conservation measures are to be established around mixed-species colonies (Oppel et al., 2018). This highlights the scales at which conservation measures should be considered from local scales of < 10 km for coastal terns, gulls, and eiders, to meso-scales up to 100 km for most alcids, and large scales of 100s of km for northern gannet and Leach’s storm-petrel. These scales are generally in agreement with previously reported foraging ranges for these species (Garthe et al., 2007; Thaxter et al., 2012; Pollet et al., 2014; Shoji et al., 2015; Soanes et al., 2016), with some exceptions (**Table 6**).

Within our study area, we documented considerable intraspecific variability in foraging ranges and distance from coastlines. Foraging effort and ranges may also be influenced by interspecific competition within colonies (Delord et al., 2020; Petalas et al., 2021) as well as density-dependent intraspecific competition and interference driven by colony size (Lewis et al., 2001; Grecian et al., 2012; Gaston et al., 2013; Jovani et al., 2016) and local prey abundance and/or prey condition (Burke and Montevecchi, 2009; Elliott et al., 2009). We were unable to formally test this with our data given the small number of tracked colonies for each species (in contrast to Wakefield et al., 2017). Intraspecific variability in foraging ranges can also be associated with prey-base differences and local foraging conditions, prey quality, and habitat characteristics, which may also vary from year-to-year (Burke and Montevecchi, 2009; Elliott et al., 2009). Additionally, there is a growing body of evidence that individual-level specialization may exist within seabird populations (Woo et al., 2008; Ceia and Ramos, 2015; Phillips et al., 2017; Maynard and Ronconi, 2018), further reinforcing the need for tracking data to include a large sample of individuals (Soanes et al., 2013; Lascelles et al., 2016). Given that some species in our study were tracked at only a few sites, a few individuals, and/or few years, considerations of data quality (**Table 4**) should be taken when interpreting results.

Predictive Models

Despite the widespread intraspecific variability in foraging ranges, it is not practical (logistically or financially) to track most species, or large numbers of individuals, from representative colonies across their range. Therefore, predictive distribution models are the most effective way to synthesize information from multiple telemetry studies to visualize the relative distribution of species over a wide area (e.g. Hindell et al., 2020). Furthermore, by incorporating location and census data from current as well as past colony sites, it becomes possible to not only delineate recent hotspots of occurrence, but also help to identify important breeding areas from the recent past. This is

important for conservation planning of endangered species such as roseate tern, where knowledge of potentially suitable sites permit the identification of candidate locations for future colony re-establishment (Environment Canada 2015).

To our knowledge, this study is the first attempt to model breeding seabird distributions for an entire community of species over such a wide area using a partially-historical collection of tracking data, though recent studies (Wakefield et al., 2017; Reisinger et al., 2018; Baylis et al., 2019; Hindell et al., 2020) have applied comparable modelling frameworks to synthesize broad-scale patterns in other contexts. Predictive models have tended to be constructed for single species, breeding at a few colonies (Grecian et al., 2012; Gaston et al., 2013), and some multi-species tracking assessments from single locations may not employ predictive modelling at all (e.g., Le Corre et al., 2012; Young et al., 2015; Requena et al., 2020). This study developed a method for modeling breeding season distributions which is: (1) applicable and comparable across species and guilds; (2) allows for broader-scale conservation assessment and supports more comprehensive priority setting; and (3) generates predictions for breeding seabirds that naturally supplements information obtained for non-breeding seabirds based on tracking (Grecian et al., 2016; Krüger et al., 2017) and at-sea survey data (Arcos et al., 2012; Wong et al., 2014). The main end product of this analytical approach was a series of large-area distribution maps.

A number of factors impinged upon the choice of analysis framework. First, there was a significant volume of data in need of processing (520 tagged individuals, yielding over 600,000 positions), which demanded a robust and flexible modelling approach. Second, the historical nature of the tracking data meant that positions had been gathered under different environmental conditions, using different protocols, and employing different types of transmitters, which resulted in variation in the quantity of information available for each species. Third, both tracking as well as colony census data were gathered over a wide time interval. The first two considerations were addressed through the use of a gridded analysis, which permitted calculation of relative densities, thereby providing a standardized way to assess distributions across species. Similarly Wakefield et al. (2017) used a gridded approach with location intensities, but modeled habitat associations with mixed-effects GLMs, possible because of the large number of locations for each tracked individual. Alternatives to analysis of gridded data (relative densities) is the use of simulated tracks which produce pseudo-absences, or areas where animals could have occupied (Hindell et al., 2020), but these required high quality tracking data which could be modeled/simulated, which was not always the case with our data (e.g. limited or infrequent time intervals to the data). With regards to the third consideration, the fact that colony sizes were defined as the maximum over a 20-year period meant that temporal variation was rolled into an aggregate summary. While this represented a loss in temporal detail, it allowed for a comprehensive summary of the biological importance of a very large number of widely-distributed breeding locations for each species. Furthermore, the results of the predictive modelling demonstrated that static variables (bathymetric and distance-based) were effective at capturing species-specific constraints

on foraging range, while at the same time acting as proxies for conditions known to affect biological productivity (Mann and Lazier, 2006).

A key aspect of the methods for predictive modelling was the use of machine learning (ML), specifically BRTs. ML-based frameworks have previously been applied to model the distribution of coastal and pelagic seabirds (Yen et al., 2004; Oppel et al., 2012; Reisinger et al., 2018; Hindell et al., 2020), primarily because of their capacity to flexibly and robustly deal with the high variability typically observed in at-sea survey data. ML techniques are adept at handling “noisy” or missing data, i.e., data which do not meet the distributional assumptions of traditional statistical models. In the case of BRT models, non-linear responses are easily accommodated, and do not require *a priori* specification of a functional form of the predictors, which is particularly useful in ecological contexts when the correct functional form (e.g., increasing linear, exponential, unimodal) is not known or cannot be assumed in advance (De'ath and Fabricius, 2000; Hochachka et al., 2007). Furthermore, specification of deeper tree depths provides a way to capture complicated, multi-way interactions.

Predictive modeling provided several key findings with respect to the environmental predictor variables that influenced distributions of breeding seabirds in Atlantic Canada. First, distance from a breeding colony was one of the primary factors contributing to all species predictions, a result consistent with other central place foragers (Wakefield et al., 2017; Baylis et al., 2019). The exception was for common eiders where seafloor slope and distance to coastlines had greater influence on predictive distributions, likely because this species is not restricted to central place foraging once broods hatch and females disperse to rear chicks (Goudie et al., 2000). Likewise, distance from coastlines was an important predictor for other near-shore foragers such as herring gull and black guillemot, as well as northern gannet which is both a long-range and nearshore forager. Bathymetry, including depth, slope, and seafloor ruggedness, showed species-specific emphasis on predictions, similar to other predictive modeling studies of these species (Wakefield et al., 2017).

Data and Model Limitations

Though the resulting species distribution models from our study provide a comprehensive layer which may be used for various conservation planning initiatives (e.g., Lieske et al., 2020), these outputs warrant careful discussion about our assumptions and data limitations, which may lead to sources of error. Errors may arise from three sources including: 1) representativeness of tracking data; 2) accuracy and completeness of colony data; and 3) ability for machine-learning models to produce ecologically realistic predictive models.

Tracking data formed the foundation of our species distribution models with the assumption that patterns observed at one or more colonies may be representative of the species more generally. However, there is a wide body of literature suggesting that, in general, seabirds show intraspecific plasticity in foraging activities (e.g., Garthe et al., 2007; Gaston et al., 2013; Camprasse et al., 2017), likely to accommodate variability in food availability

around colonies (Harding et al., 2013). As such, a large number of tracked individuals, across multiple years, may be required to properly define foraging areas at a given colony (Soanes et al., 2013; Lascelles et al., 2016; Wakefield et al., 2017). Some of the largest mean-squared prediction errors of our output models were observed for species that had few individuals tracked (e.g., black guillemot) or had less tracking data per individual (e.g., common eider, tern species). Lascelles et al. (2016) suggest that between 25 and 50 foraging trips are required within a group to be representative of a population, a target which was not met by several species in our study (black guillemot, tern species, common eider). Moreover, accuracy of different tracking devices may influence model outcomes (Quillfeldt et al., 2017); thus, problems of prediction error may have been exacerbated by use of lower-accuracy tracking data from satellite transmitters (e.g. common eider) and VHF tags (tern species), in contrast to species tracked by GPS tags. Therefore, variability in the quality and quantity of our tracking data may reduce reliability of distribution models for some species.

In addition to tracking data, species distribution models were built upon information on colony locations and population size, and consequently model outputs will be contingent on availability of complete and accurate census data. The colonial seabird monitoring program in Atlantic Canada spans more than four decades, and includes data on species which are surveyed on a three- to 10-year cycle (e.g. Wilhelm et al., 2016), others that are surveyed opportunistically at longer intervals (e.g. Wilhelm et al., 2015), as well as *ad hoc* inventory from other sources (e.g., Ronconi and Wong, 2003). Accuracy of population estimates can also vary depending on the survey methods (aerial estimates vs. ground counts). To buffer against this variability within the colony database, we invoked a decision to use the largest population size for each species and colony within the most recent 20 years. A qualitative assessment of the colony data highlights species that may be underrepresented in our models (Table 4). Specifically, species distribution models may be incomplete for black guillemot which are notoriously difficult to census because they breed in small and often widely dispersed colonies (Ronconi and Wong, 2003), as well as the common eider, which is more regularly assessed by winter aerial surveys than by breeding colony estimates (Bowman et al., 2015).

Notwithstanding the issues identified with respect to tracking and colony input data, other aspects of predictive modeling can generate additional variation in outputs. Models were based on distance from colonies, distance to coastlines, and other static environmental predictors associated with bathymetry. Soanes et al. (2016), for example, demonstrated that bathymetric constraints can help refine foraging ranges derived from a maximum radius approach. Alternatively, additional environmental covariates, such as dynamic oceanographic variables, may improve predictability of models, at a cost of increased complexity (Wakefield et al., 2017; Baylis et al., 2019). Though dynamic, local-scale environmental factors could more accurately depict distributions at the site (colony) level, this omission was deliberate and necessary to achieve our objectives of broad-scale mapping, particularly considering limited tracking data for some species. Moreover, even when dynamic

oceanographic variables are included in predictive models, distance from a colony may still be among the strongest predictors for breeding seabirds as central place foragers (Baylis et al., 2019). We suggest that our current models provide robust distribution mapping for broad-scale assessment and conservation planning initiatives (Lieske et al., 2020). However, further refinement of these models is required for local, site-level, conservation and management action (e.g. delineating MPA boundaries; Lascelles et al., 2012).

Conservation Implications

Ultimately, describing species-specific seabird distribution across a wide geographic range is beneficial for conservation planning in expanding how we think about protecting seabird habitat. Globally, there are ~ 1,600 seabird colonies designated as Important Bird Areas (IBAs, www.birdlife.org), yet these sites generally represent land-based breeding sites, sometimes including seaward boundaries associated with foraging areas that are crucial to breeding seabirds. Conservation managers should also be interested in applying conservation action to the marine areas surrounding these sites, and therefore, management and conservation actions around these sites will require practical designation of foraging areas, ideally using tracking data to identify local differences in foraging range, strategies, and habitat preferences (Oppel et al., 2018; Requena et al., 2020). Given that it is unrealistic and impractical that all birds from IBAs (or other key colonies) be tracked, the predictive modelling approach is a constructive solution.

Identifying MPAs is a key part of the Convention on Biological Diversity, which had a target of 10% marine protection by 2020 (CBD, Convention on Biological Diversity 2010), and calls for new targets for 30% marine protection by 2030 (www.campaignfornature.org). However, the ephemeral and dynamic nature of the ocean and its wildlife present obvious difficulties for creating static protected boundaries (Hyrenback et al., 2000). Inter-annual changes in behaviour or prey distribution may cause seabirds to react differently across years (e.g., northern gannet: Garthe et al., 2011; Warwick-Evans et al., 2016), potentially foraging in different locations and at different scales (e.g., if the colony grows larger). However, evidence suggests that reducing near-colony competition for forage fish, through no-take fishing zones, improves foraging efficiency (and also reduces bycatch risk) of birds living at that colony and is likely to encourage them to forage nearer home, within protected marine zones (Pichegru et al., 2012; Sydeman et al., 2021). Despite extensive mobility and variation among seabird species, MPAs with discrete boundaries around key seabird colonies can still provide foraging habitat protection for seabird species despite the patchy nature of ocean environments (Young et al., 2015). However, MPAs are just one tool for marine biodiversity conservation, and long-distance foraging ranges of some seabirds argue for greater, and perhaps increasingly innovative, ocean management beyond MPA or jurisdictional boundaries (Yorio, 2009; Lascelles et al., 2016; Oppel et al., 2018; Beale et al., 2021). Understanding seabird distributions across a wider geographic region can help frame conservation objectives and put marine spatial planning into perspective.

In summary, the analysis framework employed in this study is an approach for synthesizing empirically-derived distributional information (based on individual tracking and colony survey data), for a diverse community of organisms, to visualize spatial patterns of occurrence for a large region. By highlighting core areas of breeding activity for each of the species, planners and decision makers will now have access to a comprehensive set of tools to better understand where marine birds are actually concentrated in Atlantic Canada. Such information not only offers a way to identify gaps in protection, but can also be used to assess the potential for negative interactions with particular types of human activity (Lieske et al., 2020). This provides a landscape scale approach towards conservation planning, which can then be supplemented by region- or site-specific studies, with more precise tracking devices and fine-scale modeling, to develop more accurate and targeted conservation strategies.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: <https://zenodo.org/record/3631468#.YrIZsnbMLcs>.

ETHICS STATEMENT

The animal study was reviewed and approved by various institutional Animal Care Committees, which are detailed in the original publications of the tracking data (references in Table 2).

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AUTHOR CONTRIBUTIONS

RR, DL, LM, and SA contributed to the conception and design of the study. RR and DL organized the data and performed the analysis. RR wrote the first draft of the manuscript. DL wrote sections of the manuscript. KA, BA, AB, FB, GD, AD, DF, SG, CG, AH, MM, RM, JM, WM, ILP, IP, J-FR, PR, GR, JR, LS, KS, DS, SS, PT, and SW contributed tracking and colony data. All authors contributed to the manuscript revision and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.816794/full#supplementary-material>

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Dive Behavior and Activity Patterns of Fin Whales in a Migratory Habitat

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Efficient use of the energy budget is of fundamental importance for long-distance migrants, which must cope with seasonal energy demands and environmental conditions. Time-activity budgets can provide information on how animals balance energy use and acquisition over their annual cycle, and on the costs and benefits of different migratory strategies. Baleen whales, such as the fin whale, perform long migrations between feeding and breeding grounds. Although there are now a handful of studies describing the diving and foraging behavior of fin whales, most were carried out at their high-latitude foraging grounds, and very little is known about their behavior in wintering habitats or during migration. We analyzed time-depth recorder data to describe the diving behavior and activity patterns of fin whales in a migratory habitat. Using a hierarchical cluster analysis based on a set of dive variables, we identified six dive types. Four of these dive types (shallow exploratory, shallow active, deep exploratory and deep active) were likely associated to foraging. The other two comprised long non-active dives and dives of variable shape, which may represent resting, traveling or even vocalizing behavior. Shallow exploratory dives were the most frequent dive type (23%) and shallow active were the least frequent (5%). The two deepest dive types, deep active and exploratory, were predominantly carried out during the day, and night dives were significantly shallower than daylight dives, suggesting that fin whales tracked the vertical migration of prey. Whales spent 60% of their dive time engaged in dives associated with feeding and/or prey searching, suggesting they prioritized energy intake over energy conservation. Finally, we found that whales spent more time at or close (<15 m depth) to the surface at night (73%) than during the day (55%), indicating a higher vulnerability to ship strikes during this period. Our study provides novel information on the behavioral patterns and time-activity budgets of fin whales in a migratory habitat. This information is essential for bioenergetic analyses and to predict how fin whales respond to human activities and ongoing environmental changes.

Keywords: balaenoptera physalus, migration, baleen whales, time-depth recorders, dive classification, diving behavior, time-activity budget, foraging

INTRODUCTION

Animals live on limited time and energy, and engagement in some activities often excludes engagement in others. How individuals allocate their time to different activities (e.g., foraging, breeding, resting, traveling) can be critical to their survival and reproductive success, and trade-offs between activities depend on a range of intrinsic (e.g., sex, reproductive status, body condition) and

extrinsic drivers (e.g., food availability, density of predators and competitors) (Illius et al., 2002; Rauter and Moore, 2004; Dias et al., 2011).

Many animal populations respond to seasonal changes in resource distribution by migrating between spatially and temporally distinct ranges. Migration allows animals to track variation in food availability, favorable breeding conditions, or avoid harsh environmental conditions, thereby maximizing survival and reproductive success (Alerstam and Bäckman, 2018). However, migrants, especially long-distance migrants, also face unique energetic challenges. During migration, animals not only experience strong fluctuations in resources and environmental conditions, but also prioritize different activities with distinct energetic gains and costs. As resource availability and demands shift throughout migration, animals must adapt their behavior to manage their energy budget (Stern, 2009). Hence, the realized migratory behavior of an individual emerges from the trade-offs between external factors and individual traits. Information on time-activity budgets at different stages of animal migration and under different environmental scenarios can therefore provide valuable insights into these trade-offs, as well as on the consequences of different migratory strategies.

The annual cycle of migratory fin whales (*Balaenoptera physalus*) consists of various spatially and temporally distinct phases. Most whales spend the summer at high-latitude productive areas feeding on dense aggregations of euphausiids and small pelagic schooling fish (Christensen et al., 1992; Sigurjónsson and Víkingsson, 1997). During this period, fin whales acquire substantial quantities of energy reserves and store the surplus energy in the form of fat depots (Lockyer, 1987; Aguilar and Borrell, 1990). Food availability at these foraging grounds is highly seasonal, and fin whale migration to lower latitudes in late autumn appears to coincide with decreasing water temperatures, salinity, and ultimately prey biomass (Tsujii et al., 2016). Although locomotion costs are lower in large swimming whales, migration to breeding grounds nonetheless requires an energy investment; such investment happens during a stage of the life cycle where feeding is believed to be scarce. Moreover, reproduction in fin whales, like in other large mammals, is energetically demanding, especially during lactation (Ofstedal, 2000; Christiansen et al., 2014; Christiansen et al., 2016; Pirotta et al., 2018). As with other capital breeders (Jönsson, 1997; Stephens et al., 2009), the energy necessary for breeding and calving is believed to come mostly from the energy stores gained at the foraging grounds. Thus, fin whales must carefully manage their energy reserves throughout migration, so they can reach breeding grounds, reproduce successfully, and return to productive foraging grounds before their energy reserves are depleted (Miller et al., 2011; Williams et al., 2013; Christiansen et al., 2021).

Nevertheless, feeding outside high-latitude feeding grounds has been reported in fin whales (Silva et al., 2013; Geijer et al., 2016; Silva et al., 2019). Fin whales are commonly encountered off the Azores in spring and early summer (Silva et al., 2014), while migrating to the northern feeding grounds (Silva et al., 2013). The timing of their arrival in the Azores matches the spring phytoplankton bloom in the area (Visser et al., 2011;

Prieto et al., 2017) and their movements towards high latitudes are strongly associated with the spatiotemporal distribution of their prey (Pérez-Jorge et al., 2020), suggesting that whales adjust their movements to exploit prey availability along their migratory pathways. Feeding during migration, even if at reduced levels, may be important for the whales' energy balance. However, foraging is also a costly behavior for these whales. As air-breathing predators, fin whales are constrained by oxygen consumption during a dive, breath holding capacity, and surface recuperation time (Hazen et al., 2015). As a result, it is expected that animals weight the energetic benefit of foraging against the time, metabolic and physiological costs of diving (Boyd et al., 1997). In addition, the filter-feeding strategy (called lunging) used by fin whales to explore efficiently dense patches of small prey items is energetically demanding, limiting dive duration and the number of lunges that can be performed during a single dive, and extending the time needed to recover at the surface (Acevedo-Gutiérrez et al., 2002; Goldbogen et al., 2006; Potvin et al., 2010; Goldbogen et al., 2012). Investigating how much time migrating whales allocate to foraging and how they adjust foraging behavior in comparison to other stages of their annual cycles can provide critical insights into their energy budgets and to the potential benefits of foraging along migration.

Quantifying time-activity budgets in large baleen whales is particularly challenging because these animals are highly mobile and spend prolonged periods underwater, where directly observing their behavior is impossible. Advancements in animal-borne data loggers have enabled the collection of high-resolution data on the vertical and/or horizontal movements of animals (Evans et al., 2013). Several analytical methods using these kinematic data have been developed to infer foraging behavior (Goldbogen et al., 2006; Goldbogen et al., 2013; Sweeney et al., 2019) and describe different activities in several baleen whale species (Oleson et al., 2007; van der Hoop et al., 2017; Izadi et al., 2018; Guazzo et al., 2021). Yet, despite technological developments, most data loggers available for large whales can only stay attached for short periods of time (typically hours to a few days) and cannot be used to document changes in behavior over the annual cycle. The only way to overcome this limitation is to investigate whales' behavior at different life stages to gain a perspective of their full annual cycle.

The objective of this study is to characterize the dive behavior and activity patterns of fin whales in a migratory habitat. We used data collected from time-depth recorders (TDRs) to (1) describe the dominant dive types of fin whales and infer their potential function, (2) quantify time-activity budgets and (3) determine how these budgets vary over diel periods. This information is critical to support future investigations into the energetic constraints of baleen whale migration and for a better understanding of the relative benefits of different migratory strategies. Moreover, studying whales' behavior during their migration is essential to understand their vulnerability to impacts from human activities (Christiansen et al., 2013; Marra et al., 2015). This is of particular importance for these long-distance migrants who cross vast ocean regions during which they are exposed to various threats.

MATERIAL AND METHODS

Data Collection

Migrating fin whales were tagged off the Azores (38° N 28° W) between April and September, from 2007 to 2017 (**Figure 1**; **Table S1**). Tags consisted of a TDR (Wildlife Computers Mk9), a VHF radio transmitter (Telonics MOD125 cast3 or ATS F1835B) and syntactic foam for positive buoyancy. The TDR recorded depth data at the highest sampling rate of 1 s with a resolution of 0.5 m and precision of $\pm 1\%$. Tags were attached anterior to the dorsal fin of the whales by a suction cup (in 2007) or using umbrella darts (all other years) (**Table S1**; Domeier et al., 2005) attached subdermally, and connected to the tag by the use of a galvanic timed-release system. Darts were sterilized in an UV light chamber and by immersion in 70% ethanol and stored in a sealed sterilized plastic bag until deployment. Tags were deployed from a rigid-hulled inflatable boat using either a telescopic pole (for suction cup attachments) or a compressed air gun (ARTS/RN, Restech Norway). A VHF beacon in the tag aids in tracking and recovering the device. Tagged whales were followed for as long as weather and light conditions allowed to record their surfacing positions (**Figure 1**) and behavior. After released from the whales, the TDRs were located and recovered using VHF transmissions. Fieldwork and tagging were approved and conducted under research permits from the competent authorities (Regional Directorate of the Environment and Regional Directorate for Sea Affairs, Regional Government of the Azores) and tagging procedures followed the guidelines of the American Society of Mammalogists (Sikes and Gannon, 2011, & The Animal Care and Use Committee of the American Society of Mammalogists, 2011). A total of 21 fin whales were tagged with duration of deployments ranging from approximately 2 to 41 hours (**Table S1**).

Data Processing

TDR data were processed using the “diveMove” package in R (Luque, 2007; R Core Team, 2021). Before analysis, data were

truncated to remove periods before tag deployment and after the tag detached from the whale. A zero offset correction was first applied to correct shifts in the surface baseline of depth recordings. A dive was then defined as any submergence deeper than 15 m to exclude surface respiration activity (Croll et al., 2001). Each dive was automatically divided into three phases: descent, bottom and ascent, based on changes in vertical rate of the smoothed dive profile. A brief stop at shallow depths occurred during the descent and ascent phases in some dives. Presence of these “shoulders” led to the incorrect inclusion of a large part of these transit segments in the bottom phase of the dives (e.g., Irvine et al., 2017) (**Figure S1**). These segments were manually corrected, with the bottom phase starting at the first inflexion point following a “shoulder” in the descent phase, or ending at the last inflexion point before the “shoulder” in the ascent phase.

A total of ten variables were calculated for each dive: maximum depth, dive duration, post-dive duration, descent and ascent rate, duration of bottom phase, mean and standard deviation (SD) of bottom depth, proportion of time spent at the bottom in relation to the dive duration (hereafter bottom time proportion) and depth range of the bottom phase (hereafter bottom depth range) (**Table 1**). Univariate outliers were found for post-dive duration and the corresponding dives were removed, representing 0.4% of all dives. All variables were checked for normality and transformed when necessary. Unless stated otherwise, data are reported as median values.

Statistical Analysis

TDR data has been used extensively to quantify activity patterns in air-breathing diving vertebrates. This requires identifying specific dive types associated with different activities (e.g., feeding, traveling, resting, etc.) based on dive profiles to produce a continuous activity profile, from which time allocated to different activities can be calculated (Bodkin et al., 2007). Here, we used the dive variables listed above to classify all dives into different groups. Following Irvine et al. (2017) approach, we

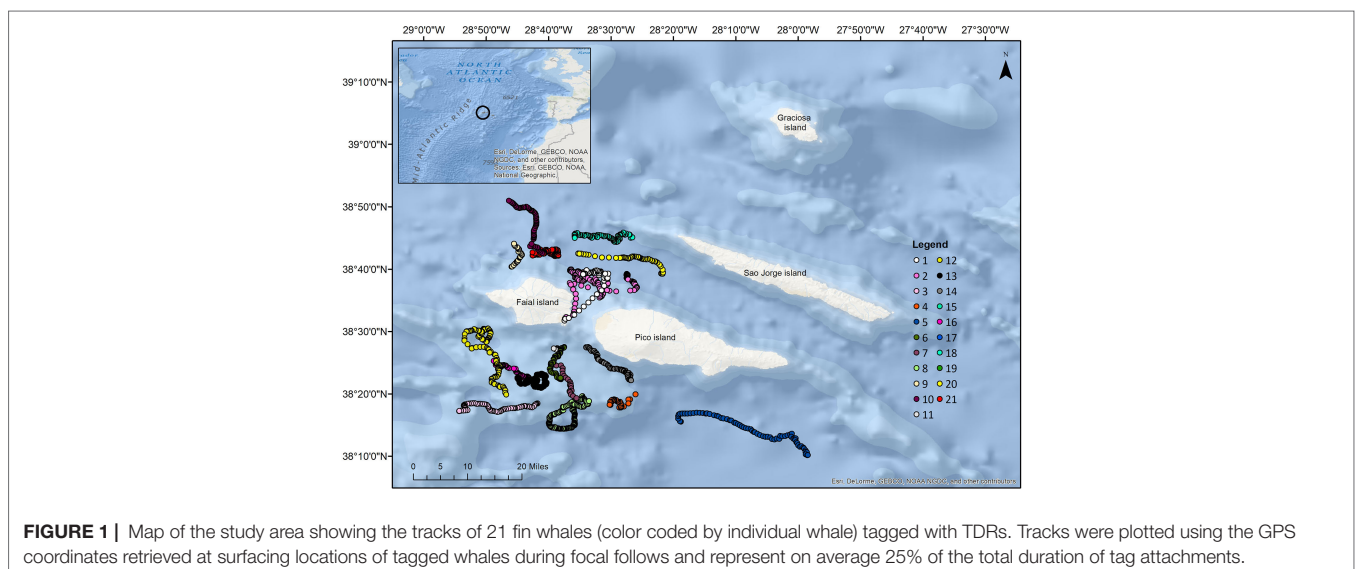


TABLE 1 | Description and summary statistics (median and range) of the dive variables analyzed in this study.

Variable	Description	Transformation applied	Median (min-max)
Maximum depth (m)	Deepest point reached during the dive	Square root	54.2 (15.0-338.8)
Dive duration (min)	Duration of the dive	Square root	3.8 (0.3-17.3)
Post-dive duration (min)	Time between the end of a dive and the start of the following dive	Log10	1.4 (0.0-83.0)
Descent rate (m/s)	Vertical rate of change in depth during the descent phase	Square root	0.9 (0.1-3.5)
Ascent rate (m/s)	Vertical rate of change in depth during the ascent phase	Square root	0.8 (0.0-3.7)
Bottom duration (min)	Duration of the bottom phase	None	1.3 (0.0-14.8)
Bottom time proportion (%)	Proportion of time in the bottom phase in relation to the total dive duration	None	39.6 (0.1-89.5)
Mean bottom depth (m)	Mean depth of the bottom phase	Log10	40.2 (6.4-336.3)
Bottom depth SD (m)	Standard deviation of the mean bottom depth	Square root	4.0 (0.0-83.2)
Bottom depth range (m)	Difference between the maximum and minimum depth in the bottom phase	Square root	13.4 (0.0-234.7)

used a Principal Component Analysis (PCA) and a hierarchical clustering analysis to identify dive groups, without *a priori* knowledge of the total number of clusters. Because some dive variables were strongly correlated, the PCA was performed on the scaled and centered data to minimize multicollinearity and reduce the dimensionality of the data. Variable loadings were calculated to determine which variables had a higher positive or negative correlation to each principal component. Then, the components explaining more variance and complying with the latent root criterion (which states that a factor must account for at least the amount of variance associated with one hypothetical variable) (McGarigal et al., 2000) were used as inputs in the clustering analysis using the Euclidean distance and Ward's method (Legendre and Legendre, 1998). The optimal number of clusters was defined by trimming the resulting dendrogram at different levels and evaluating the stability and biological meaningfulness of the resulting clusters. The cluster stability was assessed through the Jaccard similarity coefficient (hereafter Jaccard index), which ranges from 0 to 1, with values <0.6 indicating an unstable cluster, values between 0.6-0.75 indicating a pattern in the data, and those >0.75, a stable cluster (Hennig, 2014). Mean Jaccard index values were obtained through a bootstrap with 1000 iterations using the “clusterboot” function in the “fpc” R package (Hennig, 2014). A visual inspection of the dives composing each cluster was carried out to assess the presence of dominant dive shapes (e.g., squared-, U- or V-shaped) previously described in the marine mammal literature (Heide-Jørgensen et al., 2013; Irvine et al., 2017; Citta et al., 2021).

Based on the cluster analysis results, time-activity budgets were constructed by calculating the number of dives of each type as a proportion of the total dives performed by each individual whale, as well as the proportion of time allocated to each dive type as a proportion of total diving time (sum of all dive durations) and total tagging time. Percentage of time spent at the surface between dives was calculated by dividing the total post-dive durations by the duration of tag attachment. We also

calculated the percentage of time each whale remained in the first 15 m of the water column by dividing it by total tagging time. Lastly, linear mixed models (LMMs) were used to investigate diel patterns in dive type and in surface usage, using data from whales with deployments longer than 15 h. LMMs were fitted with a Gamma family distribution and a logit link function, using the restricted maximum likelihood as an optimization method and individual whale ID as a random effect to account for individual effects (“mgcv” R package; Wood, 2011). We chose this family because either the response variable clearly followed a gamma distribution and/or it provided the best fit for the model, which we assessed through residual analysis (Wu, 2005). Separate models were fit for each of the following response variables: maximum dive depth, absolute number of dives of each type, percentage of post-dive duration (hereafter surface periods) and percentage of time spent within the first 15 m of the water column. Dive type and/or diel period (Day/Night) were used as explanatory variables, with an interaction term when the models included both variables (Table S4). Dives were assigned to daylight or night-time regimes based on local sunrise and sunset times provided by NOAA Solar Calculator (<http://www.esrl.noaa.gov/gmd/grad/solcalc/calcdetails.html>). When deemed necessary, a correlation structure was applied to account for temporal autocorrelation. All numerical and statistical analysis were performed in R (R Core Team, 2021).

RESULTS

We analyzed a total of 2594 dives performed by 21 fin whales. The deepest dive reached 339 m and the longest was 17.3 min, but only 20% of the dives were deeper than 100 m and 30% longer than 5 min. Number of dives analyzed per individual whale ranged from 11 to 344, and number of dives/hour varied between 2.5 and 16.7 (Table S1). Of the 21 deployments, 10 were longer than 15 h, comprising 1930 dives.

Dive Classification and Characterization

Most of the variability in whales' diving behavior was explained by the first three principal components (84% of total variance) (Table S2). PC1 explained 40.6% of the variance and had strong positive loadings for bottom depth range, standard deviation of bottom depth, dive duration, bottom duration and bottom time proportion (Table S3). PC2 explained 28.9% of the variance and had strong negative loadings for mean bottom depth, ascent rate, maximum depth and descent rate. PC3 explained the least variance (14.6%) and had strong positive loadings for post-dive and dive durations, and a strong negative loading for descent rate.

The hierarchical cluster analysis indicated that all dives grouped into six clusters (Figure 2). According to the Jaccard similarity values, one of these clusters was stable, two clusters showed a pattern in the data and three clusters had a low degree of stability (Table 2). Cluster stability did not improve by changing the number of clusters, suggesting that the optimal number of clusters was six. Clusters were labelled: "shallow exploratory", "long non-active", "shallow active", "deep exploratory", "deep active" and "variable" (Table 2; Figure 2). Dive clusters were primarily split by: (i) depth; i.e., shallow (shallow exploratory, long non-active, shallow active) versus deep/intermediate dives (deep exploratory, deep active, variable); and (ii) the characteristics of the bottom phase; i.e., active (long bottom phase and high variability in depth), exploratory (short or inexistent bottom phase) and non-active (long bottom phase with little or no depth variability).

Shallow exploratory dives represented the most stable (Jaccard index: 0.763) and common dive type (Table 2). These dives were shallow (median maximum depth of 32.7 m) and short (1.6 min), with a short or no bottom phase, and little depth variability (Figure 3). Long non-active dives (Jaccard index: 0.626) were shallower, longer (4.3 min) and had longer post-dive durations than the remaining shallow dives. In fact, post-dive duration in these dives was within the range of that of deep dives. Vertical descent and ascent rates of long non-active dives were the slowest of all dives and bottom phase was generally long (2.2 min), accounting for about 55% of dive duration. However, compared to other dives with long bottom phases, variability in depth was considerably lower. Shallow active dives (Jaccard

index: 0.562) were the only shallow dive with an active bottom phase. Maximum depth and post-dive duration were similar to shallow exploratory dives but dives were 1.6 times longer and had a long bottom phase (48% of dive time) with high variability in depth. The bottom phase of deep exploratory dives (Jaccard index: 0.651) was short or non-existent and varied little in depth, similarly to shallow exploratory dives. The two dive types differed mostly in maximum depth (difference of ~80 m), as well as in dive and post-dive duration, respectively 2.8 and 2.3 times longer in deep exploratory dives. This was the only dive type for which descent rate was slower than ascent rate. Deep active dives (Jaccard index: 0.545) had the greatest bottom depth range and variability, and ascent and descent rates. Maximum depth and duration were similar to those of deep exploratory dives. Lastly, variable dives had the lowest degree of stability (Jaccard index: 0.471). These dives were at intermediate depths between shallow and deep dives, had the longest dive and bottom phase durations, and the highest bottom time proportion (59.1%). Similar to deep dives, post-dive duration was long (1.7 min).

Time-Activity Budgets and Diel Patterns

The majority of tagged whales performed all dive types (Figure 4A; Table S5). Overall, whales performed more deep/intermediate dives (median: 60%) than shallow excursions (40%), and more exploratory (39%) than active dives (22%), even though variability between individuals was high. Shallow exploratory (23%) and variable (20%) dives were the most frequent dive types. However, the time whales spent performing variable dives (27%) was much longer in comparison to the shallow exploratory dive type (11%) (Figure 5). Deep exploratory and deep active dives represented only 14% and 16%, respectively, of all dives. Long non-active (6%) and shallow active (5%) were the least frequent dives and represented only 8% and 4%, respectively, of whale's dive time budget.

The mixed-effects models on the absolute number of dives and maximum dive depth showed significant differences in diel patterns for most dive types (Table S4; Figure S4). Deep active and deep exploratory dives were more frequent during the day than at night (Figures 4B, C, 5), with diving depth progressively

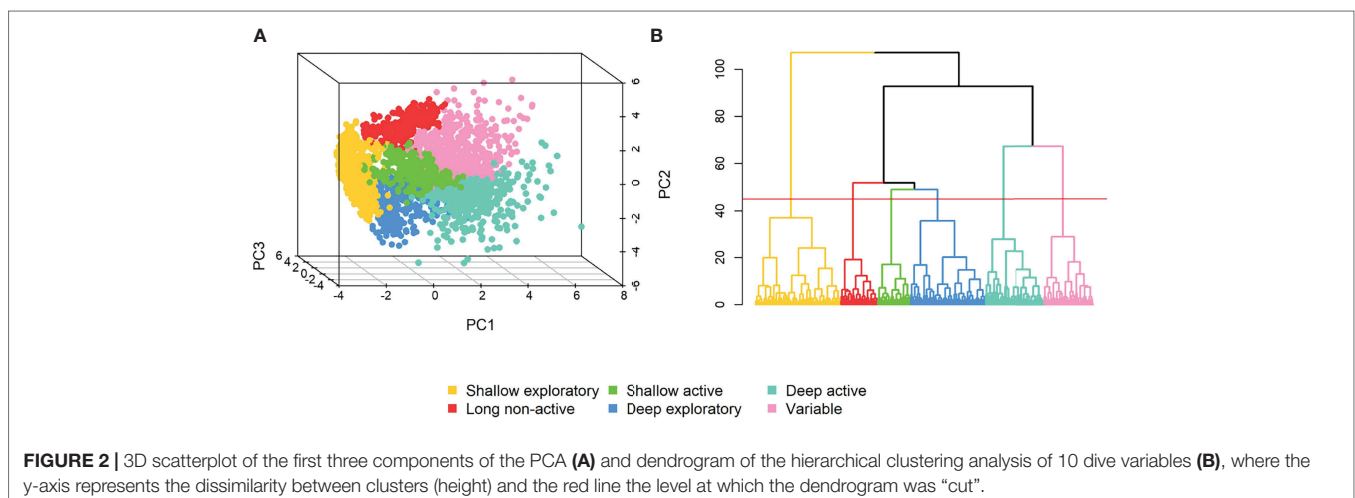


TABLE 2 | Median and range of values of each variable for the six dive types identified by the cluster analysis.

Clusters	N	Maximum depth (m)	Dive duration (min)	Post-dive duration (min)	Descent rate (m/s)	Ascent rate (m/s)	Bottom duration (min)	Bottom proportion (%)	Mean bottom depth (m)	Bottom depth range (m)	Bottom depth SD (m)	Jaccard index
Shallow exploratory	654	32.7 (15.0-102.3)	1.6 (0.3-8.0)	0.8 (0.0-62.9)	0.9 (0.2-2.8)	0.7 (0.1-3.7)	0.0 (0.0-1.0)	1.6 (0.3-50.0)	32.4 (13.9-102.3)	0.0 (0.0-6.7)	0.0 (0.0-2.1)	0.763
Long non-active	252	19.8 (15.1-59.5)	4.3 (1.4-8.0)	1.5 (0.13-83.0)	0.4 (0.2-1.2)	0.3 (0.0-1.1)	2.2 (0.4-6.7)	55.2 (10.8-85.4)	16.0 (6.4-54.7)	5.6 (0.5-30.1)	1.5 (0.1-8.9)	0.626
Shallow active	283	38.8 (15.1-74.0)	2.5 (0.7-4.7)	0.5 (0.1-9.9)	1.1 (0.2-2.3)	0.9 (0.2-1.8)	1.1 (0.2-3.3)	48.0 (11.9-78.6)	27.8 (8.9-56.6)	18.7 (0.4-56.6)	5.6 (0.1-17.9)	0.562
Deep exploratory	374	115.1 (49.7-291.3)	4.5 (0.9-12.1)	1.8 (0.1-31.0)	0.9 (0.3-3.0)	1.1 (0.4-3.2)	0.0 (0.0-3.5)	1.0 (0.1-61.3)	112.2 (41.9-278.8)	0.1 (0.0-58.1)	0.1 (0.0-22.0)	0.651
Deep active	455	110.4 (50.5-338.8)	4.9 (1.7-13.8)	1.7 (0.0-30.1)	1.3 (0.3-3.5)	1.3 (0.3-3.1)	2.4 (0.0-10.3)	50.7 (0.3-87.3)	74.6 (28.5-336.3)	49.6 (0.0-234.7)	15.1 (0.0-83.2)	0.545
Variable	576	57.5 (16.3-133.2)	5.5 (2.2-17.3)	1.7 (0.1-68.6)	0.7 (0.1-1.9)	0.6 (0.1-1.9)	3.1 (0.7-14.8)	59.1 (20.4-89.5)	33.6 (10.2-88.1)	34.8 (3.5-120.2)	10.4 (0.9-43.9)	0.471

decreasing close to sunset and increasing again towards sunrise (**Figures 6, S3**). Long non-active and variable dives were also more common during the day than at night. Only shallow exploratory dives were significantly more frequent at night than during the day. No significant diel differences were found in the proportion of shallow active dives. However, not all whales showed the same pattern, with two individuals tagged on consecutive days (12 and 13) spending most of their diving time in variable dives and night-time at the surface (**Figures 5, 7**). The mixed-effects models also revealed significant diel differences in surface usage (**Table S4**). Whales spent significantly more time in surface periods at night (median: 60%) than during the day (41%). Nonetheless, there was high individual variability in surface use at night, with the proportion of time spent in surface periods varying from ~30% to over 90% between whales (**Figure 7**). In addition, proportion of time spent in the upper 15 m of the water column was also significantly higher at night (73%) than during the day (55%).

DISCUSSION

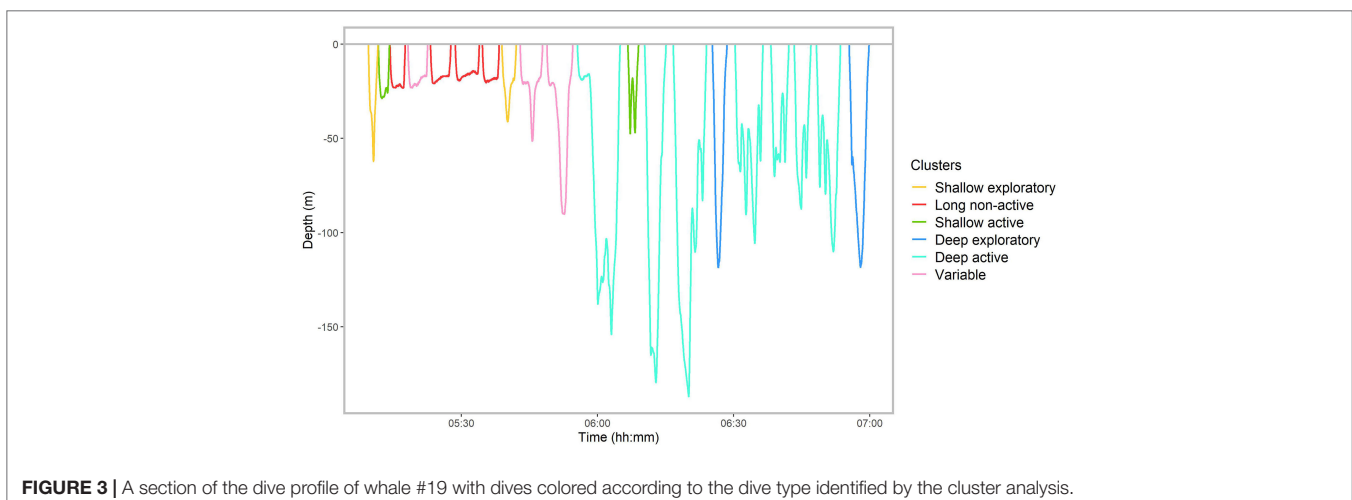
We used dive metrics calculated from TDR data to characterize different dive types, infer their potential function, and determine time-activity budgets of fin whales in a migratory habitat. To

the best of our knowledge, this represents the first detailed description of the diving behavior and activity patterns of this species in a migratory habitat.

Dive Characteristics and Function

Based on the results of the PCA, the hierarchical cluster analysis identified six dive clusters. We should stress, however, that the unsupervised classification method utilized is unable to precisely categorize each dive. While automated methods allow a fast and objective classification of dives, the classification is not free from errors, particularly for underrepresented dive classes (Thums et al., 2008). Therefore, dive types represent generalizations of the more complex dive behavior of fin whales. Additionally, characterization and discrimination of different dive types would advance significantly by using tags with tri-axial accelerometers, enabling the measurement of behavioral metrics (e.g., whale orientation, speed, acceleration, stroking activity) that can help distinguish active locomotory from inactive behaviors (Brown et al., 2013) or identify feeding lunges (Goldbogen et al., 2006; Ware et al., 2011).

Active dives had a prolonged bottom phase, sometimes reaching 10 min, and variable bottom depth, as a result of single or multiple vertical excursions (**Figure S2C**). These vertical

**FIGURE 3** | A section of the dive profile of whale #19 with dives colored according to the dive type identified by the cluster analysis.

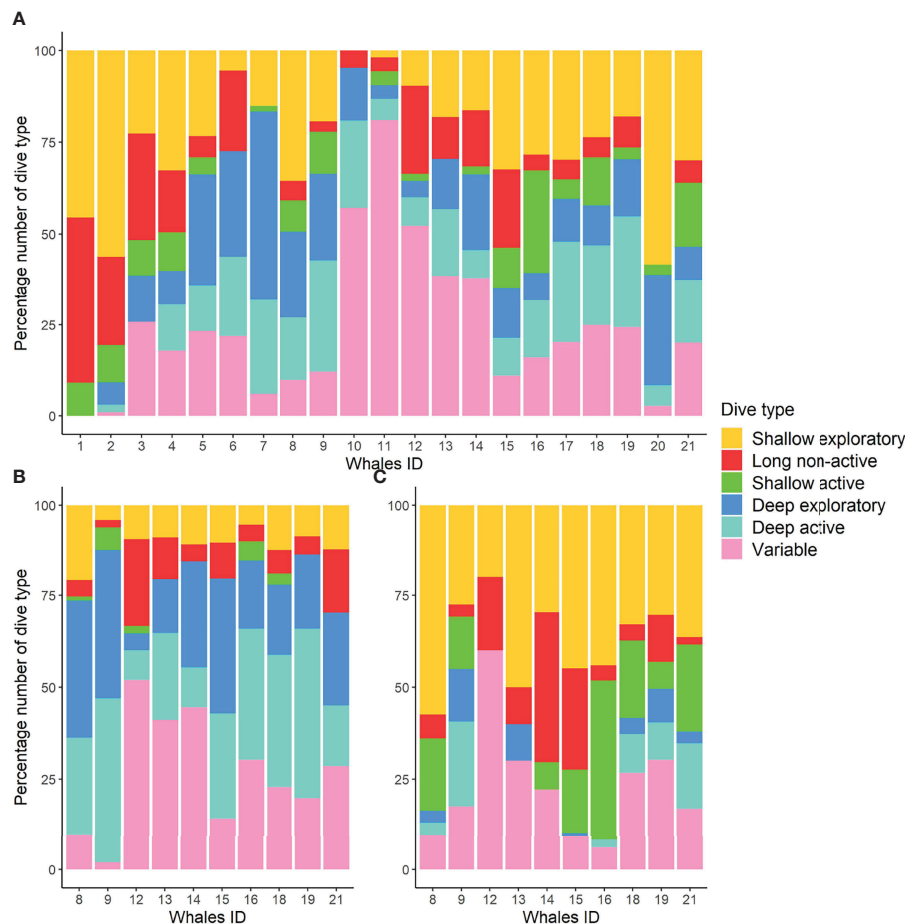


FIGURE 4 | Percentage number of each dive type (shown with different colors) by individual for 21 fin whales tagged in this study **(A)**. Percentage number of each dive type during the day **(B)** and night **(C)** for 10 fin whales with tag attachments longer than 15 h.

excursions generally occurred within a restricted depth layer at the bottom of the dive, but occasionally happened during the ascent or descent. A prolonged bottom phase is characteristic of the foraging dives of several marine predators and arises from the individuals' attempt to maximize time at a foraging patch (LeBoeuf et al., 1988; Fedak et al., 2001; Thompson and Fedak, 2001; Schreer et al., 2001; Witteveen et al., 2008). Foraging dives also have fast transit phases (Goldbogen et al., 2011), as observed here in deep and shallow active dives. In addition, in fin whales and other balaenopterid whales, vertical excursions close to the bottom are believed to represent lunging behavior, in which the whales accelerate upward towards a prey patch (Goldbogen et al., 2006; Simon et al., 2012). Finally, the clear diel pattern in active dives, where shallow dives dominated at night and deep dives during the day, is consistent with tracking the diel vertical migration of prey (see below). Taken together, these results provide strong evidence that deep and shallow active dives are associated with feeding activity. On the other hand, exploratory dives were short, with little or no bottom time, strongly resembling the stereotypical V-shaped dive described for baleen whales (Schreer et al., 2001; Heide-Jørgensen et al., 2013) (**Figure**

S2A). Shallow and deep exploratory dives reached similar depths and showed the same diel pattern as their active counterparts, suggesting they could serve to assess prey availability in the water column. They may also include aborted or failed foraging dives. Shallow exploratory dives could also encompass periods of horizontal travel. The relatively slow descent and ascent rates of these dives indicate that whales were either swimming slowly at a steep angle or more horizontally at normal speeds (Martin et al., 1998). Shallow V-dives may enable whales to avoid surface drag (see below), thus increasing swimming efficiency.

The remaining two clusters comprised a high diversity of dive shapes, although some shapes were dominant. Long non-active dives included large numbers of squared dives (**Figure S2B**), which may represent resting or traveling. The long bottom phase and small depth variability of these dives suggest that whales were either motionless or moving horizontally. Given that the impact of wave drag is lowest at depths greater than three times the body diameter of an animal (Hertel, 1966), resting and traveling under this threshold, while still remaining close to the surface, could be energetically efficient. The estimated depth threshold below which blue whales should swim to avoid wave

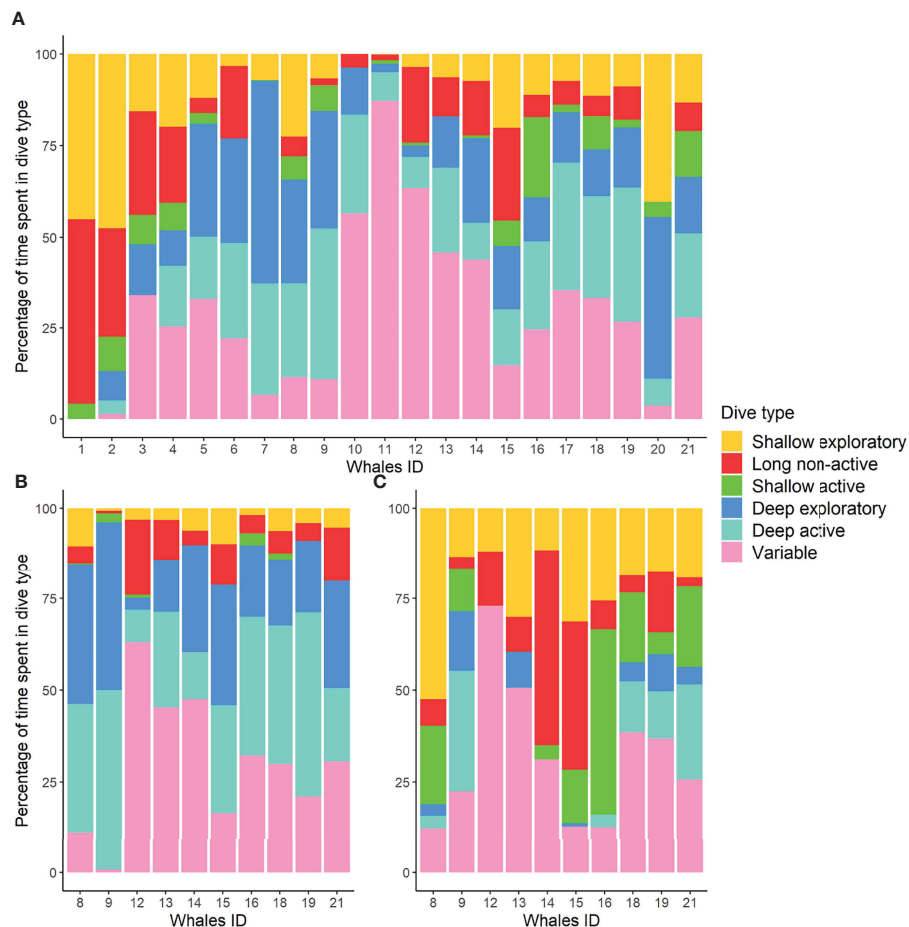


FIGURE 5 | Percentage of time spent in each dive type (shown with different colors) by individual for 21 fin whales tagged in this study **(A)**. Percentage of time spent in each dive type during the day **(B)** and night **(C)** for 10 fin whales with tag attachments longer than 15 h.

drag (12 m) (Owen et al., 2016) is close to the depth of long non-active dives. The characteristics of long non-active dives are also consistent with singing behavior. Singing fin whales generally swim slowly and display minimal body movement (Clark et al.,

2019; Guazzo et al., 2021), remaining at 15–50 m depth (Watkins et al., 1987; Aroyan et al., 2000; Stimpert et al., 2015), where they are neutrally buoyant (Goldbogen et al., 2006). Singing is also believed to be energetically demanding (Clark et al., 2019),

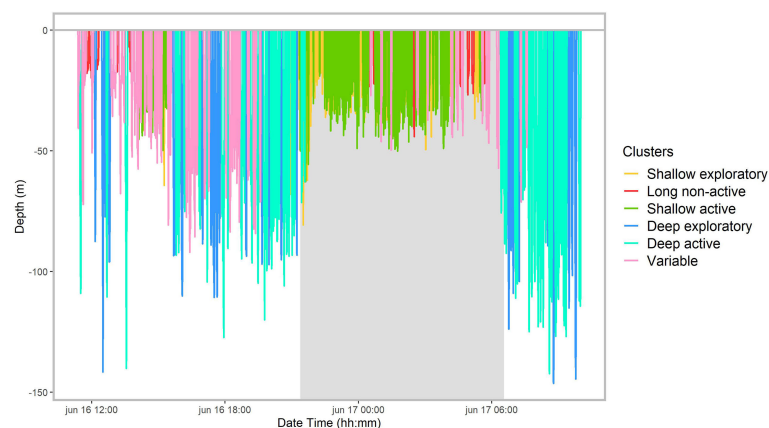


FIGURE 6 | Dive profile of whale #16 illustrating the diel pattern in diving behavior and dive types, as identified by the cluster analysis. The shaded area indicates the night period.

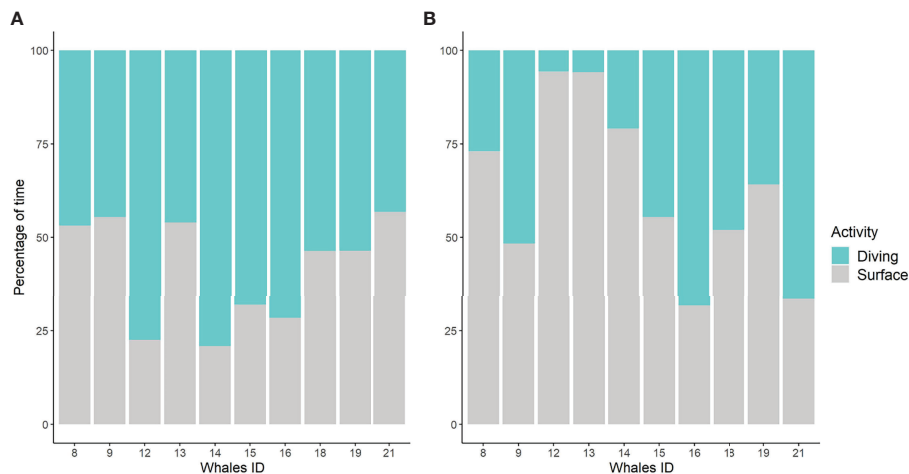


FIGURE 7 | Percentage of tag attachment time spent in surface periods during the day (A) and night (B) for 10 fin whales with tag attachments longer than 15 h.

which could explain the long surface times of these dives. Although our data were mostly collected in spring and early summer, when fin whale songs are rarely detected in the study area (Romagosa et al., 2020), this dive type could be associated with the production of other acoustic signals, like the 40 Hz call regularly emitted by foraging whales (Romagosa et al., 2021). The variable dive type encompassed dives of many different shapes, which likely serve multiple functions. The long dive, bottom and post-dive durations, high bottom time proportion and great variability in depth, also typical of active dives, suggest that variable dives include periods of feeding activity. Other dive shapes were similar to the root-square dive documented in pinnipeds (Ramasco, 2008; McIntyre et al., 2011), where whales travelled to the maximum dive depth (usually <100 m), and immediately started ascending, barely spending time at the bottom, like in V-shaped dives. The unique feature of these dives was that, before or after this “peak” in depth, whales remained a long time (up to 10 min) in the first 35 m of the water column, with little variation in depth (Figure S2D). These dives could represent exploratory dives, followed by transiting to a different prey patch, resting, or even singing activity.

Diel Patterns in Diving and Foraging Behavior

Fin whales exhibited a strong diel pattern in diving behavior, shifting between predominantly deep dives during the day and shallow dives at night. This diel pattern has been reported elsewhere in fin and other baleen whale species and is likely related to the diel vertical migration of their prey (Panigada et al., 1999; Calambokidis et al., 2007; Friedlaender et al., 2009; Friedlaender et al., 2013). Most baleen whale prey undertake vertical migrations, residing in deep waters during the day, where they form dense aggregations, and ascending to the surface at night, where they disperse to forage (Mauchline and Fisher, 1967; Raymont, 1983). Baleen whales adapt their feeding strategies to the diel changes in density and vertical distribution

of prey. Antarctic humpback whales (*Megaptera novaeangliae*) and St. Lawrence blue whales (*Balaenoptera musculus*) foraged preferentially on near-surface, less dense prey aggregations at night, presumably to minimize the energy costs and surface recovery time associated with longer, deeper dives, thereby maximizing foraging efficiency (Doniol-Valcroze et al., 2011; Ware et al., 2011; Friedlaender et al., 2013; Friedlaender et al., 2016). Conversely, fin and blue whales in the eastern North Pacific rarely foraged at night (Friedlaender et al., 2015). In fact, whales decreased the frequency of feeding dives and the number of feeding lunges when foraging on shallow, low-density prey, but increased foraging effort when targeting deep denser patches (Hazen et al., 2015; Friedlaender et al., 2020). By increasing the number of lunges on denser patches, whales can substantially increase prey intake and energy efficiency, despite of the higher costs of diving deep to reach these patches (Hazen et al., 2015; Friedlaender et al., 2020).

Our results indicate that deep active dives were longer and had more vertical excursions, which likely represent lunges, than shallow active dives. This is consistent with earlier studies (Hazen et al., 2015; Friedlaender et al., 2020) and suggests that fin whales increased their lunge-feeding rates in deep dives for foraging to become efficient. However, fin whales in this study mainly foraged in waters <100 m and the median depth of deep dives was considerably shallower than in other areas (Friedlaender et al., 2020). It is possible that the density of deeper prey was insufficient to compensate the higher costs of diving deeper to target these patches. Under these circumstances, foraging throughout the diel cycle on shallow prey may represent a more efficient foraging strategy, explaining why the frequency of deep foraging dives was similar to that of shallow foraging dives. Information on prey density and depth, as well as on consumption rates of fin whales in the area, is necessary to confirm this hypothesis and to estimate the potential energy gain of this strategy.

Nonetheless, not all whales exhibited the same pattern in foraging activity. Two individuals did not perform shallow active dives during the night and devoted less time than average to

deep diving (active and exploratory) during the day. Instead, these whales spent the majority of their tagging time (18 and 38 h) engaged in variable dives. Given the diversity of shapes of variable dives, we believe they serve more than one function, complicating the interpretation of these results. Predominance of variable dives could indicate an alternative foraging strategy to exploit different prey (Goldbogen et al., 2015), that prey density was too low to allow efficient foraging, leading to increased transiting between prey patches, or that whales prioritized resting over foraging.

The diel pattern in fin whale dive behavior implies that, at night, whales remain most of the time near the surface, and even when diving, they spend substantial time in the upper water column (<15 m). Increased surface usage exposes whales to a higher risk of ship strikes at night (McKenna et al., 2015), when whales cannot be detected by visual observers' onboard vessels. These results are in line with findings from other areas and times of year (Calambokidis et al., 2019; Keen et al., 2019), emphasizing the need to account for diel changes in whale's dive behavior when estimating the risk of ship strikes and devising mitigation measures.

Time-Activity Budgets

Tagged whales spent 56% of their time diving and 44% at or near the surface, with some variability among individuals (Figure 7). Time spent in surface activities includes surface recovery times between dives, as well as resting or traveling periods. While classifying the time spent at surface broadly as surface periods may have led to the underestimation of certain behavioral states, it is important to stress that the distinction of sub-surface activities is unfeasible with only two-dimensional dive data.

Fin whales spent about 8% of their diving time in long non-active dives, which we classified as potential horizontal traveling and resting. This value represents 4% of total tagging time, which is strikingly low when compared to the 23–35% of time spent traveling (Visser et al., 2011; Silva et al., 2013) and ~18% resting (Visser et al., 2011) previously reported for the same area. As stated above, one explanation is that traveling and resting occurs mostly in near-surface waters (<15 m), and therefore, below our dive threshold. It is also probable that traveling and resting are included in variable dives, which accounted for a median of 27% of the time-activity budget and 14% of total tagging time of fin whales.

The dominant dive types of fin whales were associated with foraging activity. Assuming that active and exploratory dives represent feeding and searching for prey, whales spent about 60% of their diving time, or 32% of total tagging time, in feeding-related activities. Our results are slightly lower than the values reported from fin whales instrumented with satellite tags in the same area, which indicated that whales spent 55% of their daily time in area-restricted search, believed to mostly represent foraging (Silva et al., 2013). However, we stress that ARS calculations also include time spent at surface, while our results reflect solely diving time.

CONCLUSIONS

Animal migrations are commonly understood as a response to the spatiotemporal variation in resources across broad scales (Dingle and Drake, 2007), but animals also respond to finer-scale variation in resources along their migrations. A wide range of terrestrial and marine migrants have been shown to track phenological variation in prey across space, thereby prolonging access to resources available and enhancing their energy gain (Armstrong et al., 2016). Recent work shows that migrating blue whales track resources by matching their movements with the long-term average phenology of the phytoplankton bloom (Abrahms et al., 2019). This work provides empirical support to modelling studies that demonstrate the emergence of blue whale migrations to track prey resources, allowing whales to support their energy demands (Pirodda et al., 2018).

Previous studies have shown that the timing of fin whale arrival in the Azores migratory habitat matches the seasonal peak in productivity (Visser et al., 2011; Prieto et al., 2017) and individuals can remain in the area for days to a few weeks (Silva et al., 2013). Movements of fin whales in the Azores and towards higher latitudes are closely linked to prey biomass (Pérez-Jorge et al., 2020), suggesting that whales track shifting hotspots of prey availability across space, similarly to blue whales (Abrahms et al., 2019). Here we examined the fine-scale behavior of migratory fin whales at a foraging hotspot. We found that whales allocate a significant proportion of their diving time to active and exploratory diving, which likely represent foraging, suggesting that whales prioritize energy intake over energy conservation. Although we were unable to quantify the energy accrued by fin whales, together these findings suggest that energy intake during migration might be higher than previously assumed. By moving to track the seasonal phenology of prey, fin whales could maximize use of the energy available to them, despite the ephemerality of individual forage patches (Abrahms et al., 2021). While the benefits of this strategy seem intuitive, they remain to be quantified. Detailed measurements of the underwater behavior of fin whales, as well as information on prey availability, will be necessary to estimate the energy gain and cost of foraging during migration. Moreover, data covering a larger spatiotemporal scale will be necessary to assess how recurrent this behavioral pattern is along the migratory route and its contribution to fin whale's annual energy budget. This knowledge will be particularly important to understand potential impacts from climate change. As climate change is modifying seasonal rhythms of resources, this may interfere with the ability of fin whales to efficiently track resources during migration, as reported across different taxa (Cohen et al., 2018). Assessing the consequences of phenological changes in prey distribution for fin whale energetics will be critical to determine effects at the population level.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by Regional Directorate of the Environment and Regional Directorate for Sea Affairs, Regional Government of the Azores.

AUTHOR CONTRIBUTIONS

CTF analyzed the data, wrote the manuscript, contributed to the methodology. SPJ contributed to the methodology, data analysis, and writing. RP conceived and designed the study, contributed to funding acquisition and project administration, undertook fieldwork and collected data. CO and MT undertook fieldwork and collected data. AS contributed to the methodology and data analysis. MAS conceived and designed the study, contributed to funding acquisition and project administration, undertook fieldwork and collected data, contributed to the methodology, and wrote sections of the manuscript. All authors reviewed the submitted version of the manuscript. All authors contributed to the article and approved the submitted version.

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Mismatches in scale between highly mobile marine megafauna and marine protected areas

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Marine protected areas (MPAs), particularly large MPAs, are increasing in number and size around the globe in part to facilitate the conservation of marine megafauna under the assumption that large-scale MPAs better align with vagile life histories; however, this alignment is not well established. Using a global tracking dataset from 36 species across five taxa, chosen to reflect the span of home range size in highly mobile marine megafauna, we show most MPAs are too small to encompass complete home ranges of most species. Based on size alone, 40% of existing MPAs could encompass the home ranges of the smallest ranged species, while only < 1% of existing MPAs could encompass those of the largest ranged species. Further, where home ranges and MPAs overlapped in real geographic space, MPAs encompassed < 5% of core areas used by all species. Despite most home ranges of mobile marine megafauna being much larger than existing MPAs, we demonstrate how benefits from MPAs are still likely to accrue by targeting seasonal aggregations and critical life history stages and through other management techniques.

KEYWORDS

dynamic ocean management, home range, life history, marine predators, marine protected areas, migratory connectivity, mobile marine protected areas, pelagic conservation

Introduction

One of the perceived benefits of marine protected areas (MPAs) has been for the conservation of megafauna (Hooker and Gerber, 2004). Many of these species are or have been targets of human exploitation or disturbance, have less resilient life histories than smaller species, and have been depleted across much of the planet (Dirzo et al., 2014; Ripple et al., 2014; Carman et al., 2015; McCauley et al., 2015). Marine megafauna are protected under a variety of international and domestic laws to conserve their important roles in maintaining the structure and function of their associated ecosystems (Estes et al., 2011; McCauley et al., 2015). Many proponents of large MPAs point to their size as a way to protect marine megafauna and their habitats (e.g., Game et al., 2009; Toonen et al., 2013; O'Leary et al., 2018; Gallagher et al., 2020). Moreover, many MPA guidelines (Lewis et al., 2017; Smyth and Hanich, 2019) as well as official MPA declarations explicitly cite megafauna protection as a key driver of establishment for large-scale MPAs, such as the Ross Sea Marine Protected Area (Commission for the Conservation of Antarctic Marine Living Resources, 2016), and expansion of Papahānaumokuākea (Executive Office of the US President, 2016) and the Pacific Remote Islands (Executive Office of the US President, 2014) Marine National Monuments in the US, though many smaller, coastal MPAs are created for other reasons. Although the protection of key habitat is a primary tool in the conservation and management of marine megafauna (Hooker et al., 2011), this perceived benefit may come with significant socioeconomic costs. This is especially true for large MPAs as they can restrict large areas of various human uses, such as fishing, mineral extraction, and vessel activity to a larger degree than smaller MPAs (Ban et al., 2017; O'Leary et al., 2018). These costs demand that the benefits of MPAs for wide-ranging megafauna be demonstrated.

Global targets for MPAs have been proposed and continue to be refined. The United Nations (UN) is actively negotiating the implementation of MPAs in regions beyond national jurisdictions (i.e., the 'High Seas') (United Nations, 2017), regions that are particularly important for marine megafauna (Harrison et al., 2018; Beal et al., 2021; Davies et al., 2021b). Moreover, in 2016 the International Union for the Conservation of Nature (IUCN) called to increase the UN Convention on Biological Diversity Aichi Biodiversity Target 11 from 10% to up to 40% of the ocean to be protected by 2030 (Hilborn, 2016; IUCN, 2016; Jefferson et al., 2021), and many countries and Tribal nations have come out in support of these goals (Allen et al., 2021; Sullivan-Stack et al., 2022). Large MPAs (> 100,000 km²) have increasingly emerged over the last decade, in part to achieve those targets (O'Leary et al., 2018), though many of the large, highly protected MPAs are placed in remote regions where threats and human conflicts are limited, while MPAs closer to human populations are often more limited in protections offered (Sullivan-Stack et al., 2022). In addition to achieving targets, the push to

establish larger MPAs has been fueled by i) the successes of coastal MPAs, ii) a recognition that most of the global ocean is not coastal, and iii) the need to protect large scale processes that characterize oceanic systems (e.g., long-distance animal movements) (Longhurst, 2010; Block et al., 2011). The various purported benefits of large MPAs also include their ability to protect entire functional ecosystems, and to help buffer these systems from climate change, large spatial-scale disturbances, and edge effects of smaller MPAs (Toonen et al., 2013; Wilhelm et al., 2014).

Despite purported benefits of MPAs, and especially large MPAs, to highly mobile marine megafauna, there remains much uncertainty about their effectiveness, in part due to observed or theorized mismatches in scale between MPA sizes and megafauna ranges or critical habitats in specific regions and cases (e.g., Agardy et al., 2011; ICES, 2011). Thus, there is a need for a comprehensive, empirical effort to explicitly evaluate the adequacy of existing MPA sizes as they relate to highly mobile marine megafauna movements. This critical first step is necessary to determine if MPAs as they are currently designed are spatially equipped to offer the protection that is necessary for highly mobile marine megafauna, and to evaluate how MPAs might be designed to be most spatially compatible.

Quantifying and understanding MPA effectiveness for megafauna will require a multi-faceted approach, requiring studies both at global scales and at smaller, regional scales. Here, our objective is to understand the extent to which global MPA boundaries align in spatial scale with the movements of highly mobile marine megafauna. This evaluation is particularly timely as the push for large MPAs continues and as an agreement for protecting biodiversity on the high seas under the UN Law of the Sea Convention (UNCLOS) develops. Here, we compiled an extensive tracking dataset from 36 species of highly mobile marine megafauna from five higher taxa (cetaceans, elasmobranchs [sharks and rays], pinnipeds, chelonoids [sea turtles], and seabirds) to quantify the congruence of global MPA sizes with home ranges and to evaluate how this congruence may fluctuate across the annual cycle and species life history. Our results identify key considerations for MPA design and management necessary to amplify the effectiveness of MPAs for marine megafauna conservation.

Methods

Data analysis

We used the following packages in R 3.5.3 (R Core Team, 2019) for all data manipulation and analyses: 'tidyverse' (Wickham, 2017); spatial analysis: 'adehabitatLT' (Calenge, 2012), 'adehabitatHR' (Calenge, 2006), 'geosphere' (Hijmans et al., 2017), 'maptools' (Bivand and Lewin-Koh, 2017), 'raster' (Hijmans and van Etten, 2018), 'rgeos' (Bivand, 2018), 'sp'

(Pebesma, 2018), 'sf' (Pebesma, 2018), and 'spatstat' (Baddeley, 2015); and visualization: 'ggplot2' (Wickham et al., 2018), 'scales' (Wickham and Seidel 2015), 'smoothr' (Strimas-Mackey, 2018).

Animal tracking data

We collected a large tracking dataset of targeted species that represented the breadth of movement patterns in high mobile marine megafauna across taxa. To do this, we gathered 43 tracking datasets from 36 species across five major taxonomic groupings of marine megafauna (elasmobranchs, cetaceans, pinnipeds, seabirds, and sea turtles) between 2001–2018 and from four of the planet's five major oceans and a few minor seas, gulfs, and channels (Figure 1; Table 1). Bony fishes were excluded due to the lack of datasets with spatial resolution that matched the rest of the dataset (e.g., bony fish locations are primarily derived from geolocation calculations vs. satellite-derived locations). Location data were obtained from species equipped with Argos satellite-linked ($n=25$

species), GPS ($n=12$ species), a combination of GPS+geolocation (GLS) ($n=1$ species), or GLS-only ($n=1$ species) tracking devices. Three species (Laysan [Phoebastria immutabilis], black-footed [P. nigripes], and short-tailed [P. albatrus] albatross) were tracked with both Argos and GPS devices, and one species (basking sharks [Cetorhinus maximus]) was tracked with Argos and GLS+GPS devices. Methodological details on specific deployments are available for most tracking datasets in previously published work (Supplemental Table S1); however, if not previously described, we provide additional deployment details in Supplemental Table S1.

Nearly all datasets were filtered and processed as described in published work (Supplemental Table S1). In brief, locations from Argos transmitters were processed through various state-space or non-state-based random walk models (Jonsen et al., 2005; Johnson et al., 2008; Tremblay et al., 2009); both types of methods provided robust estimates of animal tracks by linking mechanistic movement models with observation error. Location data estimated from geolocation (GLS) contain large spatial errors

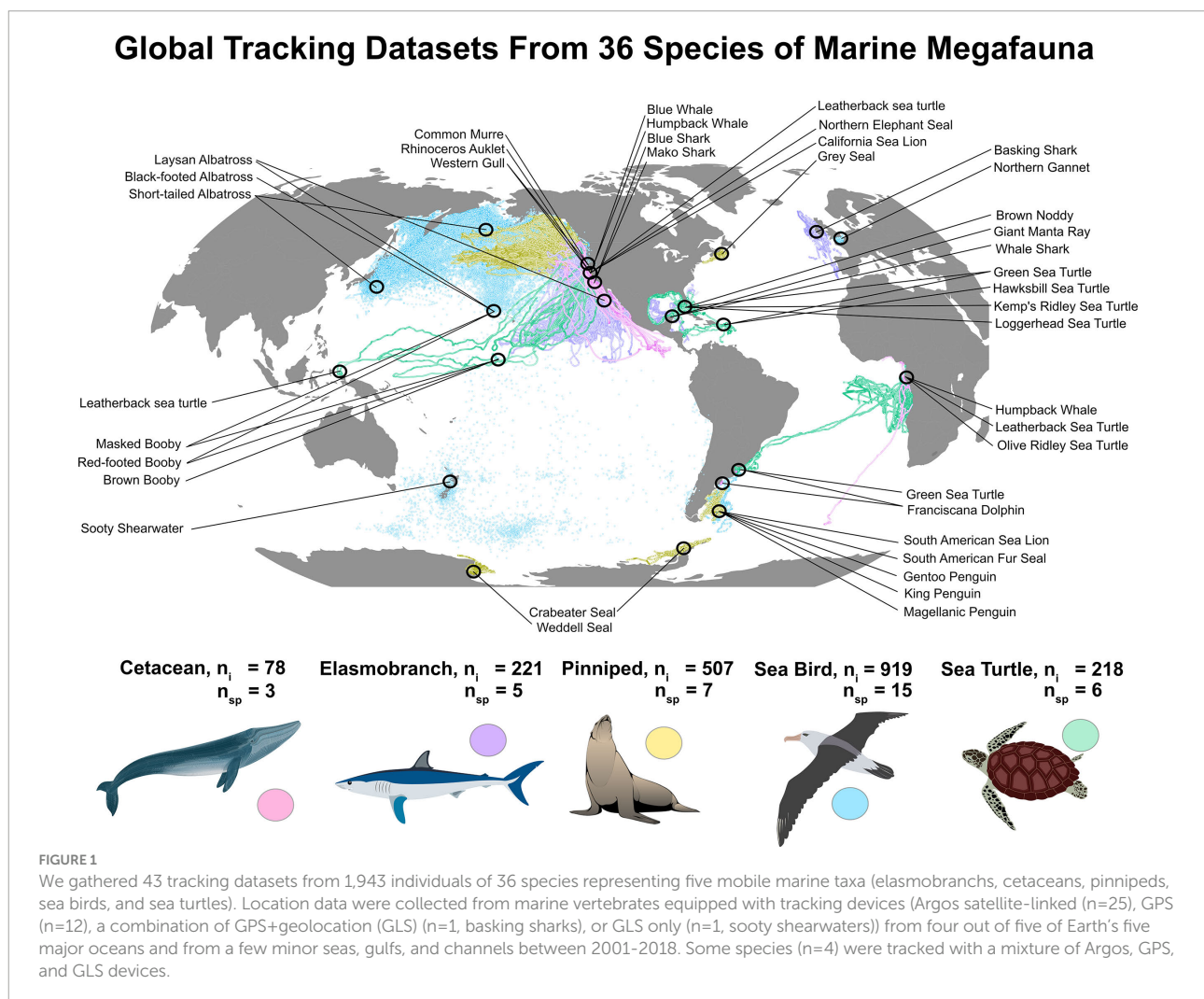


TABLE 1 Overview of 43 tracking datasets from 36 marine megafauna species.

					Deployment Duration (Days)	
Common name	Species name	Tagging site	n	Years	Range	Mean ± SD
Elasmobranchs						
Basking Shark	<i>Cetorhinus maximus</i>	Scotland	43	2012:17	12 – 420	169 ± 130
Blue Shark	<i>Prionace glauca</i>	USA	69	2004:12	9 – 737	109 ± 105
Giant Manta Ray	<i>Manta birostris</i>	Belize	4	2010	8 – 66	36 ± 24
Mako Shark	<i>Isurus oxyrinchus</i>	West Coast USA	82	2003:16	43 – 1176	372 ± 252
Whale Shark	<i>Rhincodon typus</i>	Belize	23	2013:15	6 – 276	143 ± 68
Cetaceans						
Blue whale	<i>Balaenoptera musculus</i>	West Coast USA	37	2004:07	6 – 504	112 ± 101
Franciscana dolphin	<i>Pontoporia blainvillei</i>	Argentina	15	2006:10	7 – 257	95 ± 73
Humpback whale ¹	<i>Megaptera novaeangliae</i>	West Coast USA ¹	13	2004:06	3 – 108	50 ± 29
Humpback whale ²	<i>Megaptera novaeangliae</i>	W Africa – Gabon ²	13	2002	16 – 102	42 ± 28
Pinnipeds						
California sea lion	<i>Zalophus californianus</i>	West Coast USA	105	2003:09	3 – 126	45 ± 24
Crabeater seal	<i>Lobodon carcinophagus</i>	Antarctic Peninsula	44	2001:02, 07	5 – 189	73 ± 52
Grey Seal	<i>Halichoerus grypus</i>	Sable Island	30	2009:10, 13	58 – 1222	136 ± 215
Northern elephant seal	<i>Mirounga angustirostris</i>	West Coast USA	245	2003:15	6 – 296	125 ± 71
South American fur seal	<i>Arctocephalus australis</i>	Falkland Islands	13	2015	39 – 179	123 ± 44
South American sea lion	<i>Otaria flavescens</i>	Falkland Islands	48	2011:17	1 – 90	18 ± 23
Weddell seal	<i>Leptonychotes weddellii</i>	Ross Sea	22	2011	56 – 314	234 ± 68
Seabird						
Black-footed albatross	<i>Phoebastria nigripes</i>	Tern Island	108	2006:12	1 – 29	8 ± 7
Brown booby	<i>Sula leucogaster</i>	Palmyra Atoll	9	2010	<1 – 1	1 ± 0.4
Brown noddy	<i>Anous stolidus</i>	Dry Tortugas	10	2016	<1 – 7	4 ± 2
Common murre	<i>Uria aalge</i>	Oregon coast	22	2015:17	8 – 128	60 ± 38
Gentoo penguin	<i>Pygoscelis papua</i>	Falkland Islands	25	2014:15	6 – 92	49 ± 28
King penguin	<i>Aptenodytes patagonicus</i>	Falkland Islands	8	2011	23 – 138	67 ± 36
Laysan albatross ¹	<i>Phoebastria immutabilis</i>	Guadalupe Island ¹	118	2003:06	1 – 24	5 ± 4
Laysan albatross ²	<i>Phoebastria immutabilis</i>	Tern Island ²	105	2006:12	1 – 30	10 ± 8
Magellanic penguin	<i>Spheniscus magellanicus</i>	Falkland Islands	28	2014:16	3 – 86	32 ± 23
Masked booby ¹	<i>Sula dactylatra</i>	Palmyra Atoll ¹	21	2008:10	<1 – 1	1 ± 1
Masked booby ²	<i>Sula dactylatra</i>	Tern Island ²	44	2009:12	<1 – 1	0.4 ± 1
Northern Gannet	<i>Morus bassanus</i>	Alderney	61	2011:15	<1 – 10	5 ± 3
Red-footed booby ¹	<i>Sula sula</i>	Palmyra Atoll ¹	32	2007:10	<1 – 1	0.8 ± 0.3
Red-footed booby ²	<i>Sula sula</i>	Tern Island ²	31	2009:12	<1 – 2	0.7 ± 1
Rhinoceros auklet	<i>Cerorhinca monocerata</i>	CA coast	29	2014:17	1 – 5	2 ± 1
Sooty shearwater	<i>Ardena grisea</i>	New Zealand	27	2005:06	210 – 624	281 ± 78
Short-tailed albatross	<i>Phoebastria albatrus</i>	Japan, Alaska	89	2002:15	28 – 1750	228 ± 301
Western gull ¹	<i>Larus occidentalis</i>	California coast ¹	100	2013:17	<1 – 3	1 ± 1
Western gull ²	<i>Larus occidentalis</i>	Oregon coast ²	52	2015:18	<1 – 23	7 ± 7
Sea turtle						
Green sea turtle ¹	<i>Chelonia mydas</i>	Argentina ¹	9	2008:11	65 – 360	198 ± 97
Green sea turtle ²	<i>Chelonia mydas</i>	Florida ²	36	2009:17	41 – 421	189 ± 95
Hawksbill sea turtle	<i>Eretmochelys imbricata</i>	Caribbean	33	2011:17	69 – 1030	383 ± 228
Kemp's ridley sea turtle	<i>Lepidochelys kempii</i>	Texas and Mexico	10	2003:15	153 – 1554	616 ± 404
Leatherback sea turtle ¹	<i>Dermochelys coriacea</i>	CA, Indonesia ¹	16	2004:08	45 – 947	273 ± 233
Leatherback sea turtle ²	<i>Dermochelys coriacea</i>	W Africa – Gabon ²	17	2005:09	27 – 414	183 ± 127
Loggerhead sea turtle	<i>Caretta caretta</i>	Caribbean	61	2008:18	37 – 922	252 ± 209
Olive Ridley sea turtle	<i>Lepidochelys olivacea</i>	W Africa – Gabon	36	2007:16	21 – 413	138 ± 108

Superscripts indicate where two populations of the same species are included from different tagging sites. These superscripts are used in the remaining tables.

that, even after post-processing, can be orders of magnitude greater than those of Argos satellite and GPS data (mean error, in general: 10s to 100s of kilometres (GLS), < 50 kilometres (Argos), and 10s of meters (GPS) (Wilson et al., 2002; Phillips et al., 2004; Shaffer et al., 2005; Dujon et al., 2014)). Thus we limited our inclusion of GLS data to (1) a subset of basking shark tracks (n=13 out of 43 basking shark individuals) that were processed in a robust movement model that corrected GLS locations with a subset of available GPS locations (Doherty et al., 2017), and (2)

a single case study of sooty shearwaters (*Ardena grisea*), with which we evaluated relative, not absolute, change in home range size across an annual cycle.

Location data from colony-based, central-place foragers (e.g., terrestrial breeding seabirds and pinnipeds) can artificially inflate the influence of colony location due to repeated visits to and long times spent on-land at these locations. Our focus was limited to movements at sea, so all locations from central-place foragers that fell within a designated radius from the colony/tagging location

were removed following standard practice (e.g., Maxwell et al., 2016). Radius distances were determined according to spatial error of different tag types and movement characteristics specific to each species and ranged from as low as 0.25 km for brown noddies (*Anous stolidus*) and up to 2 km for albatross species. Resulting tracks were linearly interpolated. Two interpolation schemes were used given the extremely disparate movement rates and trip durations among study taxa. Species that moved rapidly (mean speed > 40 km/hr) and had short duration trips (mean < 8 hours) were interpolated at 10-minute intervals while all other datasets were interpolated to 30-minute intervals (Supplemental Table S1). The smaller interval for high-speed, small-ranged species allowed for a sufficient sample size of locations to enable home range analyses. A handful of species (basking sharks, blue sharks, whale sharks [*Rhincodon typus*], and short-tailed albatross) had large gaps in data (weeks to months) in individual tracks. For gaps greater than a week, we did not interpolate between the contiguous portions of the track to avoid introducing erroneous boundaries in our home range estimates.

Home range utilization distributions

To determine patterns of marine space use, we conducted home range analyses using a gridded utilization distribution (UD) method which resulted in the probability of finding an animal in a defined area within its home range (Millsaugh and Marzluff, 2001; Maxwell et al., 2011; Maxwell et al., 2013). The N% UD is the smallest area in which the pixels of the UD sum to N%, and thus there is a cumulative N% probability of finding the animal within that cell at a random time. Home ranges were defined as the 90% UD to encapsulate the majority of areas visited while excluding spurious movements. Core areas were defined as areas with significant visitation and were quantified as the UD where a curve of total cumulative area used deviated the greatest from random, following Seaman & Powell (1990), indicating the UD contour where space use patterns changed distinctly. Core area UDs varied among datasets and ranged from the 75% – 90% UD depending on how uniform or clumped a population's space use was across the seascape (Table 2 and Supplemental Figure S1). Geo-computation methods were used to compute all distances and areas from animal location data. We used Haversine great circle distances to compute geographical distances on a uniform sphere. UD polygons were transformed to planar coordinates with a Lambert Azimuthal Equal Area projection centred on the mean latitude and mean longitude from each respective dataset when calculating home range and core areas.

Due to the large differences in home range size across datasets, an initial analysis of home range used an adjustable grid size that scaled with the range size of each species' dataset to avoid overly pixelated or smoothed UDs (Supplemental Figure S1). Adjustable grid sizes were equivalent to 5% of the population's median maximum distance (km) from the initial tagging location.

For the initial gridded utilization distribution analysis, dataset-specific adjusted grid sizes ranged from 1.2 km² for the highly resident Franciscan dolphins to 163.3 km² in the extremely vagile leatherback sea turtle. Tracks were normalized before gridded UD analyses to account for variable biases in tracking data (Block et al., 2011; Maxwell et al., 2011; Maxwell et al., 2013). For species with nomadic-type movement patterns and abbreviated tracking data (whales, elasmobranchs, and sea turtles), the unnatural abbreviation of trips due to tag failure or tag loss can result in a positive bias for areas near the tagging location. To correct for this potential bias, we weighted each location by the inverse number of individuals in that dataset who had locations for the same relative duration of their track (Block et al., 2011), which resulted in lower weights in locations close to the initial tagging location. This basic time-weighting scheme was modified using the 85th percentile of track lengths for a given dataset, which minimizes bias in spatial density patterns in datasets with smaller sample sizes (Block et al., 2011). Central-place foragers (pinnipeds and seabirds in our study) incur a different kind of bias since they are often tracked across multiple trips to sea from the breeding colony. This leads to a locational bias in species that exhibit at-sea site fidelity (common in seabird and pinniped species) for which we have a greater number of trips for some individuals. To correct for this potential bias in central place foragers, we weighted each location in an individual's dataset by the inverse number of trips taken by that individual. For species with datasets sourced from different colonies (e.g., different geographic origins) (n=7, Table 1), we calculated UDs separately for each dataset with the exception of Pacific Ocean leatherback sea turtles. Pacific leatherbacks from multiple colonies (tagged in both Papua Barat, Indonesia and the West Coast USA) were pooled into a single dataset, because turtle movements from both tagging origins overlapped across the entire North Pacific basin. Despite these corrections, some bias will still exist based on the region of tagging, however, random sampling of individuals and study regions within tagging studies is often either cost-prohibitive or unfeasible. Thus, the home range estimates we present here largely reflect those of the tagged population, rather than the species as a whole.

Sampling adequacy and final home range classification

To evaluate sampling bias in our home range estimates, we measured how home range area changed within a population with increasing sample sizes (sampling adequacy), following Lascelles et al. (2016) and Soanes et al. (2013). In brief, we selected random individuals starting with a sample size of one, with sample size increasing incrementally by one in each subsequent iteration until reaching the true sample size of the dataset. From the 'selected' individuals, we calculated the area (km²) of the 90% UD using the gridded utilization distribution method described above. For each iteration of sample size, we repeated this calculation 100 times,

TABLE 2 Home range sizes and percent of home range and core areas that overlap with existing MPAs.

Species	% Rep	Home range (90% UD)	Home range size class	Home range adjusted (km ²)	Core UD %	Core area (km ²)	90% UD overlap with MPAs	Core area overlap with MPAs
Elasmobranchs								
Basking Shark	71.8	532,614	Large	742,000	85	438,831	<1	<1
Blue Shark	69.1	3,031,888	Vast	4,388,000	80	2,338,647	4.0	2.6
Giant Manta Ray	45.0	2,120	Localized	4,700	85	1,771	7.5	9.2
Mako Shark	83.0	3,655,865	Vast	4,405,000	80	2,053,393	2.2	2.3
Whale Shark	55.0	443,547	Large	806,000	85	358,100	4.4	4.4
Cetaceans								
Blue whale	74.3	1,421,101	Vast	1,913,000	75	564,335	6.5	7.1
Franciscana dolphin	85.7	1,271	Localized	1,500	85	955	45.0	49.7
Humpback whale ¹	67.5	157,398	Large	233,000	75	65,389	15.4	27.3
Humpback whale ²	57.4	393,695	Large	685,000	80	288,547	<1	<1
Pinnipeds								
California sea lion	79.1	39,963	Intermediate	51,000	85	27,312	27.5	37.5
Crabeater seal	80.1	168,032	Large	210,000	85	137,021	0	0
Grey Seal	63.8	30,749	Intermediate	48,000	85	20,285	<1	0
Northern elephant seal	91.9	4,185,068	Vast	4,553,000	85	3,549,548	<1	<1
South American fur seal	51.1	243,196	Large	476,000	85	200,195	<1	0
South American sea lion	78.2	18,623	Intermediate	24,000	85	15,122	<1	0
Weddell seal	89.2	80,473	Intermediate	90,000	85	63,169	85.9	81.6
Seabird								
Black-footed albatross	73.0	3,390,952	Vast	4,645,000	80	2,113,718	11.8	15.0
Brown booby	60.9	1,976	Localized	3,200	75	1,000	100	100
Brown noddy	80.1	686	Localized	860	75	191	63.8	99.5
Common murre	77.6	40,597	Intermediate	52,000	85	31,720	14.1	18.1
Gentoo penguin	63.2	63,078	Large	100,000	80	42,264	0	0
King penguin	47.0	83,352	Intermediate	177,000	75	40,443	0	0
Laysan albatross ¹	81.2	1,298,333	Vast	1,599,000	80	728,585	1.3	2.4
Laysan albatross ²	75.9	3,598,897	Vast	4,742,000	80	2,387,119	9.8	12.3
Magellanic penguin	59.4	331,845	Large	559,000	80	221,466	1.0	1.5
Masked booby ¹	68.6	1,851	Localized	2,700	75	1,025	100	100
Masked booby ²	65.8	9,691	Intermediate	15,000	75	5,587	100	100
Northern Gannet	78.4	28,946	Intermediate	37,000	85	24,605	<1	<1
Red-footed booby ¹	70.3	10,509	Intermediate	15,000	80	6,905	83.7	97.2
Red-footed booby ²	61.4	19,520	Intermediate	32,000	80	13,741	100	100
Rhinoceros auklet	73.8	2,304	Localized	3,100	85	1,799	61.5	59.7
Sooty shearwater*	NA	NA	NA	NA	NA	NA	NA	NA
Short-tailed albatross	88.4	7,960,168	Vast	9,005,000	80	4,618,044	<1	<1
Western gull ¹	81.6	4,309	Localized	5,300	80	2,420	77.0	70.7
Western gull ²	70.1	1,280	Localized	1,800	90	1,280	0	0
Sea turtle								
Green sea turtle ¹	67.9	159,934	Large	236,000	80	107,946	<1	<1
Green sea turtle ²	83.5	4,651	Localized	5,570	85	2,488	52.4	61.3
Hawksbill sea turtle	31.3	18,964	Intermediate	61,000	90	18,964	1.9	2.6
Kemp's ridley sea turtle	53.4	54,617	Large	102,000	85	42,191	8.7	5.4
Leatherback sea turtle ¹	46.9	5,637,946	Vast	12,021,000	75	3,388,007	2.9	2.7
Leatherback sea turtle ²	49.9	1,456,521	Vast	2,919,000	70	459,271	1.6	<1
Loggerhead sea turtle	38.7	21,948	Intermediate	57,000	90	21,948	14.2	13.1
Olive Ridley sea turtle	75.0	326,577	Large	435,000	80	217,086	6.1	8.0

The sooty shearwater dataset was excluded from home range analyses due to poor resolution location data from GLS devices and was only included in the case study of the influence of annual cycle on home range, where we evaluated relative change in size rather than absolute home range size. The extent to which home range calculated from each tracking dataset represented its estimated population home range is given as '% Rep' (see 'sampling adequacy' in methods). 'Adjusted Home Range' was derived from adjusting the calculated home range of each dataset with its respective percent representation of the population (% Rep). The overlap of home ranges and MPAs (90% UD MPA Overlap and Core MPA Overlap) was calculated as the proportion of a species range within MPA boundaries in geographic space. Superscripts are used when two populations of the same species are included from different tagging sites; the tagging sites can be found in Table 1.

with a different set of randomly selected individuals. For central place foragers with individuals tracked across multiple trips, we selected a single trip (that with the largest maximum range) per individual for this analysis. A nonlinear regression fitting home

range area as a function of $n/n+1$ (n =sample size) was then used to estimate how representative the tracking dataset was to its population (Supplemental Figure S2). We approximated the nonlinear fit to a sample size of 100 individuals and calculated

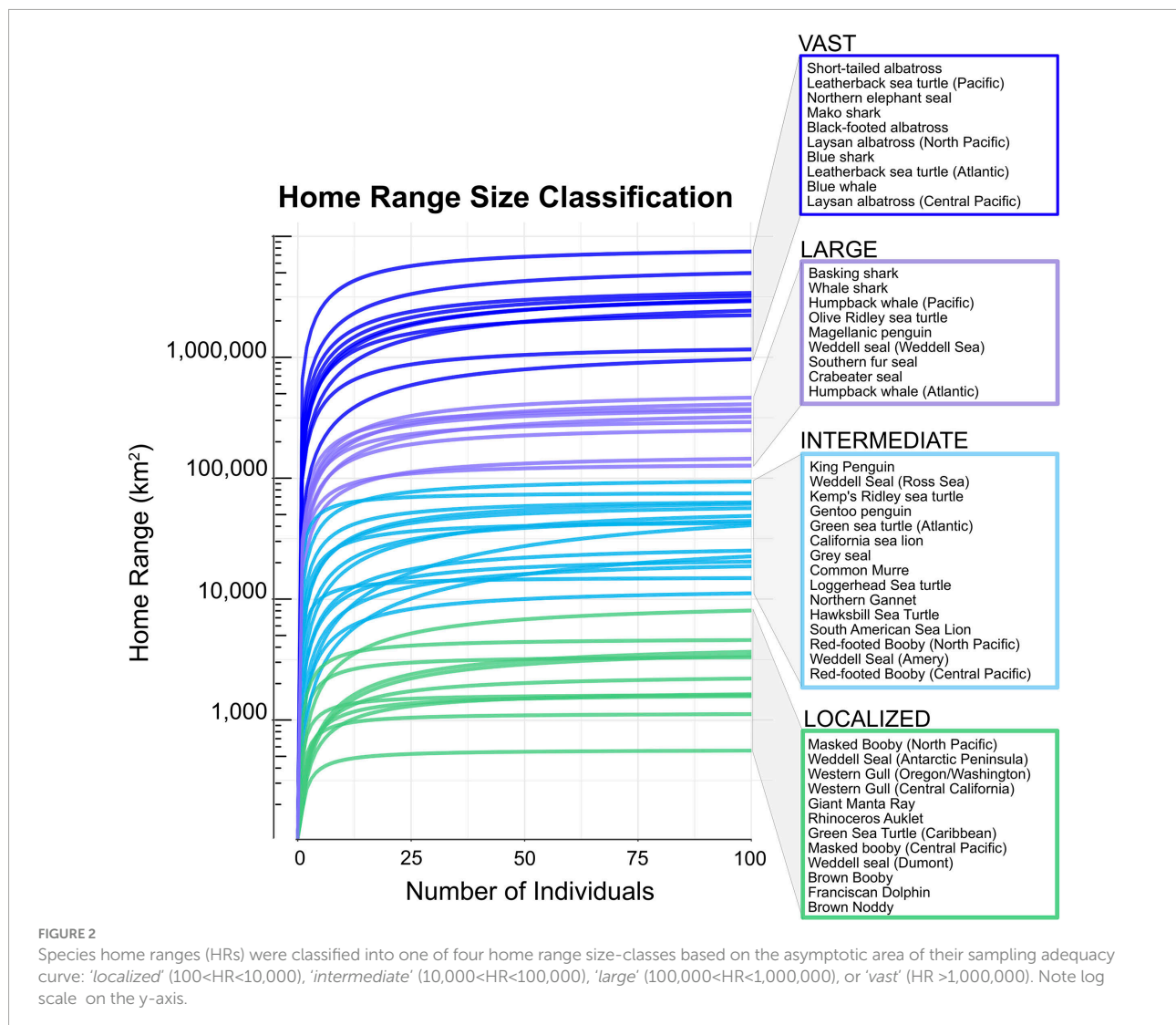
the ratio of the home range area estimated from the true sample size to the home range area of 100 individuals estimated by the ensuing function. The resulting percentage conveyed the degree of sampling bias in home range estimates and was used to evaluate both the robustness of each dataset also as a correction factor to adjust home range size estimates by multiplying the original home range area with the correction factor fraction (Table 2 and Supplemental Figure S2).

Nonlinear regression functions were used to visualize and define home range size classes. These functions were calculated separately for each species' dataset, and then visualized together on a single axis in log-scale (Figure 2). We did not observe distinct groupings of home range size in the aggregated plot, so we defined four home range size classes by order of magnitude, as the following: 'localized' (0–10,000 km²), 'intermediate' (10,000–100,000 km²), 'large' (100,000–1M km²), and 'vast' (> 1M km²). Final home ranges, and final core areas, were calculated

for all datasets using a grid size defined by the home range size class of each dataset. We used 5, 10, 25, and 50 km² grids for 'localized', 'intermediate', 'large', and 'vast' home range size classes, respectively. One exception was made for Pacific leatherback sea turtles (*Dermochelys coriacea*) which required a larger grid size (75 km²) than all other species because of their expansive, trans-ocean basin movements.

Spatial scales of global MPAs and highly mobile marine megafauna

MPA boundaries and metadata were sourced from the 'Atlas of Marine Protection' database (www.mpatlas.org) maintained by Marine Conservation Institute, accessed June 2018. Although this database is derived from the Protected Planet database at the United Nations Environment World Conservation Monitoring



Centre, it is specific to marine protected areas and subjected to more rigorous quality control than the Protected Planet database (www.protectedplanet.net) in determining if areas meet IUCN guidance for an MPA (Morgan et al., 2018). We limited our dataset to those MPAs defined as ‘designated’ and ‘implemented’ by the ‘Atlas of Marine Protection’ (Morgan et al., 2018). Boundaries of current MPAs less than 100 km² in size were excluded from analyses because 100 km² was smaller than the smallest core area across all species (brown noddies: 191 km²) and would have negligible impacts on results, and because the vast majority of MPAs were < 100km², a spatial scale minimally relevant to that of highly mobile marine megafauna core and home ranges. We acknowledge that MPAs even as small as < 100km² may influence megafauna protection, particularly those that may target specific critical threats within populations that occur on smaller spatial scales; however, our broader-scale objectives required a focus on larger MPA boundaries. The boundaries of MPAs that were contained within another MPA, or had a boundary immediately adjacent to another MPA, were merged, so that one size was calculated for contiguous MPAs. This resulted in 456 discrete MPA polygons for analysis. To conceptualize the global congruence between MPA size and marine megafauna space use, binned distributions of global MPA sizes (km²) were used to quantify the percentage of MPAs large enough to encompass home ranges of highly mobile marine megafauna in each home range size class.

Overlap of megafauna community aggregate home ranges with MPA networks

To evaluate overlap between megafauna communities and MPAs in real space and time, we isolated three regions in our dataset where communities of tracked megafauna species co-occurred with networks of MPAs: (i) the U.S. West Coast National Marine Sanctuary complex (USNMS) where MPAs overlapped with 12 tagged species; (ii) the confluence of the Gulf of Mexico and the Caribbean Sea (GOM) where MPAs overlapped with 6 tagged species; and (iii) the Pacific Remote Islands (PRI) where MPAs overlapped with 6 tagged species. In these regions, a community-aggregate UD was calculated from merged tracking data following methods of Maxwell et al. (2013) and overlap between individual and community-aggregate UDs and MPA boundaries was calculated. To define core areas of species aggregates, we used the 50% UD contour since individual species display different distribution patterns and core area UD thresholds calculated within individual species varied. We summed the UDs within each cell across all species, and then normalized the summed layer by maximum UD values across all cells. UDs were weighted by multiplying the grid value by the number of species that occurred in each cell to emphasize regions of greater species overlap. We then calculated the percentage of

home range and core areas that occurred within and outside the boundaries of any MPA that overlapped with the range of the species aggregate.

The influence of the annual cycle and Life history on spatial scales of protection

To evaluate the influence of seasonal cycles and discrete population subsectors (e.g., sex and age classes) on megafauna movement patterns, we targeted a subset of datasets (n=14 species) that represented multiple taxa and that contained sufficient tracking data from enough individuals across population subsectors or seasonal cycles (Supplemental Table S2). For central place foragers (albatrosses, gulls, auklets, penguins, sea lions) we identified individuals with tracking data from different parts of the breeding cycle (e.g. incubation, brood-guard, chick-rearing, post-breeding in albatrosses). A single central-place forager dataset (sooty shearwater) was composed of tracking data from individuals that spanned an entire annual cycle: breeding (Nov–Mar), the spring migration (Apr–May), moulting/post-breeding grounds (May–Sep), and the fall migration (Sep–Oct). For non-central-place foragers (sea turtles, elephant seals, and whales), the metrics ‘residence time’ and ‘day of year’ were used to determine nesting/interesting movements (sea turtles only) versus migrating movements (low residence time) versus foraging movements (high residence time). Residence time is a scale-dependent metric that imposes a virtual circle with a user-defined radius over each consecutive location and sums the time spent along all track segments within the circle, both forward and backward (Barraquand and Benhamou, 2008). Residence time was calculated using a 50 km radius and a maximum time outside the circle of 24 hours. Tracks were interpolated to 1 point a day and transformed to a Lambert’s Equal Area projection before residence time analysis. For elephant seals that forage continuously along their migrations to their core feeding grounds (Robinson et al., 2010; Robinson et al., 2012b), ‘high’ residence time was considered to be the top 30th percentile of all residence time values; for whales and turtles that have a more discrete migration before exhibiting more localized movements, ‘high’ residence time was considered to be the top 50th percentile of all residence time values. Once datasets were divided into different life history segments, we ran the gridded utilization distribution analysis to determine home range and core area of species under different sex, age, and seasonal conditions. For all species, except for sooty shearwaters (due to a spatial resolution limitation), we then calculated the percentage of current MPAs that were theoretically large enough to encompass the core area of a population across different life history conditions. For all but sooty shearwaters, core areas were used to highlight the times and places where marine megafauna distributions aggregate and are thus, in theory, more feasible to protect spatially. Individual home ranges, rather than core areas, were used in the sooty shearwater

case study to emphasize dramatic seasonal changes in the overall space use of individuals.

Results

Animal tracking data and home ranges

In total, our study included 1,709,042 raw locations from 1,943 individuals and 36 species in 43 population-level datasets, ranging from 78°S to 66°N latitude and over 220 degrees of longitude (Figure 1, Table 1). Seabirds were the most extensively represented taxa (15 species; 919 individuals; average track length: 40 d \pm 79), followed by pinnipeds (7 species; 507 individuals; average track length: 108 d \pm 72), sea turtles (6 species; 218 individuals; average track length: 279 d \pm 156), elasmobranchs (5 species; 221 individuals; average track length: 166 d \pm 126), and cetaceans (3 species; 78 individuals; average track length: 75 d \pm 34). Estimated megafauna home ranges varied from <1,000 km² for breeding brown noddies (*Anous stolidus*) to just over 12,000,000 km² for Pacific leatherback sea turtles (*Dermochelys coriacea*) (Table 2).

Spatial scales of global MPAs and highly mobile marine megafauna

Less than 1% of all existing MPAs were large-scale MPAs (>100,000 km²). Indeed, the vast majority (n=8,788, 86.8%)

were considered too small (< 100 km²) to be relevant to the scale of mobile marine megafauna ranges and were subsequently excluded. Our final MPA dataset of 456 MPA boundaries ranging in size from 100 km² (Pensacola Bay, USA) to 1,513,723 km² (Ross Sea Protected Area, Antarctica), with a median size (5th percentile, 95th percentile) of 727 km² (130, 93626). After excluding MPAs < 100 km², 43% of MPAs were large enough to encompass localized species ranges while only 12, 5, and 1% were large enough to encompass the home ranges of intermediate-, large-, and vast-ranging species, respectively (Figure 3). Home ranges of megafauna community aggregates overlapped minimally (< 5%) with their associated MPA networks. Home range overlap was <1, 4, and 1%, for the USNMS, GOM, and PRI, respectively (Figure 4). These small levels of overlap were primarily driven by the occurrence of large- and vast-ranging species in each region. While community-level MPA overlap was low, MPA overlap of many individual species was high (Figure 4 inlaid barplot, Table 2).

The influence of the annual cycle and life history on spatial scales of protection

Movement patterns often changed markedly with season, sex, and life stage in some cases resulting in marked expansion or contraction of home range size (Figure 5, Supplemental Table S2). The most pronounced change in the congruence of spatial scales of MPAs and home ranges was that for olive ridley sea turtles (*Lepidochelys olivacea*), where > 50% of existing MPAs

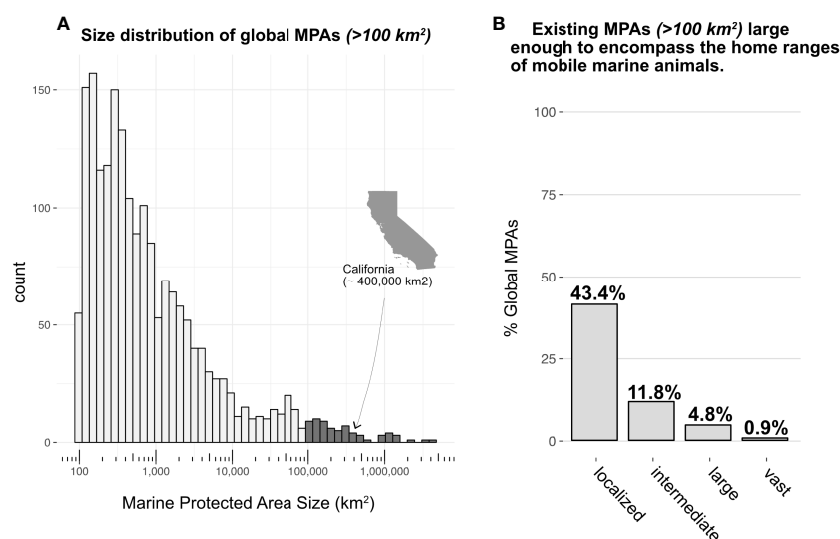
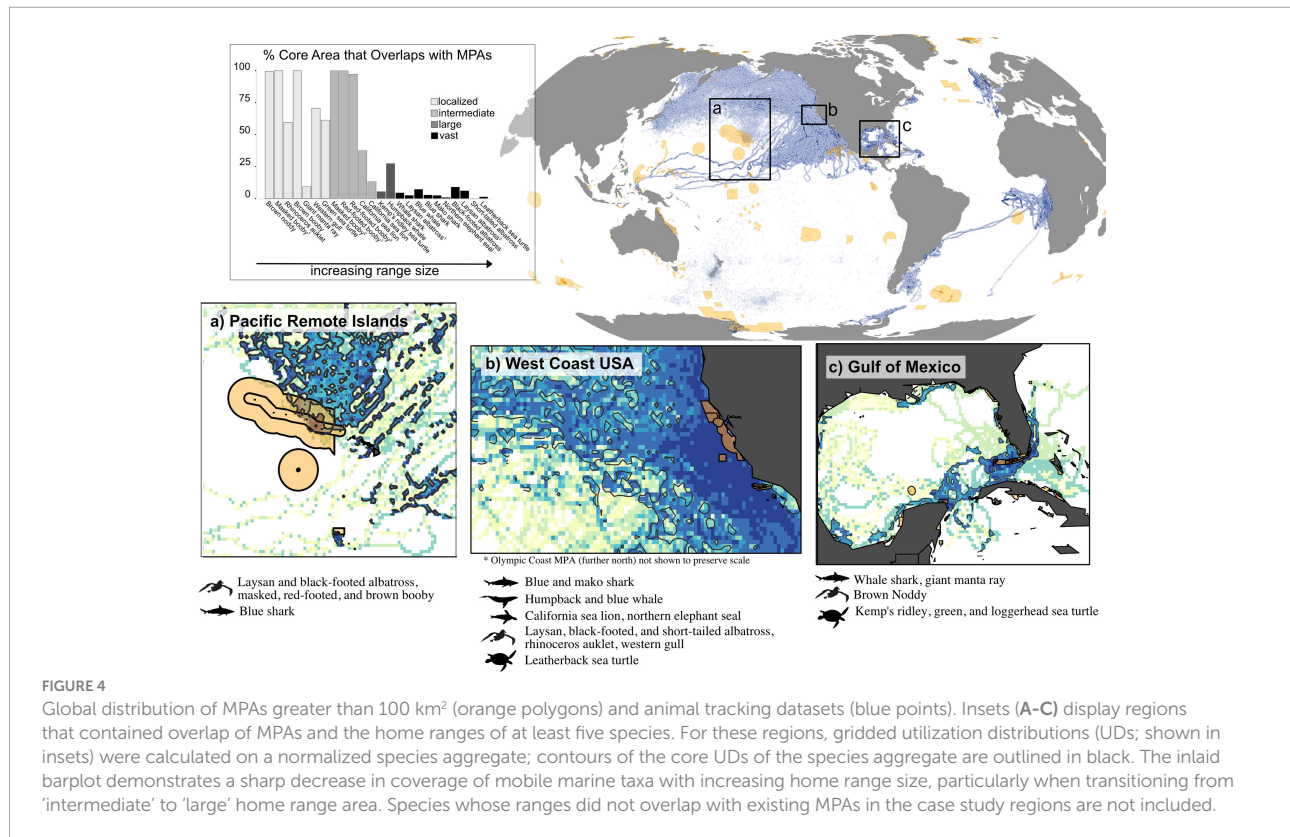


FIGURE 3

Size distributions of existing marine protected areas relative to home range sizes of mobile marine species. Less than 1% of all existing MPAs of all sizes (including those < 100 km² – not shown in histogram) can be classified as large MPAs (greater than 100,000 km², dark grey shading, (A); California is included as a point of reference for size for large MPAs. Excluding MPAs that are less than 100 km², just over 43% of remaining MPAs were large enough to encompass the home ranges of 'localized' species, but MPA coverage dropped off rapidly for species with 'intermediate', 'large', and 'vast' home ranges (B).



were large enough to encompass turtle core areas during nesting, compared to only 5% of MPAs during migration and only 8% while turtles were on their feeding grounds. The influence of life stage, season, and sex on other datasets was highly variable, and in general, less pronounced than seen in olive ridley sea turtles. For some species (e.g., elephant seals, short-tailed albatross), the potential for spatial protection through MPAs remained low across sexes, seasons, and life stages (Figure 5).

Discussion

MPAs and marine megafauna conservation at scale

Despite the recent global increase in large MPAs, there remains a considerable mismatch between the size of marine areas used by megafauna species and the size of marine areas managed for biodiversity protection. For these highly mobile species, size does indeed matter; however, MPA size quickly hits a ceiling of what is practical and affordable to implement. For example, in the Papahānaumokuākea Marine National Monument (PMNM), one of the largest MPAs worldwide, the home ranges of three intermediate-ranged breeding seabird species were nearly fully enclosed in protected waters (Figure 4 inlaid barplot, Table 2). Nonetheless, this expansive MPA with a footprint greater than 1.5 million km², remained too small to provide much at-sea

protection for the two vast-ranging albatross species that breed there, despite protection of critical seabird habitat being cited as part of the designation of this MPA (Executive Office of the US President, 2016).

While this would seem to bode poorly for the utility of MPAs in the conservation and management of megafauna, more nuanced considerations suggest that MPAs can have an important role. For example, while PMNM alone did not provide significant at-sea protection for black-footed albatross, this species was additionally found in the West Coast National Marine Sanctuary network, an important foraging destination, which includes some protections for seabirds as part of its regulations (NOAA, 2008). These MPAs are separated by half an ocean but combined they overlapped with 11.8% of the albatross's total home range, and 15.0% of their core area, a sizable amount for a species with a total home range of over 4 million km² (Table 2). Despite this, many black-footed albatross breeding populations additionally depend on habitats that fall under the sovereignty of Japan and Russia, as well as international waters, exemplifying that cooperation within and among nations may be necessary for successful conservation outcomes for some wide-ranging species (Harrison et al., 2018; Beal et al., 2021; Davies et al., 2021a).

Not all marine megafauna move at this basin-level scale, however, and over 40% of existing MPAs would be large enough to encompass the entire home ranges of localized species, for

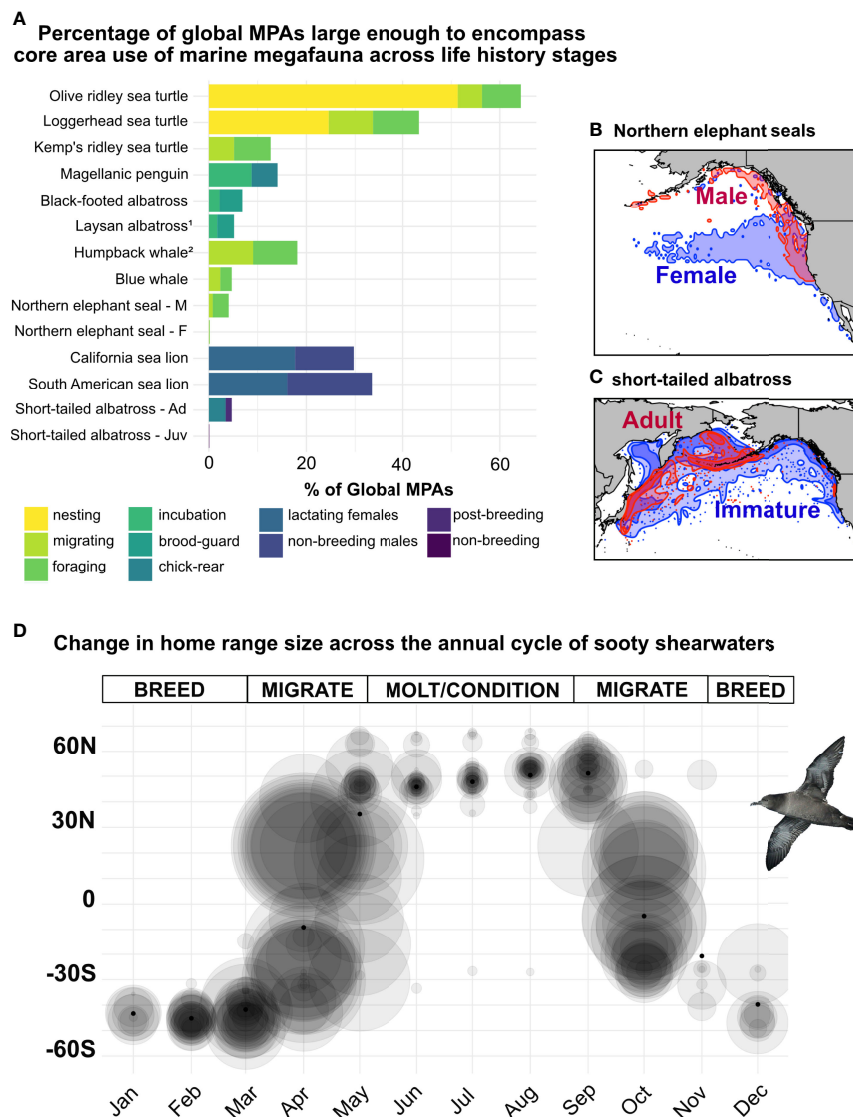


FIGURE 5

Tracking datasets from fifteen species demonstrate how the size distribution of current MPAs relates to the potential spatial protection of marine megafauna species under different sex, age, and seasonal contexts (panel A). Male northern elephant seals strictly forage along the northeast perimeter of the North Pacific Ocean, along the continental shelf, while females primarily target the pelagic North Pacific Transition Zone, far offshore (panel B). Immature short-tailed albatrosses are far more pelagic than their adult conspecifics, resulting in larger home range and core use areas (panel C). The annual cycle of sooty shearwaters includes vast trans-equatorial migrations in which birds travel from breeding grounds in the high latitudes of the south Pacific to their foraging and molting grounds in high latitudes of the North Pacific in the boreal summer (panel D) (Shaffer et al., 2006). Individual shearwater home ranges are plotted, by month, as a transparent grey circle whose radius was scaled to home range size; each individual home range circle was overlaid monthly with their position on the y-axis displaying the average monthly latitude of that individual. Mean latitude of all shearwaters was overlaid on each month as a black dot. ¹ Tagging Site, Tern Island; ² Tagging Site, West Coast USA.

example masked boobies (*Sula dactylatra*) and Franciscana dolphins (*Pontoporia blainvillei*). This suggests that with proper placement and appropriate management measures, single, ‘average-sized’ MPAs could still play an important role in the conservation of some megafauna populations. Indeed, developing and enforcing protected areas and no-take zones are among the priority actions in the International Whaling Commission’s conservation management plan for Franciscana dolphins (IWC,

2016). Furthermore, the potential for comprehensive inclusion in protected MPA waters isn’t wholly limited to localized populations. Nearly 12% of existing MPAs are large enough to encompass the home ranges of intermediate-ranged species and there are some MPAs large enough encompass the home ranges of even large-and vast-ranged species (Figure 3). However, a clear incongruence in the sizes of megafauna home range and existing MPAs becomes plainly evident around spatial scales greater than 10,000 km².

Placement and connectivity of MPAs for marine megafauna

Placement of MPAs is critical for their effectiveness; and, when done effectively, MPAs can support even large-ranged species. For example, U.S. National Marine Sanctuaries encompassed nearly 30% of the core area of large-ranged humpback whales (*Megaptera novaeangliae*) in stark contrast to large-ranged Kemp's ridley sea turtles (*L. kempii*), whose core areas overlapped less than 5% with the MPA network in the Gulf of Mexico (Figure 4). Even with suitable placement, potential for overlap with MPAs may remain minimal for those species with vast ranges. For example, movements of Pacific blue whales (*Balaenoptera musculus*) paralleled the west coast of the US, as did nearby MPAs, but their core areas only overlapped with these MPAs by only 7% (Table 2). Thus, even for species with movement patterns amenable to protection (e.g., those that parallel coastlines and thus are within national waters), the spatial scale of their movements – even core areas – may be well beyond that of most available MPAs, though international collaboration may aid in protection.

This underscores the importance of identifying critical habitats throughout annual cycles and understanding migratory connectivity of populations for effective area-based conservation measures for marine megafauna (e.g., Dunn et al., 2019). Networks of MPAs have been shown to be effective for less mobile species, particularly fishes (Gaines et al., 2010), and may similarly prove effective for megafauna because many, if not most, large- and vast-ranged species aggregate seasonally and by life stage, sex, or season, and these aggregations that occur at smaller spatial scales have greater potential to benefit from MPAs (Hooker et al., 2011; Carneiro et al., 2020). For instance, the average individual home range of sooty shearwaters was 80% smaller during the vulnerable moulting period and 50% smaller during the breeding period than during peak trans-equatorial migrations (Figure 5D). Spatial protection can be particularly effective for central-place foragers that return repeatedly to the same location (Table 2) (Young et al., 2015; Maxwell et al., 2016; Handley et al., 2020; Gilmour et al., 2022). Across taxa, ranges typically contracted during breeding seasons (Figure 5A), increasing the capacity for spatial protection during this critical life stage. For example, the highly restricted ranges of nesting sea turtles are in strong contrast to their long post-breeding migratory journeys (Witt et al., 2011; Dawson et al., 2017). Indeed, over half the core area of nesting olive ridley turtles in this study overlapped with MPAs in Gabonese waters, likely a direct result of both their smaller ranges during this life stage and that their tracking data was explicitly incorporated into the MPA siting process with the Gabonese government (Maxwell et al., 2011; Dawson et al., 2017; Hays et al., 2019; Metcalfe et al., 2022). Conservation impacts from MPAs may compound when there is potential to protect multiple species during critical life history stages, such as in the Gulf of Mexico where loggerhead (*Caretta caretta*), green (*Chelonia*

mydas), and hawksbill sea turtles (*Eretmochelys imbricata*) were found to select for areas within protected boundaries while transiting and foraging, despite having alternate habitat available to them (Roberts et al., 2021).

Similarly, age-classes and sexes within populations may also translate into varying capacity for area-based conservation. This may be particularly relevant to conservation planning when sub-sectors act as bottlenecks in population recovery or stability (Crouse et al., 1987). For example, male northern elephant seals (*Mirounga angustirostris*) primarily ranged along the continental shelf, close to coastal waters, and thus may be easier to protect through area-based conservation measures than their highly pelagic female counterparts (Figure 5B) (Robinson et al., 2012; Kienle, 2022). Similarly, adult short-tailed albatrosses (*P. albatrus*) formed dense aggregations around the continental shelf year-round, while juveniles ranged transiently across the entire North Pacific basin (Figure 5C) (Suryan et al., 2007; Orben et al., 2018). Despite relatively smaller ranges of male seals and adult albatross than their intra-specific counterparts, the spatial scale of these populations still far exceeded that of the majority of existing MPAs (Figure 5A). For many vast-ranged populations, sector-based conservation measures, such as bycatch mitigation policies or increasing prey stocks through sustainable fisheries management, may have a greater impact than area-based measures.

Conservation measures for marine megafauna: Beyond MPAs

A critical consideration is the level of protection afforded by MPAs, as well as what threats they limit, as MPAs vary widely in the protections they offer or enhanced. For example, in the US, 96% of the largest MPAs are highly protected meaning they limit extractive activities, however these occur almost exclusively in remote Pacific regions where extractive activities were limited to begin with (Sullivan-Stack et al., 2022). Additionally, in some cases, populations of the species studied herein are increasing (e.g., northern elephant seals), despite mismatches in scale of MPA protections, suggesting that other, non-MPA management interventions are positively impacting their recoveries. For those species for which area-based measures are a tractable option, MPAs may not confer benefits if they don't (or can't) effectively address key threats to the population. For example, ship strikes are a primary threat to many baleen whale populations, but even highly protected MPAs rarely exclude shipping transport (Wiley et al., 2011), though modifications to shipping lanes or ship speeds have occurred within MPAs (Freedman et al., 2017). Pollution (e.g., plastics, persistent organic pollutants, ghost nets, noise) is another key threat to many marine megafauna populations (Maxwell et al., 2013; Nelms et al., 2021), but the diffusive nature of pollutants often belies MPA boundaries. Despite limitations in the protective capacity of MPAs and the reality that their benefits

will vary across species and regions, area-based conservation measures, including MPAs, have been repeatedly identified as a key strategy for the protection of all marine megafauna taxa presented here (e.g. Scott et al., 2012; Lascelles et al., 2014; Gallagher et al., 2020; Handley et al., 2021; Nelms et al., 2021). As larger MPAs become increasingly common and established, it will become critical to quantify explicit population-level impacts of these MPAs on marine megafauna, as has been done for less mobile species (e.g., Halpern, 2003). This currently remains challenging given the extreme longevity, low intrinsic rates of increase, and a host of issues in effective sampling and population estimation unique to highly mobile megafauna. However, if MPAs provide mechanisms to reduce human impacts and/or strengthen the prey base used by megafauna, a population-level impact is likely. The most effective strategy for most highly mobile marine megafauna species may be a combination of traditional area-based conservation measures (e.g., MPAs) with alternative strategies, such as those that are sector-based and target specific threats across space (e.g., bycatch mitigation techniques, rerouting shipping lanes). Complicating matters, effects of climate change on megafauna distributions and habitat may necessitate an adaptive approach to MPA boundaries through time (Bruno et al., 2018). Dynamic management (Maxwell et al., 2015) or mobile MPAs (Maxwell et al., 2020) may prove to be particularly effective in buffering effects of climate change for marine megafauna, particularly those that require large, dynamic habitats, such as the high seas.

Conclusion

Tracking data, such as those used here, have advanced megafauna conservation around the world, including in the creation of MPAs (Hays et al., 2019). Using tracking data to identify areas of significant importance to multi-species megafauna assemblages in the high seas [e.g., the North Atlantic Current and Evlanov Seamount proposed MPA (Davies et al., 2021b); Areas of Ecological Significance in the Southern Ocean Ecosystem (Hindell et al., 2020)] is becoming more commonplace as data across megafauna species accumulates over time and across regions (Sequeira et al., 2019). Given the wide-ranging nature of most marine megafauna species, a first step for managers and decision-makers in making management decisions to protect marine megafauna is to gather datasets that link spatial data on animal ranges with existing metadata on colony, sex, age, and life stage (Carneiro et al., 2020). Though gathering datasets with this level of detail can be a challenge, large, global databases of aggregated tracking data are multiplying [e.g., Movebank (ca. 2007), MegaMove (ca. 2021)] along with repeated calls for establishing a standardized framework for the collection and aggregation of tracking data to optimize conservation gains (Campbell et al., 2016; Sequeira et al., 2021). It is important to recognize that in this study, our tracking dataset was not exhaustive

and datasets were selected based on availability and on those that, together, represented the range of movement patterns observed across marine megafauna taxa; thus, not all regions or life history stages are represented for all species and taxa. Furthermore, the species and MPAs in this study reflect a diversity of marine systems, human impacts, and conservation strategies; in some cases, MPAs were established with megafauna in mind using the tracking data herein to design MPAs (e.g., Metcalfe et al., 2022), while in other cases megafauna were not included in the planning or justification of MPAs. Our objective was not to consider specific conservation goals of individual MPAs and region/species-specific threats, but rather to: 1) evaluate the agreement or mismatch of spatial scales between global MPAs and those of highly mobile marine megafauna; and, 2) to highlight spatial considerations needed for area-based conservation measures to effectively support highly mobile marine megafauna. Despite some evidence that even large- and vast-ranged species could benefit from MPAs when properly sized, placed, and networked, these findings underscore that MPAs, as currently designed, may not be effective for many megafauna species by virtue of just existing, even if deliberately large. This point is underscored by Mason et al. (2018) who demonstrated that large MPAs in Australia did not necessarily protect critically-endangered albatrosses simply as a result of being large, and rather, performed more poorly at protecting critical habitat than those located randomly.

Data availability statement

All major scripts, functions, utilization distributions (core and home range) for all species and MPA shapefiles used in this study will be available online at https://github.com/melindaconners/megafauna_mpas. Most of the raw tracking datasets are archived in public data repositories and available by request; see **Supplementary Table S1** for database location and dataset IDs. Tracking data will not be made public for some species to protect sensitive information (e.g., species that could be exploited by use of the fine-scale resolution of tracking data), however the utilization distributions for these species are still provided.

Ethics statement

The animal study was reviewed and approved by relevant ethics committee for individual studies of datasets included.

Author contributions

MC conducted analyses and led manuscript creation; MC and SM conceived and executed the study; NS uploaded datasets to various data repositories. All authors contributed data and contributed to the writing and editing of the manuscript.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.897104/full#supplementary-material>.

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Spatiotemporal Overlap of Baleen Whales and Krill Fisheries in the Western Antarctic Peninsula Region

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In Antarctica, abundant consumers rely on Antarctic krill for food, but krill are also the subject of a commercial fishery. The fishery overlaps in time and space with the foraging areas of these consumers, thus potential competition between krill fisheries and krill consumers is a major management concern. The fishery is managed by the Commission for the Conservation of Antarctic Marine Living Resources with an ecosystem approach, according to which fishing should not interfere with either the population growth of krill, or krill-dependent consumers. Krill catches have become increasingly spatially concentrated in a small number of hotspots, raising concerns about how local depletion of krill impacts consumers. Such concentrated fishing demonstrates that there is a mismatch between the spatial and temporal scale at which krill fisheries are currently managed, and that at which fisheries operate and consumers forage. Information on the seasonal dynamics of predator abundance and their foraging behaviour is fundamental to future precautionary management of the krill fishery. We analysed the spatiotemporal distribution of two major krill consumers – humpback and minke whales – and that of krill fishing, off the Western Antarctic Peninsula. We used whale tracking data (58 humpback whale tracks and 19 minke whale tracks) to develop spatial random forest models predicting the monthly distribution of whale foraging areas from January–July. Using these predictions, we calculated spatiotemporally-explicit geographic overlap between whales and fisheries, the latter represented by krill fishing effort and catch data. Over the krill fishing season, fishing effort and catch hotspots shifted to the southwest, into the Bransfield Strait where effort and catch was highest. Predicted humpback whale foraging areas increased in the Bransfield Strait over the same period, while predicted minke whale foraging areas showed an opposite trend. For both we predicted a whale-fishing interaction hotspot in the Bransfield Strait, strongest in April and May. Our results illustrate the fine spatial scale of likely interactions between baleen whales and the krill fishery, and their concentration over the season, underlining the need for fishery management more closely aligned to the spatiotemporal scale of likely predator-fishery interactions.

Keywords: humpback whale (*Megaptera novaeangliae*), Antarctic krill (*Euphausia superba*), Antarctic minke whale (*Balaenoptera bonaerensis*), competition, fishing, tracking

INTRODUCTION

Large marine vertebrates, like marine mammals, frequently occupy high trophic levels and often rely on prey that are also subject to human fishing. Thus, spatial overlap between large marine vertebrates and fishing is apparently widespread (e.g., Queiroz et al., 2019; Hindell et al., 2020), but can be more acute when and where prey are aggregated (e.g., Scales et al. 2018). Fisheries impact large marine vertebrates through direct interactions (targeted or incidental capture, e.g., Lewison et al., 2014) and indirect interactions (provisioning, resource competition, e.g., Grémillet et al., 2018) and potential interactions are consequently a conservation concern for marine top predators as well as for fishery management.

The Antarctic Krill Fishery and Krill Consumers

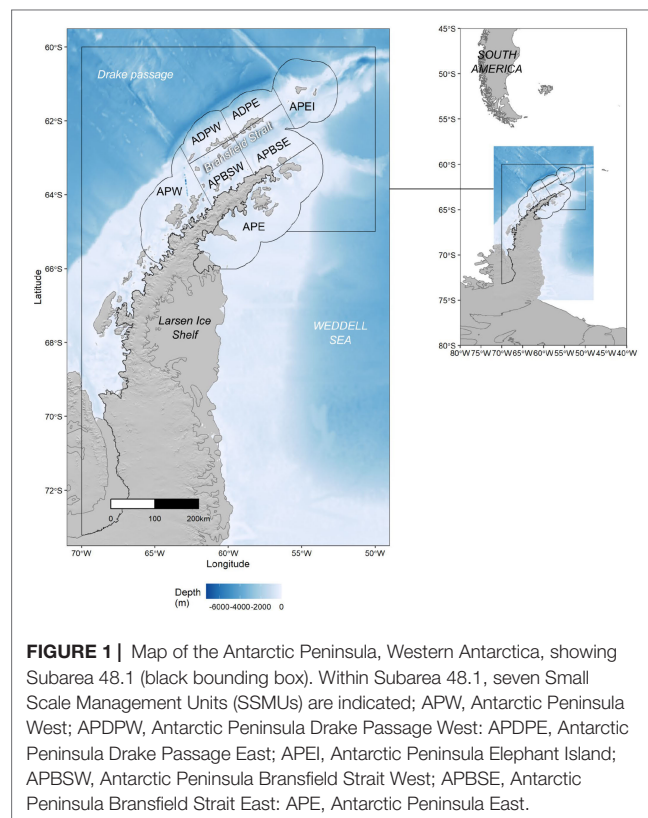
In Antarctica, abundant consumers rely on Antarctic krill (*Euphausia superba*, hereafter 'krill') for food, and the top-down and bottom-up interactions between krill and its consumers play a key role in structuring Antarctic marine ecosystems (Trathan & Hill, 2016). Krill are also the subject of a commercial fishery (Nicol et al., 2012) that overlaps in time and space with foraging of consumers and the potential competition between krill fisheries and krill consumers is thus a major management concern (e.g., Trivelpiece et al., 2011; Forcada et al., 2012; Trathan & Hill, 2016; Weinstein et al., 2017; Warwick-Evans et al., 2018; Watters et al., 2020; Bamford et al., 2021; Krüger et al., 2021).

The krill fishery is managed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) with an ecosystem approach, according to which fishing should not interfere with the population growth of krill, or krill-dependent consumers, including those that are recovering from historical exploitation (Constable et al., 2000). Almost all krill catches are from the southwest Atlantic sector of the Southern Ocean, FAO Area 48, where the krill population is concentrated (Atkinson et al., 2017). In some years small amounts have also been taken from the Indian Ocean sector of Antarctica. The current (annual) total allowable catch (precautionary catch limit) for the southwest Atlantic, based on an acoustic estimate of stock biomass undertaken in 2000 (Hewitt et al., 2004; SC-CCAMLR, 2010), is currently 5.61 million tonnes. Over recent years, catches have been increasing, reaching a maximum of 450,813 tonnes in 2020, with a mean catch of 267,386 tonnes over the period between 2010 and 2020 (CCAMLR, 2021). As such, krill is "one of the world's largest known underexploited marine stocks" (Nicol et al., 2012) and could account for about 10% of future marine landings (Trathan et al., 2022).

Now, with the potential expansion of the krill fishery, there is increasing pressure on this shared resource, since populations of many krill consumers are changing (Bestley et al., 2020; Strycker et al., 2020). In line with their precautionary, ecosystem approach to management, CCAMLR has set an interim catch limit (or 'trigger level') of 620,000 tonnes for the southwest Atlantic krill fishery (Hill et al., 2016; Trathan et al., 2022). This trigger level has been set until such a time that CCAMLR has agreed a way

in which to spatially (and temporally) subdivide the much larger precautionary catch limit. Although catches are considered to be low compared to overall krill abundance (the interim catch limit is ~1% of the total estimated biomass across the southwest Atlantic [SC-CCAMLR, 2019]), catches are expected to keep increasing into the future with the development of new processing and fishing technologies. Further, due to interannual variability in total krill abundance and spatial distribution, local catch limits based on a single year assessment or even average assessments across multiple years, may exceed local krill abundance in some years. In recent years, krill catches have become increasingly spatially concentrated in a small number of hotspots (Weinstein et al., 2017; Santa Cruz et al., 2018; Krüger, 2019; Santa Cruz et al., 2022; Trathan et al., 2022), raising concerns about how local depletion of krill impacts its consumers (e.g., Weinstein et al., 2017; Watters et al., 2020; Krüger et al., 2021; Santa Cruz et al., 2022).

CCAMLR has recognized that this increasingly concentrated krill fishing necessitates a smaller-scale management approach that better reflects the scale of krill-predator interactions and the current behaviour of the fishing fleet (i.e., at the scale of tens of kms) (SC-CCAMLR, 2016, paragraph 3.62 and 3.106). However, catches are still managed at the Subarea scale (658,730 km² - 1,033,248 km² for Subareas 48.1-48.4), even though 'Small Scale Management Units' (16,000 km² - 440,000 km² (Figure 1) have been designated. In the southwest Atlantic (Subareas 48.1, 48.2, 48.3 and 48.4) harvesting is limited to 25%, 45%, 45% and 15%, respectively, of the trigger level. These interim Subarea limits sum



to 130% of the overall trigger level to allow spatial flexibility for the fishery, but the overall catch across these four Subareas is still limited by the overall trigger level (Trathan et al., 2022).

Competing with the commercial krill fishery are numerous natural krill consumers including fishes, squid, seabirds and marine mammals, not to mention the numerous invertebrate species that feed on early life-history stages of krill (Trathan and Hill, 2016). The air-breathing consumers adjust their foraging areas in response to prey availability and accessibility, but are spatially restricted due to their intrinsic ecology, such as migratory patterns in baleen whales or the central place foraging constraints associated with breeding on land for penguins and seals. This means that consumers usually shift their foraging areas (e.g., Trathan et al., 2018) over an approximately annual timescale and over spatial scales of 10s – 100s or 1000s of kms. Accompanied by these changes in the areas foraged by consumers are changes in their energy requirements. Together this produces a dynamic pattern of space-use and energy requirement that must be incorporated into the risk assessment framework for managing the Antarctic krill fishery (e.g., Hinke et al., 2017a; Weinstein et al., 2017). Integral to the finer scale (10s of km and hours to weeks) space-time structuring of these patterns is the way in which predators find and exploit patchily distributed prey. Predators initially search for prey using faster, more linear movements but when they encounter prey they slow down and turn more often to remain in the prey patch. Predators forage in these patches until prey reaches some ‘giving up’ density below which foraging is no longer profitable. It is at these spatiotemporal scales that we might expect to detect predator-prey overlap, as well as overlap with fisheries, since similar dynamics seem to operate in the krill fishing fleet. Vessels must locate large, dense krill swarms that they exploit before moving to search for a new krill swarm (Santa Cruz et al., 2018). Such dynamics may also be intensified if fishing vessels also use cues similar to those used by dependent predators, for example the presence of other foraging predators such as baleen whales. Krill fishing vessels exploit krill hotspots for about 3–17 days, whereafter they move on due to declining catches indicating local krill depletion (Santa Cruz et al., 2018). However, in some hotspots close to shore off the Western Antarctic Peninsula, concentrated fishing can last longer, but still with evident declines in catches towards the end of the event, which differed for different vessels within the fishing hotspot (Trathan et al., 2016).

Such concentrated fishing demonstrates a mismatch between the spatial and temporal scale at which krill fisheries are currently managed, and that at which fisheries operate and consumers forage. Information on the seasonal dynamics of predator abundance and their foraging behaviour is fundamental to future precautionary management of the krill fishery. Improved analyses on both spatial and functional overlap of consumers with the fishery and how they both interact with krill will be extremely informative, especially for key predator groups about which foraging information is limited. In particular, baleen whales are not included in CCAMLR’s management approach even though they are known to be major krill consumers (e.g., Savoca et al., 2021). Importantly, baleen whales are also not

included in the CCAMLR Ecosystem Monitoring Program which monitors other krill consumers (Agnew, 1997).

Thus, there is a clear and urgent need to better understand the spatiotemporal characteristics of potential interactions between krill consumers and the krill fishery. This is perhaps most urgent for those species that have not previously been considered in detail and which are known to be recovering rapidly from previous exploitation. Krill-eating baleen whales are therefore probably the most important taxonomic group for which CCAMLR needs information (Trathan et al., 2022). Moreover, recent by-catch of whales in the krill fishery demonstrate that fishing vessels and baleen whales do not always easily coexist (CCAMLR Secretariat, 2021; Delegations of Norway and the United Kingdom, 2021). Understanding the spatiotemporal distribution of both whales and fishing vessels is now urgent. Fortunately, animal biologging and vessel tracking provides data that can be used to address this need.

Humpback and Minke Whales

One of the most important consumers of krill in the Southern Ocean is the humpback whale (*Megaptera novaeangliae*), a medium sized (~15 m) baleen whale which, migrates annually from low latitude overwintering grounds to mid and high latitude summer feeding grounds (Clapham, 2018). Southern hemisphere humpback whale populations were severely depleted by catches of ~215,000 animals during industrial whaling from 1900–1979 (Rocha et al., 2015). Circumpolar surveys suggest a total Southern Ocean abundance >55,000 in 2011 (Branch, 2011). Most populations are increasing (albeit at different rates) and some are estimated to be near their pre-exploitation abundance (International Whaling Commission, 2016). The humpback whale population that uses waters off the Western Antarctic Peninsula is increasing rapidly (Pallin et al., 2018) and unprecedentedly dense ‘super-aggregations’ have been observed in this region (Nowacek et al., 2011). Spatial abundance models estimate around 19,000 individuals in this region in early summer (Johannessen et al., 2022; see also Warwick-Evans et al., 2022), a 5.1% per annum increase from the estimated 7,000 individuals in the same region in 2000 (Hedley et al., 2001; Johannessen et al., 2022). Their global IUCN Red List classification is Least Concern (Cooke, 2018).

Another major Southern Ocean krill consumer is the smaller (~8m) but much more abundant Antarctic minke whale (*Balaenoptera bonaerensis*) (Friedlaender et al., 2014). Their Southern Ocean population has been estimated to be around 500,000 individuals, based on circumpolar surveys from 1993–2004 (International Whaling Commission, 2013). This represents a 13% decline from the 1986–1991 survey estimate of around 700,000 animals, although both estimates are imprecise [due largely to minke whales’ affinity for sea ice (Williams et al., 2014; Herr et al., 2019)] and the trend is thus not significant (International Whaling Commission, 2013). Nonetheless, the apparent decline is one of the reasons for their current IUCN Red List classification as Near-Threatened (Cooke et al., 2018).

Habitat modelling of humpback and minke whale sighting data in the Western Antarctic Peninsula showed that the

distribution of these whales was best explained by krill distribution (Friedlaender et al., 2006; Friedlaender et al., 2011). Using tracking data from five humpback whales, Curtice et al. (2015) showed that their distribution changed over their feeding season from January to June. Individuals moved inshore and their movements became more concentrated, likely a response to the inshore movement and aggregation of krill over the same period (Curtice et al., 2015), given krill are thought also to follow a seasonal migration (Siegel, 1988).

Weinstein et al. (2017) used tracking data from 33 humpback whales in the Western Antarctic Peninsula (Subarea 48.1) to map the month-by-month foraging areas of whales in relation to krill catches. Individuals used some of the Small-Scale Management Units significantly more than expected, suggesting that a uniform krill catch limit for all SSMUs in Subarea 48.1 is overly broad and ignores important variation in humpback whale distribution and critical foraging areas. The authors recommended that two Small Scale Management Units particularly – Antarctic Peninsula West and Bransfield Strait West – deserve special attention if fine scale management is to be implemented (Weinstein et al., 2017). However, this work did not account for the dynamic behaviour of the fishery on a predator-relevant timescale. Friedlaender et al. (2021) showed that humpback whales range throughout continental shelf waters and nearshore bays along the Western Antarctic Peninsula, while minke whales prefer sheltered bays and areas where sea ice is present. Minke whales thus occupy areas within the areas used by humpback whales (Friedlaender et al., 2021).

Aims

This simultaneous concentration of krill, whales and fisheries inshore late in the fishing season (late austral summer into autumn) heightens the possibility of local depletion and disruption of whale populations, but new information is required to address this issue in light of CCAMLR's Risk Assessment Framework for krill fishery management. Here, we address this information gap by investigating the spatiotemporal distribution of humpback whale and minke whale foraging behaviour in the Western Antarctic Peninsula as well as that of krill fishing in the same region. We do this using recent whale tracking data and fishing catch and effort data. We develop spatial models to predict monthly whale distribution from January–July, thereby calculating spatiotemporally explicit geographic overlap between whales and fisheries.

METHODS

Computation

All analyses were performed in the R environment (R Core Team, 2022). Scripts used to conduct the analyses can be found in the Github repository <https://github.com/ryanreisinger/whaleKrillOverlap>.

Whale Movement Behaviour

We collated published and unpublished satellite tag tracking data for humpback and minke whales. For humpback whales, we used a circumpolar dataset of tracks (Reisinger et al., 2021) totalling

367 tracks and 214,865 locations. Individuals were tagged on Antarctic foraging grounds as well as lower latitude breeding grounds (Reisinger et al., 2021). For minke whales, we used published tracks from tags deployed off the Western Antarctic Peninsula (Friedlaender et al., 2021), as well as unpublished tracks from tags deployed in the Weddell Sea and off the Western Antarctic Peninsula. Together these totalled 20 tracks and 10,286 locations. The tags were all Argos-linked satellite tags in various configurations (see Curtice et al. (2015); Weinstein et al. (2017); Weinstein & Friedlaender (2017) and Friedlaender et al. (2021) for specific details). For both species, we restricted the dataset to tracks from 1 January 2012 onwards, with locations within CCAMLR statistical Subarea 48.1: 58 humpback whale tracks (2012–2018) and 19 minke whale tracks (2013–2017) (**Supplementary Table S1**).

Argos-linked tags provide geographic location estimates at irregular intervals due to the dive behaviour of whales and the availability of overhead satellites. Argos location estimates have some geographic uncertainty, categorised by system Argos into four classes with error radiuses from <250 m (class 3) to >1,500 m (class 0) (CLS, 2016). To estimate locations at regular intervals, while accounting for location uncertainty, we fitted state-space models to the tracking data. Specifically, we chose a behaviour-switching state-space model (Jonsen et al., 2005), which also estimates a behavioural parameter (b) for each location. The behavioural parameter b is estimated using the turning angles and persistence in speed and direction from the fitted tracks (Jonsen et al., 2007). Low b values are associated with faster, straighter movements indicative of 'transit' behaviour, while high b values indicate slower, more tortuous movements, assumed to be associated with 'Area-Restricted Search' behaviour (Jonsen et al., 2007). The rationale is that, when prey is heterogeneously distributed, consumers initially search for prey using faster, more linear movements; when they encounter prey they then slow down and turn more often to remain in the prey patch (e.g., Kareiva & Odell, 1987; Benhamou, 1992; Fauchald et al., 2000; Fauchald and Tveraa, 2003). Thus, locations with high b values – hereafter 'restricted' behavioural state – are assumed to represent areas where whales have encountered prey.

Before fitting the state-space models, we split tracks with temporal gaps greater than three days into track segments and treated these separately to avoid excessive interpolation. We also filtered the data using a speed filter (retaining positions with apparent speeds less than 5 m s⁻¹). Behavioural-switching state space models were fitted using the *bsam* R package (Jonsen et al., 2005; Jonsen, 2016). We estimated locations 3-hourly. Locations with b values $1.0 \leq b \leq 1.4$ were classified as transit, $1.6 \leq b \leq 2.0$ as restricted, and $1.4 < b < 1.6$ as uncertain (a slightly relaxed threshold cf. Jonsen et al., 2007).

Since the satellite tracking data depict only the behaviour of the tracked individuals, we fitted spatial random forest models (Hengl et al., 2018) to predict the behaviour of whales over the entire study area in each month where there was sufficient tracking data. These models relate the behavioural state in the tracks to a set of environmental covariates as well as a set of covariates capturing the spatial relationships among the tracking locations. Hengl et al. (2018) show that spatial random forests

perform at least as well as state-of-the-art Kriging methods, but with greater flexibility.

Following Hengl et al. (2018), our spatial random forest is represented as:

$$Y(s) = f(X_g, X_e)$$

The response variable Y at point s is the behavioural state b , either 'transit' or 'restricted'; X_g are predictors/covariates accounting for geographic proximity among points, in this case the distance (km) from the given point s to all other points, calculated using the *gdistance* R package (Van Etten, 2017), X_e are environmental predictors/covariates at the given points, in this case: ocean depth, distance to shelf, sea surface temperature (mean and coefficient of variation), sea ice concentration (mean and coefficient of variation) and distance to the sea ice edge (mean and coefficient of variation) (Table 1). These are among the covariates that have previously been linked to the occurrence of minke (Friedlaender et al., 2006; Ainley et al., 2012; Friedlaender et al., 2014; Williams et al., 2014;

Ainley et al., 2017; Herr et al., 2019; Ainley et al., 2020; Friedlaender et al., 2021) and humpback (Andrews-Goff et al., 2018; Bestley et al., 2019; Riekkola et al., 2019; Friedlaender et al., 2021; Reisinger et al., 2021) whales around Antarctica. The primary aim of our modelling was spatial prediction, and in addition to the spatial covariates we therefore included only some environmental covariates from a variety of possible ones (e.g., Reisinger et al., 2021). For dynamic covariates (sea surface temperature, sea ice concentration, distance to sea ice edge), monthly mean and coefficient of variation were calculated using daily data from the respective months over the period December 2015 - November 2020. Additionally, we included one- and two-month lags of these covariates, since lagged sea ice covariates have been linked to humpback whale movements previously (Andrews-Goff et al., 2018; Riekkola et al., 2019). Environmental data were extracted from a data collection maintained by the Australian Antarctic Division, using the *raadtools* (Sumner, 2021) and *raster* (Hijmans, 2020) R packages. The latter package was used for most raster manipulations. Random forests were fitted using the *ranger* package (Wright & Ziegler, 2017). The number of trees was set to 500 and

TABLE 1 | Environmental covariates used as predictors of whale behavioural state in spatial random forest models.

Variable	Description	Unit	Spatial resolution	Temporal resolution	Source
Depth	Ocean depth	m	30 arc-second	–	GEBCO 2020 grid GEBCO Compilation Group, 2020
Distance to shelf	Distance to 500 m ocean depth contour.	km	30 arc-second	–	Calculated from: GEBCO 2020 grid GEBCO Compilation Group, 2020
Sea surface temperature mean	Sea surface temperature - monthly mean climatology from daily values.	°C	0.01° x 0.01°	Monthly summary of daily values	Calculated from: GHRSSST Level 4 MUR Global Foundation Sea Surface Temperature Analysis v4.1 http://podaac.jpl.nasa.gov/dataset/MUR-JPL-L4-GLOB-v4.1 https://doi.org/10.5067/GHGMR-4FJ04
Sea surface temperature CV	Sea surface temperature - monthly CV – climatology from daily values.	–	0.01° x 0.01°	Monthly summary of daily values	Calculated from: GHRSSST Level 4 MUR Global Foundation Sea Surface Temperature Analysis v4.1 http://podaac.jpl.nasa.gov/dataset/MUR-JPL-L4-GLOB-v4.1 https://doi.org/10.5067/GHGMR-4FJ04
Sea ice concentration mean	Sea ice concentration per grid cell monthly mean climatology from daily values.	%	25 km, regridded to 0.1° x 0.1°	Monthly summary of daily values	Calculated from: https://nsidc.org/data/NSIDC-0051/versions/1 Cavalieri et al. (1996)
Sea ice concentration CV	Sea ice concentration per grid cell monthly CV climatology from daily values.	–	25 km, regridded to 0.1° x 0.1°	Monthly summary of daily values	Calculated from: https://nsidc.org/data/NSIDC-0051/versions/1 Cavalieri et al. (1996)
Distance to sea ice edge mean	Distance to 15% contour in sea ice concentration. Monthly mean climatology from daily values. Positive distance in open water; negative distance within sea ice.	km	25 km, regridded to 0.1° x 0.1°	Monthly summary of daily values	Calculated from: https://nsidc.org/data/NSIDC-0051/versions/1 Cavalieri et al. (1996)
Distance to sea ice edge CV	Distance to 15% contour in sea ice concentration. Monthly CV climatology from daily values. Positive distance in open water; negative distance within sea ice.	–	25 km, regridded to 0.1° x 0.1°	Monthly summary of daily values	Calculated from: https://nsidc.org/data/NSIDC-0051/versions/1 Cavalieri et al. (1996)

prediction error was assessed with the Brier score. Covariate importance was assessed with the Gini index. We assessed the temporal trend in predictions by calculating Kendall's tau for each grid cell over months, using the spatialEco package (Evans & Murphy, 2021).

Krill Fishing

We compiled data on Antarctic krill fishing in statistical Subarea 48.1 from two sources: CCAMLR fine-scale catch and effort data for trawl fisheries ("C1 data") obtained from (<https://www.ccamlr.org/en/node/74767>) and Global Fishing Watch global fishing effort data version 2.0 (<https://globalfishingwatch.org/data-download/datasets/public-fishing-effort>) (Kroodsma et al., 2018). The C1 data are reported to CCAMLR on a haul-by-haul basis. We used data from December 2015 - May 2020 (2016-2020 fishing seasons), summing the krill catch (tonnes) per haul onto an aggregated $0.1^\circ \times 0.1^\circ$ (approximately 11.1 km x 5.6 km at 60°S) spatial grid by month, using the haul set end locations. The Global Fishing Watch effort dataset is based on AIS-detections that are identified as fishing using a suite of algorithms, including a neural network classifier; these detections are binned onto a spatial grid and effort is calculated per grid as the time between the current and previous position (Kroodsma et al., 2018). We filtered these effort data for the same period as the catch data, summing fishing effort (hours) on the same spatial grid. We calculated temporal trends in krill fishing catch and effort as for the whale behaviour predictions.

Overlap Between Important Whale Areas and Fishing

We calculated an overlap index between whales and fishing by multiplying the predicted probabilities for whales to be in a restricted behavioural state in a given grid cell, by the monthly krill catch.

RESULTS

Whale Movement Behaviour

After limiting the 367 humpback whale and 20 minke whale tracks to our study area, splitting tracks with time gaps > 3 days into track segments, and fitting behaviour-switching state-space models to regularise the locations in time accounting for the errors inherent to satellite tracking data, we retained 52 humpback whale track segments totalling 18,236 locations (Figure 2A) and 25 minke whale track segments totalling 4,188 locations (Figure 2B). The distribution of b values for each species is shown in Supplementary Figure S1.

Movements of humpback whales were more extensive than those of minke whales, with humpback locations distributed throughout Subarea 48.1 (Figure 2A). Minke whale locations, in contrast, were mainly close to the Antarctic Peninsula coast, often in bays (Figure 2B). Humpback whales typically

switched from transit to restricted behaviour upon reaching the South Shetland Islands or Bransfield and Gerlache Straits, where there were high concentrations of restricted behaviour locations (Figure 2A). Most whale locations were within the seven CCAMLR SSMUs, although both humpbacks and minke recorded locations further south along the Peninsula.

Prediction error (Brier score, which can range from 0 [all cases correctly predicted] to 1 [no cases correctly predicted] of the random forest models ranged (best-worst) from 0.02-0.06 for humpback whales and from 0.03-0.08 for minke whales, indicating very low error when predicting the datasets used for model fitting.

The trend in random forest predictions over the season was very different for humpback and minke whales. For humpback whales (Figure 3A) there is an increasing trend in the Bransfield Strait West, Antarctic Peninsula West and Antarctic Peninsula Pelagic SSMUs over the season, with a decreasing trend elsewhere. For minke whales (Figure 3B) there is a decrease in the Bransfield Strait East SSMUs, strong decrease in the Antarctic Peninsula West SSMU nearshore and Antarctic Peninsula East SSMU (around James Ross Island), with a strong increase in the pelagic SSMU, off Adelaide Island.

Among the environmental covariates, 1- and 2-month lagged mean sea surface temperature followed by 1-month lagged mean sea ice concentration had the highest to third-highest mean variable importance for humpback whales (Figure 4). For minke whales, 1-month lagged sea surface temperature mean, followed by 2-month lagged mean sea ice concentration had the highest mean importance (Figure 4).

Fishing

Fishing effort and catch took place in the Drake Passage near the South Shetland Islands (SSMUs ADPW and ADPE), near Elephant Island (SSMU APEI) in the Bransfield Strait (SSMUs APBSW and APBSW) and in the Gerlache Strait (SSMU APW) (Figure 5). The greatest effort (up to 34 hours in a grid cell) and greatest catch (up to 12,908 tonnes in a grid cell) was located in a cluster of grid cells around the shelf edge of the Antarctic Peninsula within the Bransfield Strait (near Lafond Trough), straddling SSMUs APBSW and APBSE with a size in the region of 30×60 km.

Each Antarctic krill fishing season lasts from 1 December to 30 November, but Subarea 48.1 is usually closed early, because the local catch limit is reached, usually in May, June or July of a given year. We calculated the spatial trend (Kendall's tau) in krill catch (Figure 5) and fishing effort (Figure 6) over the season (for a given calendar month, summing the data over all years). Figures 5, 6 show the clear seasonal progression from areas in the Drake Passage off Elephant Island (APEI SSMU) and King George Island (APDPE SSMU) to more south-westerly areas in the Drake Passage (APDPW SSMU) and areas in the Bransfield Strait (APBSW and APBSE SSMUs). Monthly, interannual variance in fishing effort was highest in the Bransfield Strait in April and May (Supplementary Figure S2).

Overlap

Overlap index values reveal a clear seasonal progression in potential interactions between predicted whale foraging and krill fisheries. For humpback whales, overlap early in the season, in January, is located in the Elephant Island (APEI) and Drake Passage (APDPW and APDPE) SSMUs (**Figures 7A, 8**), while from February, overlap for humpback whales develops in the Bransfield Strait. For minke whales, overlap is highest in the Bransfield Strait (APBSE and APBSW),

firstly, and off the South Shetland Islands (APDPE and APDWE), secondly (**Figures 7B, 8**). For both humpback (**Figure 7A**) and minke (**Figure 7B**) whales, the highest overlap occurs in April and May, concentrated in the Bransfield Strait (**Figure 8**), driven by high krill catch in this area (see **Figure 5**). An approximate comparative phenology of whales – using the tracking data and International Whaling Commission whaling catch dataset (Allison, 2016) south of 60° S – and fisheries – using the effort data – is shown in **Figure 9**.

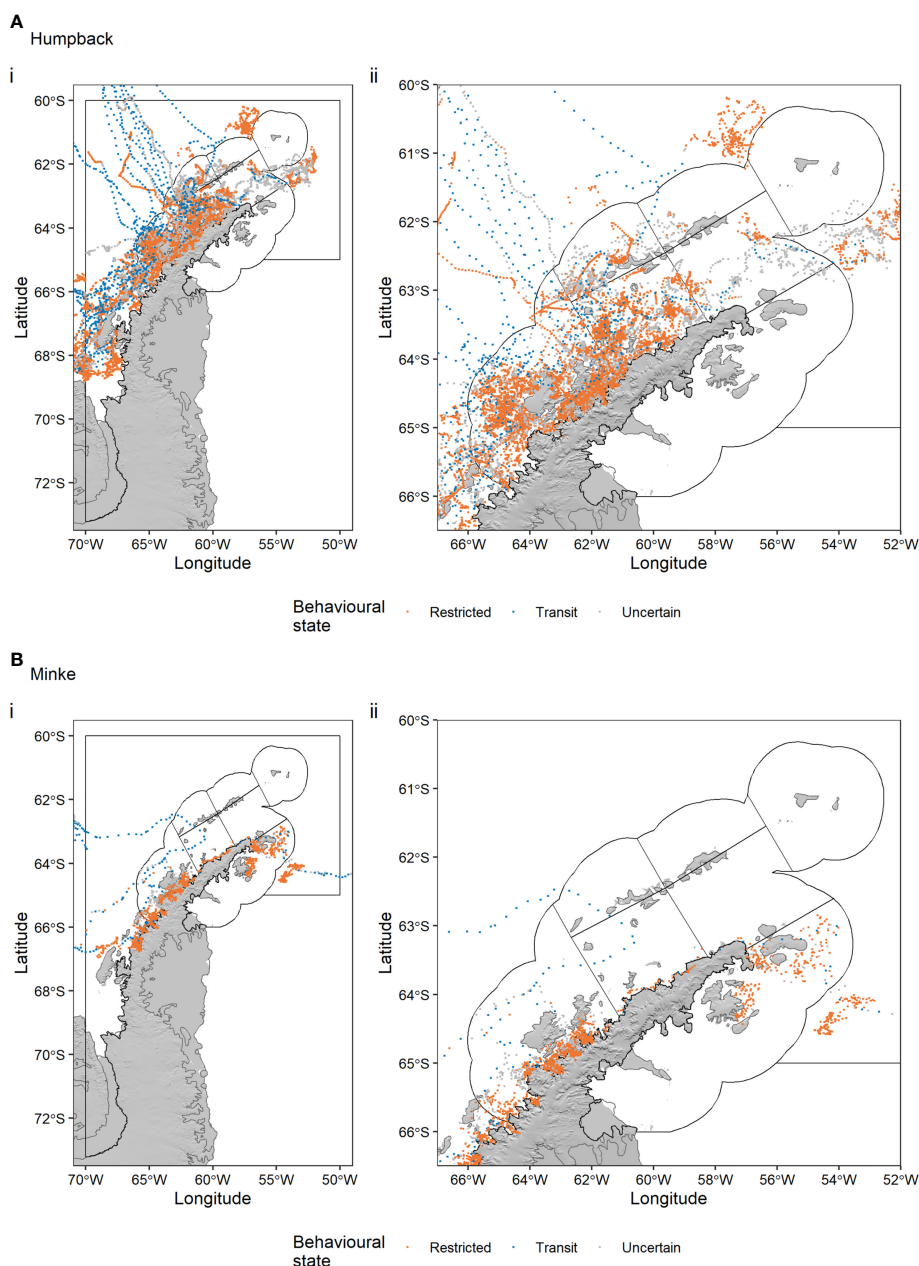


FIGURE 2 | Humpback whale (**A**) and minke whale movement (**B**) tracks off the Antarctic Peninsula. A behaviour switching state-space model was used to regularise the locations in time (6-hour timestep), to account for errors associated with satellite tracking data, and estimate the behavioural state of whales. Black polygons indicate the seven CCAMLR Small Scale Management Units (SSMUs) within Subarea 48.1, which is delineated by the outer black polygon.

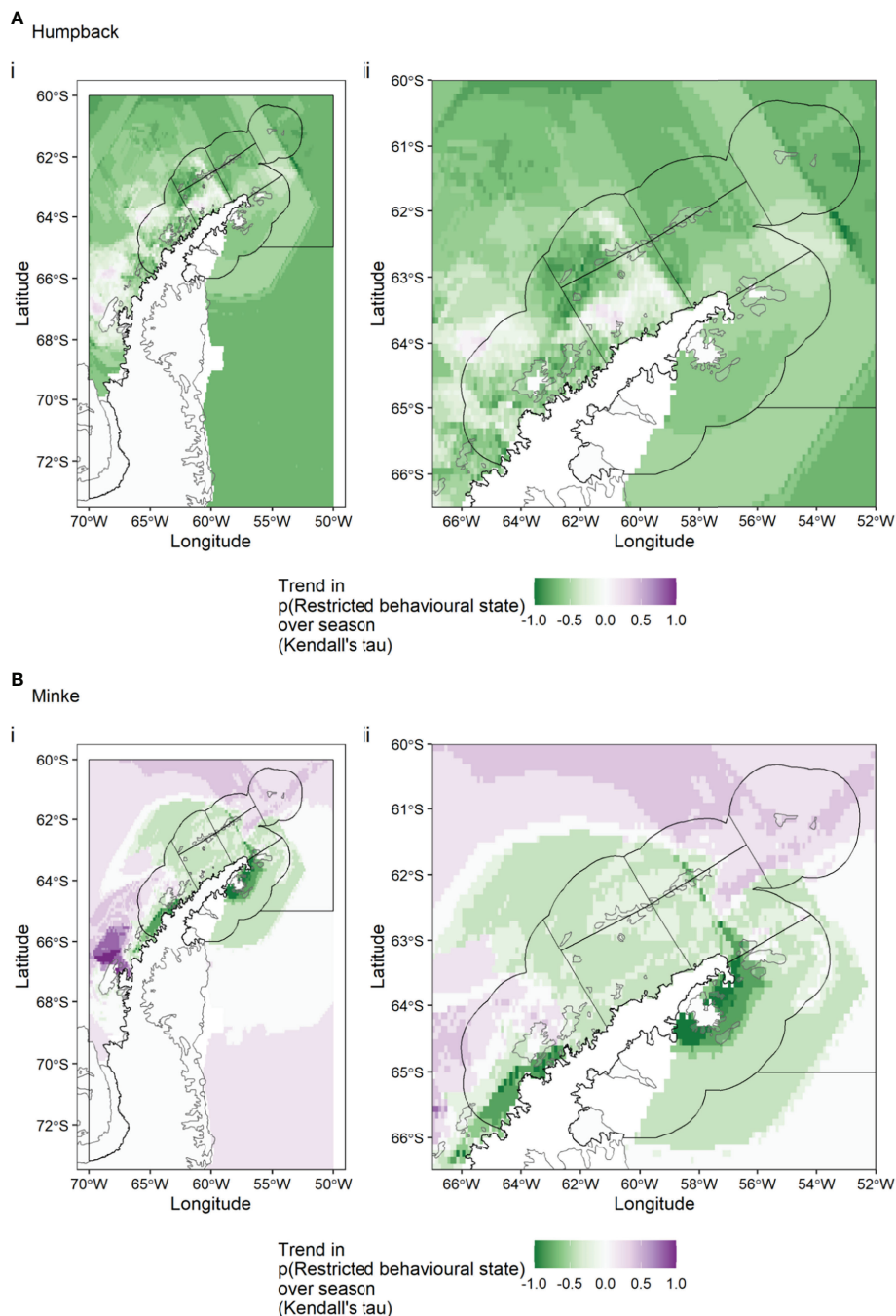


FIGURE 3 | For humpback whales (**A**) and minke whales (**B**), the trend in behavioural state predictions over the season. A negative trend (green colours) means that, in a given grid cell, whales were decreasingly likely to be in a restricted behavioural state as the season progressed, while a positive trend indicates the opposite.

DISCUSSION

Using humpback whale and minke whale tracking data, we fitted spatial random forest models to predict the monthly distribution of whale behavioural state over the summer foraging period in the Western Antarctic Peninsula region. For humpback whales, we predicted a shift towards a concentrated foraging area in the

Bransfield Strait. For minke whales, there was a more subtle trend suggesting diffusion from their early season foraging area in the Gerlache Strait. We used fine-scale data on krill fishing effort and catch to examine the monthly spatial distribution of the krill fishery in the same region. These data show that fishing effort and catch is highly concentrated in relatively small areas, as shown by Santa Cruz et al. (2018) (see also Weinstein et al., 2017 and

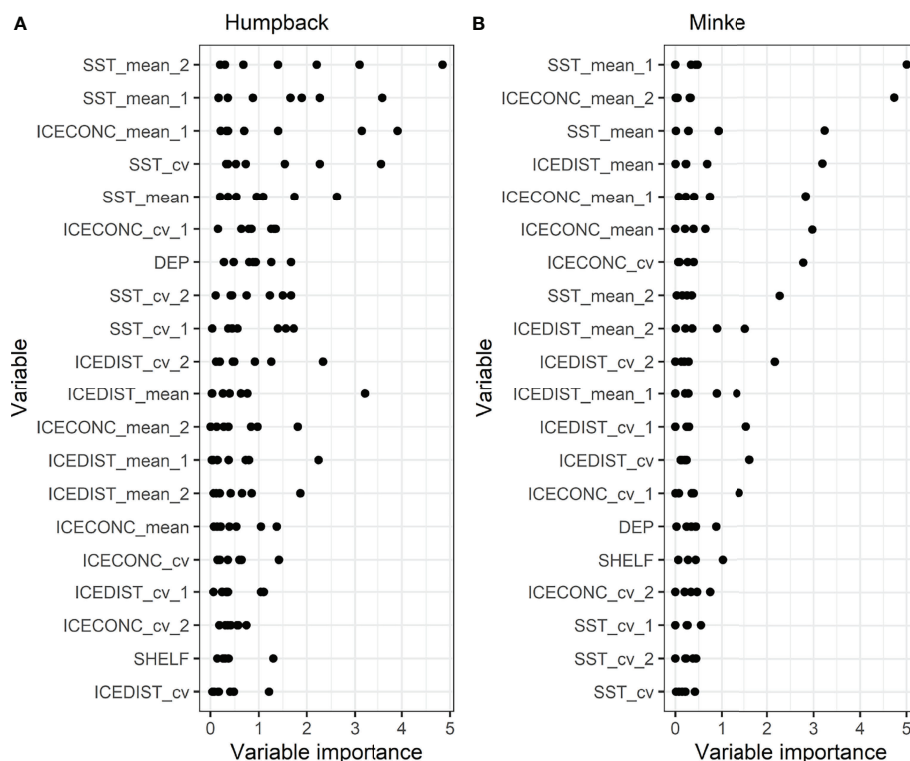


FIGURE 4 | Importance of environmental covariates in random forest models predicting the behavioural state of (A) humpback and (B) minke whales. Covariates are ordered from lowest (bottom) to highest (top) mean importance, with each point representing a monthly random forest model (seven models for humpback whales and five models for minke whales). SST_mean, mean sea surface temperature; SST_cv, coefficient of variation of sea surface temperature; ICECONC_cv, coefficient of variation of sea ice concentration; ICEDIST_mean, mean of distance to sea ice edge (15% sea ice concentration contour); ICECONC_mean, mean of sea ice concentration; DEP - ocean depth; SHELF, distance to shelf (500 m bathymetry contour); ICEDIST_cv, coefficient of variation of distance to sea ice edge (15% sea ice concentration contour). Suffixes _1 and _2 indicate 1- and 2-month time lags.

Krüger, 2019). Krill fishing is particularly concentrated in two SSMUs in the Bransfield Strait: Bransfield Strait West (APBSW) and Bransfield Strait East (APBSW) (see also Weinstein et al., 2017; Santa Cruz et al., 2018).

Several studies (e.g., Trivelpiece et al., 2011; Forcada et al., 2012; Trathan & Hill, 2016; Warwick-Evans et al., 2018; Watters et al., 2020; Bamford et al., 2021; Krüger et al., 2021) highlight overlap between krill consumers and krill fisheries as a serious management concern. However, most work has so far focussed on penguins and seals while baleen whales, despite being major krill consumers (Savoca et al., 2021), have received comparatively little attention (*cf.* Weinstein et al., 2017; Johannessen et al., 2022; Trathan et al., 2022). Indeed, baleen whales are not explicitly included in CCAMLR's ecosystem approach to fishery management or in the CCAMLR Ecosystem Monitoring Program that monitors other krill consumers (Agnew, 1997). Indeed, by the time that the CAMLR Convention was negotiated, populations of baleen whales had already been exploited to such levels that management concerns principally focused upon land-based krill predators. However, negotiation of the CAMLR Convention did allow for the restoration of previously depleted populations, which clearly must now include baleen whales.

Our results indicate the likely overlap between humpback and minke whales and the krill fishery at fine spatial scale on the order of tens of km. Further, the temporal changes in humpback whale foraging distribution and krill fishing distribution are likely to result in intensified potential competition as both krill consumers and krill fisheries track the movement of krill in coastal regions as the summer progresses. This underlines the importance of including information on baleen whales in managing the krill fishery. Moreover, our results further emphasise that management of the krill fishery should move towards understanding actual impacts on krill consumers at fine temporal and spatial scales, as well as being adaptive by, for example, using spatial models similar to those we present to predict overlap between krill consumers and the krill fishery. This is now increasingly urgent as the ecosystem changes with changing predator populations and rapid environmental change in this region, but also in the context of an expanding krill fishing (Trathan et al., 2022).

Having recognized the increasing spatial concentration of krill fishing and the typical spatial scale of krill-predator interactions, CCAMLR designated SSMUs ranging in size from 16,000 km² - 440,000 km² (Figure 1). However, krill catches are still managed by Subarea, for Subarea 48.1 an area of 658,739

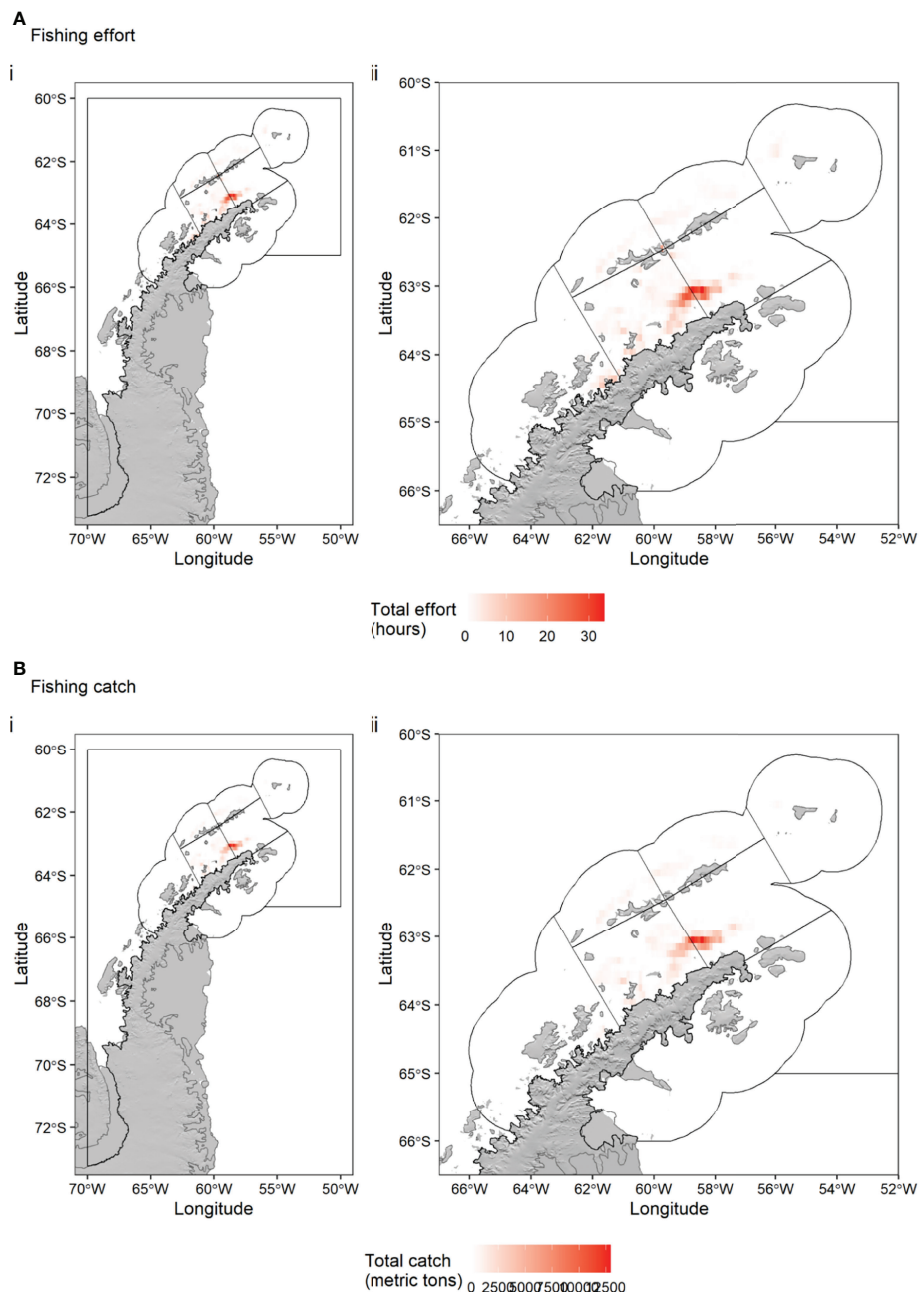


FIGURE 5 | Total Antarctic krill fishing effort (hours) **(A)** and catch (tonnes) **(B)** per $0.1^{\circ} \times 0.1^{\circ}$ grid cell in statistical subarea 48.1 over the period December 2015 – May 2020. Black polygons indicate the seven Small Scale Management Units (SSMUs) within the Subarea, named in **Figure 1**. Catch data: CCAMLR. Effort data: Global Fishing Watch.

km². Even if catch were to be managed by SSMU, our analyses show that potential interactions are concentrated in hotspots in only a few SSMUs. Weinstein et al. (2017) showed that humpback whales used the Antarctic Peninsula West (APW), Bransfield Strait West (APBSW), and Drake (APDP) Passage West SSMUs more often than expected, spending more time in a restricted behavioural state in these SSMUs. Similarly, density modelling of humpback whale sightings data likewise identifies the Bransfield

Strait and northern Gerlache Strait as areas of high humpback whale abundance, at least during December (Johannessen et al., 2022). In the last decade, krill fishing has shifted spatially into the Bransfield Strait (Santa Cruz et al., 2018), representing the primary krill fishing hotspot in our analysis (**Figure 5**). Thus, these areas represent hotspots of likely high overlap between humpback whales and the krill fishery (**Figures 7, 8**). Minke whales had a more restricted distribution, with most of their

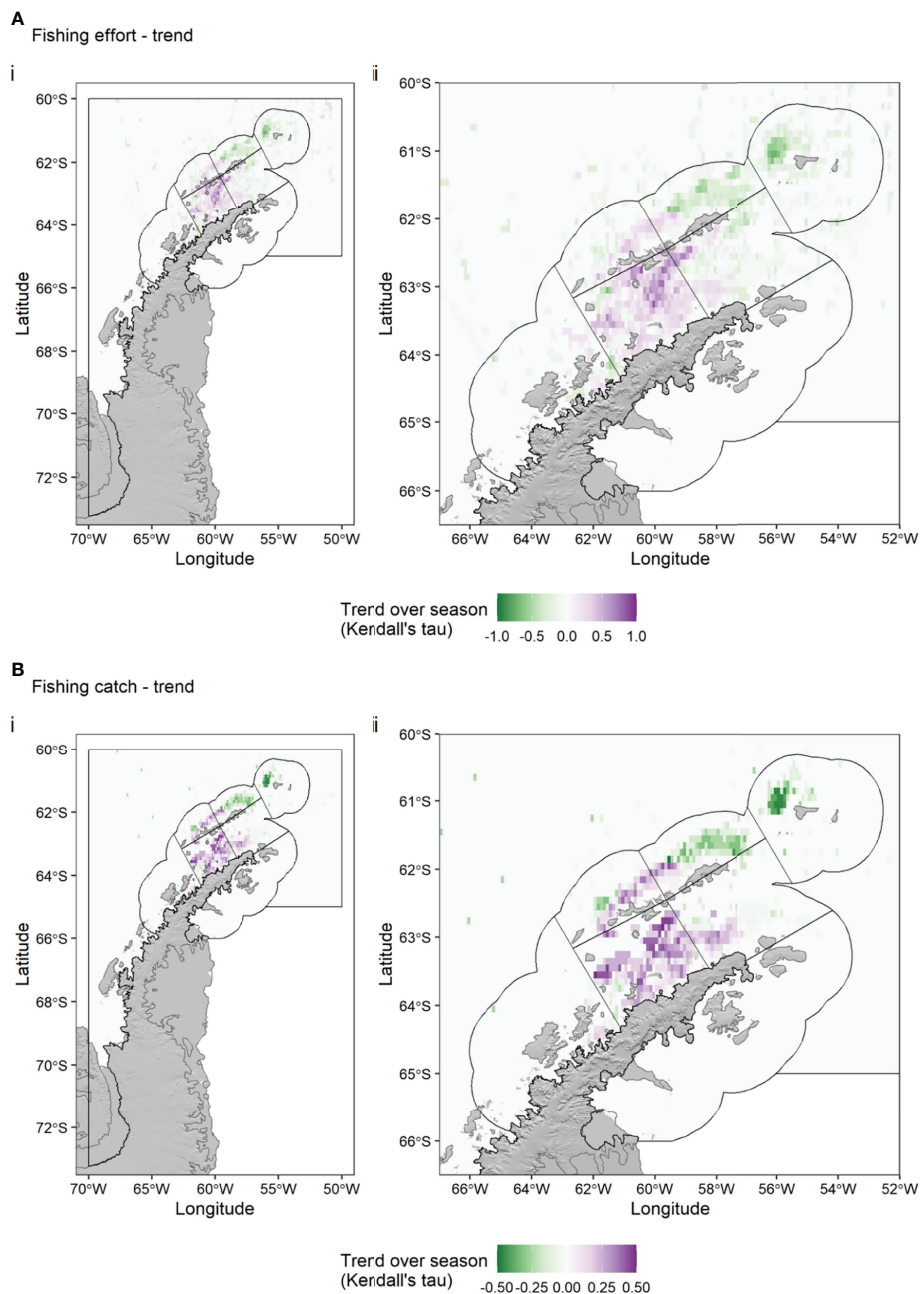


FIGURE 6 | Trend (Kendall's tau) in Antarctic krill fishing effort **(A)** and catch **(B)** over all fishing seasons (December – July), 2015–2020, depicting the average movement of the fishing effort (top) and catch (bottom) within seasons. Green colours indicate a decrease in effort (top) or catch (bottom) in a given $0.1^\circ \times 0.1^\circ$ grid cell over the season, while purple colours indicate an increase. Black polygons indicate the seven Small Scale Management Units (SSMUs) within the Subarea. Effort data: Global Fishing Watch. Catch data: CCAMLR.

restricted-behaviour locations in the nearshore waters of the Gerlache Strait (Danco Coast) and Grenadier Channel (Graham Coast and Loubet Coast). There was some fishing effort in the northern Gerlache Strait, but little further south, and consequently overlap between predicted minke whale foraging areas and the krill fishery was much lower than for humpback whales. A caveat is that fewer tracking data for whales in some months – mainly April but also May for minke whales, and March for humpback

whales – resulted in less informative models with somewhat uniform predictions in those months. The trend in predictions across months is likely to be robust despite this, but, for minke whales, extending the seasonal data window in this region should be a priority in light of projected environmental changes in the Western Antarctic Peninsula (see below). Further, tagging may have been biased towards smaller individuals more likely to feed in protected bays, and our study did not include information

on Antarctic blue (*Balaenoptera musculus intermedia*) and fin (*Balaenoptera physalus*) whales, two important krill consumers likely to overlap with the krill fishery in more open waters (Santora et al., 2010; Santora et al., 2014; Herr et al., 2016). Lastly, behavioural differences between humpback and minke whales could influence the definition of 'restricted' and 'transit' locations estimated from the state-space models, with minke whales likely switching behavioural states in a manner that is more difficult to detect with a state-space switching model. Further, directed work, where satellite tracking is augmented with accelerometry to detect foraging more directly, is required to investigate this fully.

Predator foraging behaviour is highly variable, including seasonally, depending upon animal status (e.g., for different phases of the penguin breeding season, Warwick-Evans et al., 2018). As such, the scale and intensity of habitat used by a predator can change. This has important consequences for management of the krill fishery (e.g., see Trathan et al., 2022, for a broader discussion of scale in the management of the krill fishery). Briefly, the dynamic mosaic of predator demand across time and space and across species presents a number of challenges to CCAMLR, particularly as habitat use preferences are unknown for many species, or are only partially known for others. For most species, there is a lack of understanding about how predators use their habitat in winter. How predators interact with the available krill in an area now requires deeper understanding, particularly where carryover effects may be important (Trathan et al., 2021).

Our analysis shows that as the season progresses, fishing shifts south and inshore, similar to the predicted seasonal movement of humpback whale foraging areas. Tracking data from five humpback whales analysed by Curtice et al. (2015) showed that whales used smaller more concentrated areas and moved nearer to the coast over the foraging season. Since both fishing vessels and humpback whales are targeting krill, a similar progression of their hotspots should be expected if krill distribution shifts through the year, and especially if krill behaviour or ecological drivers of krill habitat use have a seasonal component. Indeed, Atkinson et al. (2008) note that krill density peaks in the middle of summer (January) and declines thereafter, reflecting the pulse of recruitment from larvae during spring–summer and subsequent mortality. However, adult krill are also thought to migrate from shelf waters to deeper oceanic waters at the edge of the shelf to spawn in summer, returning at the end of the summer to winter in shelf or coastal waters (Siegel, 1988; Trathan et al., 1993; Siegel, 2005). Apparently, krill overwinter in coastal waters, regardless of sea ice cover (Reiss et al., 2017). In this context, Lascara et al. (1999) have also reported that at the Western Antarctic Peninsula, there is a strong decrease in krill biomass, with altered aggregation characteristics between spring (November) and winter (August–September). As such, in summer (January–February), there are widespread, dense aggregations of smaller size, which are located in the upper water column. Whereas, in autumn (March–May), there are larger, less dense aggregations that are located deeper in the water column. Such a change in krill aggregation state could, at least partially, be associated with predator foraging behaviour (Tarling and Fielding, 2016), particularly if krill show differential responses to different feeding behaviours, by for example, baleen

whales or penguins, and these predators remain seasonally in the region for different periods of time. Krill behaviour will also be affected by complex dispersal and retention of krill due to local currents (Trathan et al., 2022). Krill may concentrate near to local bathymetric features, entrained by local oceanographic flows (Capella et al., 1992; Piñones et al., 2013b). In late autumn/winter, massive, extremely dense aggregations of krill have been documented in the nearshore bays on the western side of the Antarctic Peninsula (Nowacek et al., 2011) coincident with where the krill fishery is known to operate at these times (Weinstein and Friedlaender, 2017). Baleen whale concentrations (Johnston et al., 2012) mirror these summer aggregations of krill and whales consistently distribute in these places and forage in a manner that optimises energy gain (Friedlaender et al., 2013; Friedlaender et al., 2016; Tyson et al., 2016).

Johannessen et al. (2022 see also Warwick-Evans et al., 2022) estimate peak potential competition (calculated as humpback whales' per capita consumption multiplied by their abundance through the season, and krill catch through the season) in April, which corresponds with the highest values in our monthly spatial overlap index. Based on the assumption that whales spend 120 days in their Southern Ocean foraging areas (Lockyer, 1981), Johannessen et al. (2022) calculated very limited humpback whale-fishery competition by May, but tracking data in this study and Weinstein et al. (2017) shows that some individuals remain in the region as late as July. Further, minke whales may remain in the Western Antarctic Peninsula region much longer, and can overwinter in the area (Dominello and Širović, 2016). Thus, as vessels increasingly fish the region later into the year, it is unlikely that any overlap with baleen whales will be limited to just the summer. This will likely be exacerbated by the increasingly ice-free environment (e.g., Turner et al., 2016) that is likely to result in a longer season for fisheries and whales in future. Indeed, Trathan et al. (2022) show that peak fishing effort is now in May, highlighting the need for more intensive studies on predator-prey interactions at this time.

Minke whales occur within the foraging habitat of humpback whales (this study, Friedlaender et al., 2021). The seasonal movement of humpback whales closer inshore (this study, Curtice et al., 2015; Weinstein and Friedlaender, 2017) could thus increase potential competition between minke whales and humpback whales as the season progresses, congruent with increased fishing effort inshore.

Humpback whales, minke whales and krill fisheries are not the only consumers of krill in the study region, and as the humpback whale population that uses the Western Antarctic Peninsula region appears to be increasing (Pallin et al., 2018), it suggests that prey availability is not currently a limiting factor for baleen whales. However, changing populations of other krill consumers, suggest that species interactions should be considered as part of CCAMLR's revised krill management approach, particularly given the ongoing expansion of the krill fishery. Further, as other baleen whale populations recover, competitive effects may increase, both amongst krill predators and with the krill fishery. Currently, catch levels in the study area remain low in real terms (~155,000 tonnes) compared with estimates of local krill biomass (~19.2 million tonnes in 2019; Krafft et al., 2021). However, the

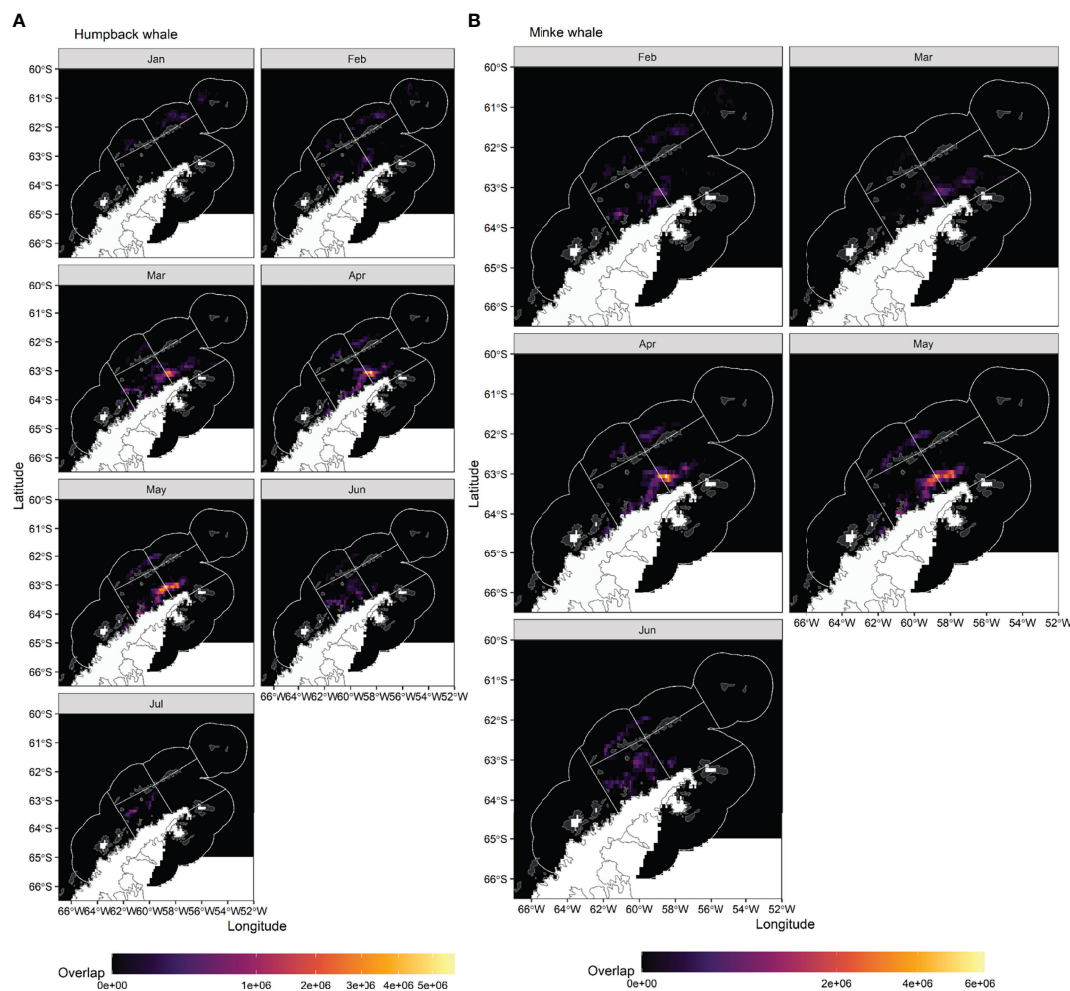


FIGURE 7 | Monthly overlap between **(A)** humpback whales and krill fishing and **(B)** minke whales and krill fishing, estimated as predicted probability of whales being in a restricted behavioural state in a given grid cell in a given month, multiplied by monthly fishing catch.

fishery regularly operates in favoured areas where krill biomass is predictable, but which are also areas used by krill predators (Trathan et al., 2022). Although Cox et al. (2018) argue that krill density was stable from 1976–2016, several studies have reported declines in krill density in the southwest Atlantic in the late 20th century (Atkinson et al., 2004; Atkinson et al., 2019; Hill et al., 2019), raising the possibility of increasing fishing of a declining resource. Future expansion of the krill fishery must therefore follow a precautionary approach to ensure krill predators are not disadvantaged. A key issue for managers will be ensuring replenishment of krill by ocean currents remains adequate for predator needs, and that retention and carry over of krill in certain areas is sufficient across time (Trathan et al., 2022). In the Western Antarctic Peninsula, many Adélie (*Pygoscelis adeliae*) and chinstrap (*Pygoscelis antarcticus*) penguin populations are decreasing (Cimino et al., 2016; Hinke et al., 2017b; Strycker et al., 2020). Understanding the drivers of these population changes, whether through increased competition with other krill predators, climate change or local fishery impacts is now required.

Recently, the international fishing fleet targeting Antarctic krill agreed to voluntarily avoid catches in the vicinity of large *Pygoscelis* penguin colonies situated in the Western Antarctic Peninsula region (e.g., Trathan et al., 2022; Godø & Trathan, 2022). This was based on the recognition that land-based predators are potentially most vulnerable to the competitive effects of fishing and any possible depletion of the resources predators need to provision both themselves and their offspring during the breeding season. The focus of the so-called ‘Voluntary Buffer Zones (VBZ)’ was penguin colonies, as these are the most numerous central-place foraging predators breeding on the Antarctic Peninsula. The VBZ are seasonal so only reduce competitive effects with the fishery during the penguin breeding season. Each VBZ extends from the penguin colony location to either 30 km or 40 km, depending upon the penguin species (see details in Trathan et al., 2022). The VBZ include the majority of the penguin foraging habitat during breeding for colonies within Subarea 48.1, including ~74.3% of chinstrap, ~97.5% of gentoo and ~91.4% of Adélie penguin colonies. Thus, approximately 74,160.8 km² of ocean is protected:

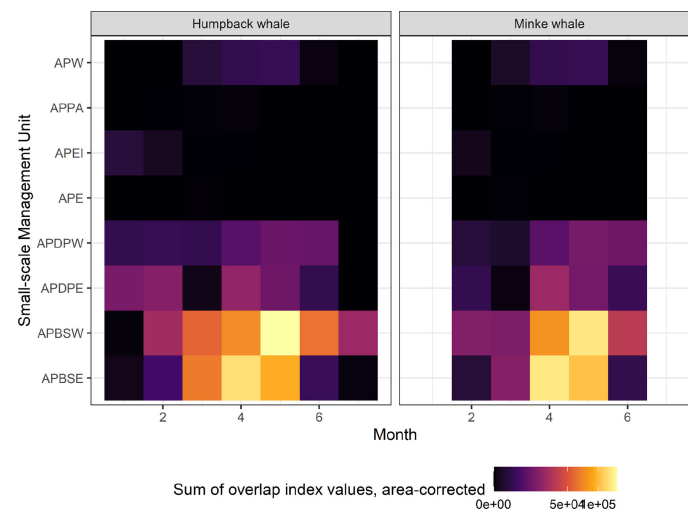


FIGURE 8 | Heatmap of the summed fishing-whale overlap index values (mapped in **Figure 7**) in each Small-Scale Management Unit (vertical axes), by month (horizontal axes). The summed values were divided by the number of grid cells in each Small-Scale Management Unit, to correct for size differences. APW, Antarctic Peninsula West; APPA, Antarctic Peninsula Pelagic Area; APEI, Antarctic Peninsula Elephant Island; APE, Antarctic Peninsula East; APDPW, Antarctic Peninsula Drake Passage West; APDPE, Antarctic Peninsula Drake Passage East; APBSW, Antarctic Peninsula Bransfield Strait West; APBSE, Antarctic Peninsula Bransfield Strait East.

~13,131.9 km² within the Gerlache Strait; ~37,055.6 km² around the South Shetland Islands; and ~23,973.3 km² around the tip of the Antarctic Peninsula (Godø & Trathan, 2022). Inevitably, protection, though voluntary, also provides significant levels of protection for baleen whales, including both humpback and minke whales. Stricter protection would be provided by a proposed Marine Protected Area in the Western Antarctic Peninsula and South Scotia Arc (Delegations of Argentina and Chile, 2020). The proposed MPA includes protected zones encompassing areas in the Bransfield and Gerlache Straits and areas in the Bellingshausen Sea, important for krill, birds and marine mammals. The MPA would also include zones where commercial krill fishing is permitted (Delegations of Argentina and Chile, 2020). Still, there is at present no understanding

about functional overlap between the fishery and krill predators, as opposed to simple spatial overlap. To determine levels of functional overlap, we need to better understand how predators (and the fishery) target krill.

As such, there is now a real need to examine the characteristics of krill patches targeted by the fishery, compared with patches targeted by natural krill consumers. Exploitation of large, dense patches of krill by the fishery may be similar to the patches required by large baleen whale species, or other predators. Minkes potentially can exploit less dense patches, but their habitat is restricted, and may become even more restricted as the polar regions continue to warm (Constable 2022). Minkes may currently escape competition with fisheries (and humpbacks to some extent) due to their high affinity for sea ice and the capability

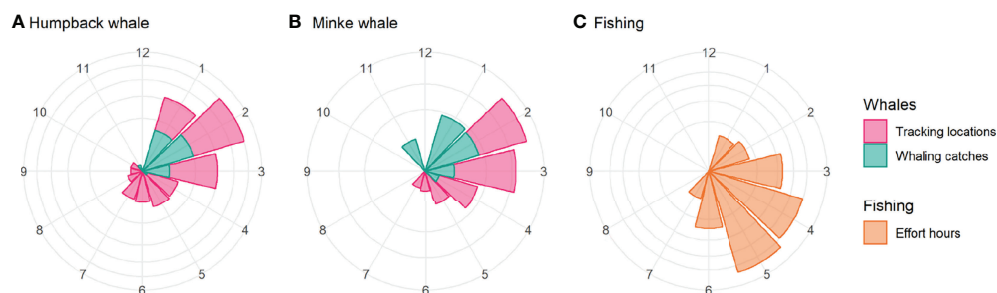


FIGURE 9 | Approximate phenology of humpback whales (A), minke whales (B) and fisheries (C) in the Western Antarctic Peninsula by month. The figure shows an approximate comparative phenology for whales – using the monthly number of satellite tracking location estimates in the study area (magenta) and the monthly number of whaling catches south of 60° S from 1900–2015 (Allison, 2016) (cyan) – and fisheries – using the monthly hours of effort (orange). Values were normalised for presentation, and the y-axis is square root-transformed. The whale phenology will be biased towards tagging activity during the summer and autumn, and whaling catches will be biased against catches in winter and spring. Minke whales (Antarctic and common) were only caught in large numbers from around 1960 onwards, around which time humpback whale catches declined (Rocha et al., 2015).

to exploit less dense krill patches. However, decreasing sea ice means baleen whales (see discussion in Friedlaender et al., 2021) and fisheries (Krüger, 2019) are likely to experience increasing niche overlap. In contrast, Pickett et al. (2018) show that climate changes may not increase competition between gentoos and Adélies in the Western Antarctic Peninsula region, due to fine scale niche partitioning. This illustrates that increased potential competition is not a foregone outcome, given the fine-scale partitioning resulting from different foraging mechanics in humpback and minke whales and with other predators of krill. However, overall depletion of krill remains a concern despite any ability of consumers to partition resources at fine spatial scales in four dimensions, i.e., in space and time.

The primary aim of our modelling was spatial prediction, and we therefore used spatial random forests (Hengl et al., 2018), which incorporate distances among observations in the dataset. However, we included a limited number of environmental covariates to add some information on the physical environment and its correlation with whale behavioural state. In the humpback whale models, sea surface temperature variables were the most important environmental covariates. This likely reflects the transition of humpback whales from migratory (transit) to foraging (restricted) behaviour as they reach the South Shetland Islands and Peninsula. Sea surface temperature has been found to be an important covariate influencing the habitat selection of humpback whales in the Southern Ocean (e.g., Andrews-Goff et al., 2018; Bestley et al., 2019; Riekkola et al., 2019; Reisinger et al., 2021). Johannessen et al. (2022) observed a positive correlation between humpback whale presence and sea surface temperature in the Bransfield Strait region, and interpret this as a preference for the warm, nutrient-rich Circumpolar Deep Water that is delivered onto the continental shelf (Martinson & McKee, 2012; Wang et al., 2022), driving marine productivity (e.g., Ducklow et al., 2012).

In contrast, sea ice variables were more often among the most important environmental variables in the minke whale models, reflecting the species' closer relationship with sea ice (Friedlaender et al., 2006; Ainley et al., 2012; Friedlaender et al., 2014; Williams et al., 2014; Ainley et al., 2017; Herr et al., 2019; Ainley et al., 2020; Friedlaender et al., 2021). For example, sightings and density of whales, mainly minkes, along surveys in the Amundsen and Bellingshausen Seas were best explained by sea ice concentration and distance to the marginal ice zone (Ainley et al., 2007) and Williams et al. (2014) observed most minke whales in the Weddell Sea near the sea ice edge. Similarly, Herr et al. (2019) found that minke whale distribution was best explained by distance to the sea ice edge – with most whales observed at the sea ice edge and through to medium sea ice concentrations. However, waters off the Western Antarctic Peninsula are comparatively ice-free (Ducklow et al., 2013), and becoming more so (Turner et al., 2016). Minke whale abundance off the Western Antarctic Peninsula is lower than in surveyed areas in the Weddell Sea (Herr et al., 2019) and minke whales tracked off the Western Antarctic Peninsula spent a great deal of time in open water

(sea ice concentration <20%) with few locations in dense sea ice (>20% concentration) (Linsky et al., 2020). Minke whales thus have a facultative rather than obligate link with sea ice.

In the sea-ice zone there is a tight coupling between sea-ice melt and ocean productivity, but there is a weeks-to-months lag between sea ice retreat, phytoplankton increase and then the accumulation of zooplankton, including krill, which finally attracts birds and marine mammals (e.g., Fauchald et al., 2017). The movement of humpback whales in their Antarctic foraging areas has been linked to sea ice concentration one month prior (Andrews-Goff et al., 2018) and to distance to the sea ice edge two months prior (Riekkola et al., 2019). Our results indicate a lagged relationship in minke whales too. In both species, our results indicate a link with lagged sea surface temperature that may suggest water masses may also be influential in driving productivity and the distribution of krill.

Habitat selection modelling of some of the humpback whale and minke whale tracking data used by Friedlaender et al. (2021), and also included in our study, showed similar differences in the habitat selection of humpback and minke whales. Humpback whales showed decreasing preference as sea ice concentration increased, but also as distance from the sea ice edge increased (meaning they preferred areas near the sea ice edge but not in sea ice). They also preferred shallower, onshelf areas. Minke whales showed a comparatively flat preference-response for distance to the sea ice edge and depth. Both species had strong preferences for enclosed bays (Friedlaender et al., 2022). Such known habitat relationships informed by surveys and tracking can help to predict and project overlap between krill consumer and the krill fishery in adaptive management frameworks. This is increasingly urgent as the Western Antarctic Peninsula ecosystem changes (Clarke et al., 2007) with changing predator populations and rapid environmental change in this region, but also in the context of an expanding krill fishing (Trathan et al., 2022). An outlook is that continued decreases in sea ice (Turner et al., 2016) may in future increase favoured humpback whale habitat. Increases in chinstrap penguin populations have been attributed to decreases in the number of years with extensive winter sea ice (Fraser et al., 1992), raising the question of whether the same may happen for humpback whales, although more recently, chinstrap populations are now decreasing (Strycker et al., 2021). Foraging areas may also be accessible to whales for longer, as it will for fishing vessels and, ultimately, krill could become more accessible to consumers and fisheries in their key overwintering habitats. Conversely, habitat favoured by minke whales may decrease. However, the impacts of sea ice loss on krill abundance and distribution will be significant (Flores et al., 2012; Hill et al., 2013; Piñones & Fedorov, 2016; Veytia et al., 2020) with knock-on effects for consumers.

Broadly, our work illustrates the importance of integrating time as well as space when assessing overlap between fisheries and marine predators. Moreover, we show that overlap can be characterized by small spatial scales, and that fisheries should where possible be managed at these small scales, typical of predator foraging scales.

DATA AVAILABILITY STATEMENT

The datasets presented in this article are not readily available because Antarctic krill fishing catch data should be requested from CCAMLR. Fishing effort data are publicly available from Global Fishing Watch. Whale tracking data are available from the authors without undue reservation.

Requests to access the datasets should be directed to CCAMLR (<https://www.ccamlr.org/en/node/74767>; catch data) and Ryan Reisinger (r.r.reisinger@southampton.ac.uk; tracking data).

ETHICS STATEMENT

The animal study was reviewed and approved by Duke University Institutional Animal Care and Use Committee (A049-122-01), the University of California Santa Cruz Institutional Animal Care and Use Committee (friea1706), Oregon State University Institutional Animal Care and Use Committee (4513) and the SWR/PIR Regional NMFS Institutional Animal Care and Use Committee. Research was conducted under NMFS Permits 14907, 14809, and 14856, ACA Permits 2009–013 and 2015–011, Duke University IACUC A049-122-01, UCSC IACUC friea1706, and OSU ACU 4513.

AUTHOR CONTRIBUTIONS

Conceptualization: RR, PT, CJ, AF. Data curation: RR, TJ. Formal analysis: RR; Funding acquisition: RR, PT, CJ, AF, JD. Investigation: RR, PT, CJ, TJ, JD, RP, AF. Writing - original draft: RR, PT. Writing - review and editing: RR, PT, CJ, TJ, JD, RP, AF. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.914726/full#supplementary-material>

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North Pacific minke whales call rapidly when calling conspecifics are nearby

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North Pacific minke whale (*Balaenoptera acutorostrata*) boing calls are commonly detected in Hawaiian waters. When producing boing vocalizations, minke whales seem to be in one of two calling behavioral states. Most often minke whales produce boings with inter-call intervals of several minutes, but sometimes minke whales call rapidly with inter-call intervals of less than a minute. Since minke whales are difficult to detect visually, cue-rate-based density estimation using passive acoustic monitoring has been proposed. However, the variables that influence cue rate or calling rate are poorly understood in most whales, including minke whales. We collected passive acoustic recordings from 47 bottom-mounted hydrophones at the Pacific Missile Range Facility's instrumented range off the coast of Kaua'i, Hawai'i to test the hypothesis that minke whales call more rapidly when closer in proximity to other calling conspecifics. A total of 599 days of data were recorded between August 2012 and July 2017 and were automatically post-processed to detect, classify, and localize calls. Localized calls were grouped into tracks and manually validated, resulting in 509 individual tracks composed of 36,033 calls within a 16 x 39 km focal study area. Tracked minke whales exhibited a strong bimodal call rate with means of one call every 6.85 min ($\sigma = 2.54$ min) and 0.63 min ($\sigma = 0.36$ min). We ran hidden Markov models to quantify the relationship between call rate and the distance to the nearest calling conspecific. Overall, the probability of the higher call rate occurring increased as the distance to the nearest conspecific decreased, and the probability of the lower call rate occurring increased as the distance to the nearest conspecific increased. We also examined individual track data and found that minke whales may also exhibit other responses (i.e. increased speed, changes in heading, and cessation of calling) when calling conspecifics are nearby. These findings provide new information about minke whale calling behavior in what is likely a breeding area.

KEYWORDS

minke whale (*Balaenoptera acutorostrata*), inter-call interval (ICI), calling rate, cue rate, bioacoustics, passive acoustic monitoring, animal behavior, marine ecology

1 Introduction

North Pacific minke whale (*Balaenoptera acutorostrata*) boing calls are commonly detected in Hawaiian waters from fall to spring, but the animals that produce them have rarely been sighted and little is known about their behavior in this area. The minke whale boing call was first detailed by Wenz (1964) using recordings from submarines operating off the coast of San Diego, California and in Hawaiian waters and also from two bottom-mounted hydrophones off the coast of Kāneʻohe, Hawaiʻi. Although it was suspected that the boing was produced by a whale species (Thompson and Friedl, 1982), it took about 40 years until the source of the boing was determined to be from a minke whale (Rankin and Barlow, 2005). Minke whales are difficult to detect visually, so passive acoustic monitoring (PAM) is an important methodology for learning about the behavior and life history of this species.

Thompson and Friedl (1982) recorded boing sounds from two bottom-mounted hydrophones off the coast of Oʻahu. They observed two calling states with distinct inter-call intervals (ICIs). They proposed that the whales produced calls with ICIs of approximately 30 s when in acoustic contact with another calling whale, and 6 min when not in acoustic contact with another calling whale, but this study was limited by a low sample size and the inability to localize calls and measure distances between individuals (Thompson and Friedl, 1982). The significance of the boing call is currently unknown. However, since humpback whales (*Megaptera novaeangliae*) in Hawaiian waters use song for breeding purposes (Tyack, 1981) and have a similar seasonal and spatial overlap with minke whales, past researchers have suggested that the minke whale boing is also a mating call (Oswald et al., 2011; Martin et al., 2015), but this hypothesis is yet to be tested. Learning more about the calling rate of whales in different contexts can help us better understand the function of calls in whale behavior.

The central North Pacific boing call produced by minke whales in Hawaiian waters (as opposed to the eastern North Pacific boing call, which has a slightly different pulse repetition rate and call duration) has an onset transient component followed by a long call (mean duration of 2.6 sec) with both frequency and amplitude modulation (Rankin and Barlow, 2005). The 1,350 to 1,440 Hz band contains the majority of energy from the boing call with 115 Hz pulse repetition rate harmonic bands (Wenz, 1964; Rankin and Barlow, 2005; Martin et al., 2015). The peak frequency in this band has been termed the dominant signal component (DSC) (Martin, 2009), and has been identified as a feature to attribute calls to individual whales in some situations (Martin et al., 2013).

The life history of minke whales that spend time in Hawaiian waters is unknown, but acoustic detections and visual sightings in other areas can give clues about their migratory patterns. In the Chukchi Sea, Delarue et al. (2012) detected a small number

of central North Pacific boings in the early fall (n=44), and boings resembling the eastern North Pacific type in the late summer and fall (n=10). In the North Pacific, pulse trains and downsweep calls have been documented in the presence of minke whales during the summer in Cormorant Channel, British Columbia, Canada which is likely a feeding area (Nikolich and Towers, 2020). Minke whales sighted off Vancouver Island and central British Columbia often have scars characteristic of cookiecutter sharks (*Isistius brasiliensis*) which are only in tropical and subtropical waters (Towers et al., 2013). Based on these observations and acoustic detections, the minke whales detected in Hawaiian waters probably migrate north to arctic or subarctic waters to feed, similar to the migration patterns of other large baleen whales.

In addition to helping us understand whale behavior, calling rate, or cue rate, is a necessary variable for PAM cue-rate-based density estimation (Marques et al., 2009). Visual surveys are currently the primary method to estimate marine mammal abundance, but minke whales are difficult to see due to their small size, minimal surface cues, and tendency to be alone, and so it is very challenging to estimate their abundance precisely (Zerbini et al., 2006). In addition, the visual ship-based surveys for marine mammals in Hawaiian waters are usually conducted during summer and fall, and since minke whales are rarely visually or acoustically detected during this time, no total abundance estimate exists for minke whales in this region (Carretta et al., 2014). Quantifying the minke whale cue rate and the variables that influence it may make it possible to estimate the abundance of minke whales using PAM for applications when tracking individuals is not possible.

In this paper, we investigate the hypothesis proposed by Thompson and Friedl (1982) that minke whales call more rapidly when closer to other calling minke whales. We recorded and localized boing calls off of Kauaʻi, Hawaiʻi between fall and spring for 5 years, and spatio-temporally grouped these localized calls into acoustic tracks. Using these tracks, we quantified individual minke whale ICIs and modeled ICI as a function of distance to the nearest tracked calling conspecific. This paper summarizes the calling behavior of minke whales using 36,033 boing calls from 509 tracks.

2 Methods

2.1 Study area and data description

The Pacific Missile Range Facility (PMRF) is a U.S. Navy training and testing area northwest of the island of Kauaʻi, Hawaiʻi. For this analysis, we analyzed recordings from 47 bottom-mounted hydrophones spread over a grid approximately 20 km to the east-west and 58 km to the north-south (Figure 1) to detect, classify, and localize minke whale

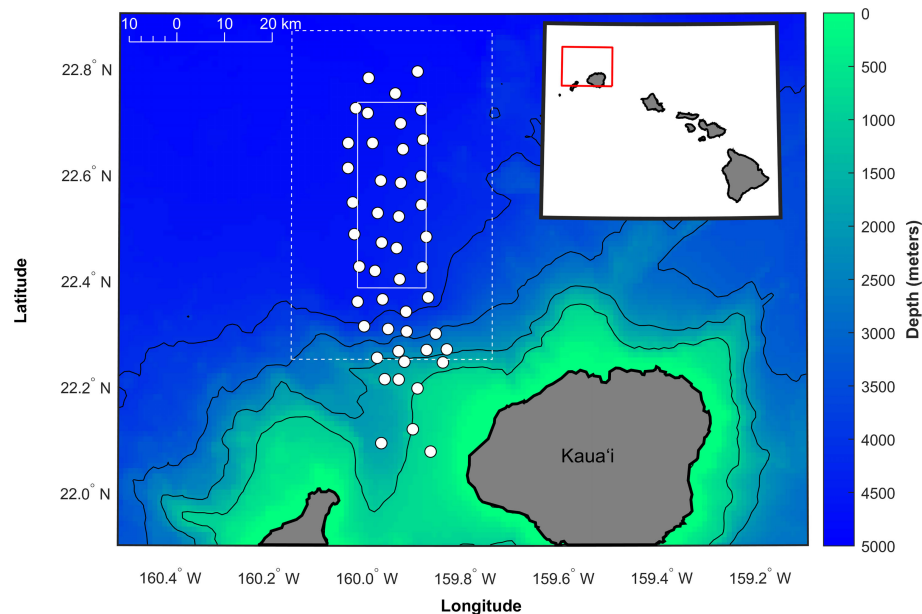


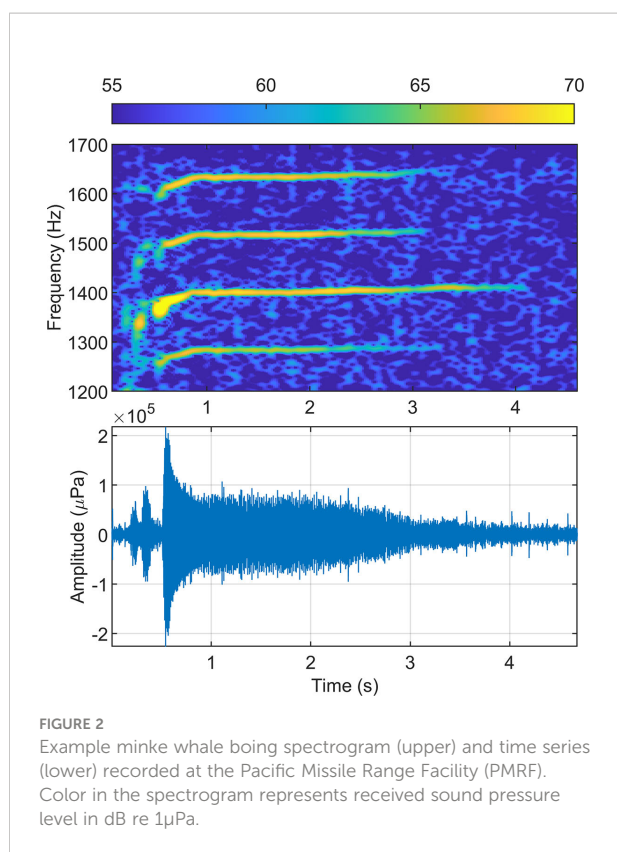
FIGURE 1

Map of the approximate locations of the 47 hydrophones used in this analysis (white circles) at the Pacific Missile Range Facility (PMRF) off Kaua'i, Hawai'i, as shown by the red box in the inset map. The focal study area of the array extends approximately 16 km to the east-west and 39 km to the north-south (boundaries shown by a solid white box). The 15 km search area outside the focal area is shown with a dashed white box. The depth contours are every 1,000 m (1 km spatial resolution, Hawaii Mapping Research Group, The School of Ocean and Earth Science and Technology, the University of Hawai'i at Mānoa, <http://www.soest.hawaii.edu/hmrg/multibeam/bathymetry.php>).

boing calls (Figure 2) from data collected between August 2012 and July 2017. This period from 2012 to 2017 was chosen because the broadband hydrophone array configuration was consistent during this time. As detailed by Martin et al. (2015), the depths of the hydrophones ranged from 650 m to 4,700 m and had a suitable frequency response to detect calls from minke whales. A custom personal computer-based recorder described by Martin et al. (2013) and updated with a second 32-channel analog-to-digital converter was used to record a total of 62 hydrophones and two inter-range instrumentation group time code channels. Full bandwidth data were collected at a 96 kHz sample rate with 16-bit samples. Starting in August 2014, the collection of additional long-term recordings at a 6 kHz sample rate increased the recording effort to monitor low-frequency whale calls, including the minke whale boing call. Recordings at the 96 kHz sample rate typically had maximum durations of 1.9 days of continuous data, while recordings at the 6 kHz sample rate had maximum durations of 10.9 days. The recording limit was a function of sample rate, bit depth, the number of channels recorded, and a maximum hard disk drive capacity of 2 terabytes supported by the recorder. No recordings during known U.S. Navy training or testing activities were included in the analysis. This work only analyzed tracks from unclassified recordings. Of the focal tracks analyzed, two started within 24 hours after U.S.

Navy training and testing activities ended. Based on previous work by Durbach et al. (2021), between 24 hours and 4 days after the last sonar transmission, the kinematic behavior of minke whales on PMRF is similar to baseline behavior.

In order to investigate the impact of conspecifics on minke whale calling rate, we had to ensure that if a minke whale was vocalizing within a certain distance from another whale, both whales would be detected, localized, and tracked in all expected noise conditions. Based on the geometry of the PMRF array and the probability of detection of minke whale calls as a function of location, we designated an inner rectangular focal area where, if a whale called from a distance of 15 km or less from the focal area boundaries, we would be able to detect, localize, and track it. In other words, we could detect nearest calling conspecifics for whales tracked within the focal area out to 15 km. The focal area extended approximately 16 km to the east-west and 39 km to the north-south (indicated by the solid white box in Figure 1) with approximate latitude boundaries of 22.38°N and 22.74°N, and longitude boundaries of 160.02°W and 159.87°W. The 15 km search area was smaller than that defined by Harris et al. (2019) which conservatively encompassed the area where minke whale calls could be accurately detected, localized, and tracked based on expected noise conditions, source levels, and transmission properties of the boing call.



2.2 Post-processing and validation

The automated minke whale boing call detection and classification algorithms developed to process recordings collected at the PMRF instrumented range have been previously described (Mellinger et al., 2011; Martin et al., 2013; Martin et al., 2015) and are briefly reiterated here. The central North Pacific minke whale boing call detection and classification process operated in multiple stages. The first stage detected the near-continuous wave portion of the call by measuring if the energy in the detection band (1,320–1,450 Hz) exceeded a long-term spectral average noise estimate in the detection band for more than 0.8 sec. The second stage computed a spectral correlation to locate the onset time of the frequency modulated portion of call, and was used as the measured time of arrival (TOA) in the model-based localizer (discussed in the next paragraph). The third stage reprocessed the raw time series data with a longer fast Fourier transform (FFT) length to produce an FFT bin resolution of less than 1 Hz. The average power in the 1,350–1,440 Hz range over the duration of the signal was calculated and compared to the peak power in the same frequency and time range. The resulting value was termed a quasi-signal-to-noise ratio (QSNR) since the average power in the 1,350–1,440 Hz range

also included the peak signal. If the QSNR exceeded a user-defined value of 2.0, the signal was classified as a boing call detection, and a high resolution measurement of the DSC was made. To our knowledge, the central North Pacific boing call is the only call associated with minke whales that has been recorded on PMRF.

The model-based localization algorithm for data processing was previously described by Martin et al. (2015) and is briefly described here. To localize calls, we compared the measured time difference of arrivals (TDOAs) of each call across the hydrophones with the modeled TDOAs. The onset times for automatic detections on multiple hydrophones were the measured TOAs, and were subtracted from each other to calculate measured TDOAs. Modeled TDOAs were calculated from theoretical source locations. An iterative spatial gridding process minimized the weighted least square error between measured and modeled TDOAs to spatially locate a call. The least square error was weighted by order of TOA with earlier arrivals weighted more than later arrivals, and was also normalized by the number of hydrophones in the localization solution. Only localizations with a weighted least square error value between measured and modeled TDOAs of less than or equal to 0.075 sec were used in this analysis. In addition, the DSCs of the first four detections for a candidate localization were required to be within 5 Hz to initiate grouping of detections. Currently, ground-truth whale positions to determine localization accuracy do not exist. However, Martin et al. (2015) noted that surface ship hull-mounted mid-frequency active sonar transmissions within the hydrophone array at PMRF that were localized with the same algorithm were typically within 50 m of ship positional data. The accuracy with which the start of a signal is detected influences the accuracy of localization. Despite mid-frequency active sonar transmissions being a higher frequency than minke whale boings, the start of both signals have an onset transient with a sharp rise time that is detected well.

An automatic tracking algorithm (previously described by Klay et al. (2015) and used by Harris et al. (2019); Helble et al. (2020b); Durbach et al. (2021) to track minke whales) spatially and temporally grouped localized calls into individual tracks by recursively examining distance and time between successive candidate localizations. The following user-defined values were tuned for tracking minke whales: a track had to be composed of 12 or more localizations, a localization solution required automatic detections from 8 or more hydrophones, the distance between localizations had to be less than or equal to 0.06 decimal degrees in both latitude and longitude (approximately 6.7 km), and the maximum time allowed between any two localizations before terminating a track was set to 40 min. Gaps between recordings could vary from minutes to weeks. In this study, we did not group calls into tracks across individual recordings.

For every localized call, we searched for the closest localized call from another track within the past 10, 20, and 30 min. If at least one other vocalizing minke whale was present during that time window and within the 15 km search area from the focal study area, we calculated the straight-line horizontal distance between the focal track's call and the neighboring track's calls. The distance to the nearest calling conspecific or "nearest neighbor" was the distance to the closest localized call from another track during that time window. For statistical analysis, nearest neighbor distances were assigned to categories of 0–5 km, 5–10 km, 10–15 km, or 15+ km. If there were no other tracks within the search area and time window, then the nearest neighbor for the focal track was assigned to the 15+ km category given that there were additional whales beyond 15 km. Grouping nearest neighbor distances into categories allowed us to keep observations from all tracks, including those that did not have a detectable nearest neighbor, without assuming an arbitrary large value for its nearest neighbor distance. The 5 km distance bins were small enough to see changes in calling behavior across distances, but large enough to have large sample sizes and small confidence intervals for each category. We only searched for nearest neighbors within the same recording as that containing the focal track. We tested multiple nearest neighbor time windows (10, 20, and 30 min) to account for variability in call timing and location (e.g. if an animal skipped calls or if some calls from the nearest neighbor were outside of the study area). Since the maximum time between subsequent calls before terminating a track was 40 min, we did not test window sizes larger than 30 min to avoid potentially declaring a whale as its own nearest neighbor.

We manually validated all tracks to ensure that a track was generated by an individual whale since spurious tracks could be generated under certain conditions. Specifically, a single track could be classified as two or more tracks in close proximity to each other when the ICI decreased or the number of co-occurring tracks in the study area increased. During the validation process, it was important to inspect and rectify potential duplicate tracks by removing or combining them since they could produce artificial minimum distances between conspecifics (i.e. a whale could be its own nearest neighbor). An interactive program was used to systematically examine the movement, DSC, and ICI of tracks in close proximity to each other. We combined tracks if the overall track path appeared to be a single animal which was evidenced by a relatively stable DSC and a call rate distribution that fell within the expected bimodal call rate distribution. Alternatively, we removed a track if it did not satisfy these criteria and appeared to be produced by multiple animals. No tracks were split since parsing calls from an individual track to multiple individuals is difficult and subjective without other data from tags or visual sightings. The validation process reduced the total number of focal tracks by 15.7%. Using

unmodified tracks has the advantage of adding no subjectivity from the analyst, but a fraction of these automatic tracks are likely spurious or split from the same animal. To test the sensitivity of the results to the validation process and ensure call rate results were not biased by combining or removing tracks, both validated and unvalidated tracks were run through the same statistical analyses and the overall trend of the results were similar. From this analysis we determined that any subjectivity introduced from the validation process was minimal and using validated tracks for the statistical analyses provided the most accurate information on minke whale calling behavior and distances to conspecifics.

In addition to validating how calls were grouped into tracks, we also quantified the performance of the entire detection, classification, localization, and tracking process in a way similar to Helble et al. (2020a). We randomly selected 5% of all tracks from the full range of seasons and years. The corresponding raw acoustic data during the times of these tracks from four hydrophones centered and evenly spaced in the study area were imported into Raven Pro (Center for Conservation Bioacoustics, 2019) to generate spectrograms. The TOAs for tracked calls were also imported and colored boxes were overlaid on the signals in the spectrogram, with each color associated with an individual whale track. Sequential calls from the same individual had similar delay patterns across the four hydrophones. If an unmarked call recorded on the four channels had the same delay pattern as other calls along a known track, the call was counted as a missed localization. A missed localization means a call along a track should have been detected, localized, and tracked, but was missed or excluded in one of the automated stages. If detections coincidentally arrived at the correct delay patterns to warrant a localization but did not appear to be a minke boing or if boings were detected but suspected to be from multiple minke sources (based on the signal characteristics and/or source level), they were marked as false localizations. Any missed or false localizations were noted from each of these tracks. In reality, there was no evidence that false localizations occurred along a track, which is not surprising because calls from different whales would need to arrive in near-perfect delay sequences on 8 or more hydrophones to be considered a valid localization. Missed localizations did occasionally occur, and so a "stress test" dataset was created to determine how sensitive subsequent analyses were to missed localizations. To test this sensitivity, 30% of all calls along each track were randomly deleted, and this decimated dataset was also used to see if any changes in the calling behavior statistical analysis could be mistakenly skewed by any missed localizations. In practice, the average missed localization rate was nearly an order of magnitude smaller than 30%, and so the stress test marked a worse-case scenario for any missed localizations to skew the behavioral statistical analysis.

2.3 Changes in calling behavior statistical analysis

We used hidden Markov models (HMMs) to quantify the relationship between calling rate and distance to the closest calling conspecific. For each localized call, we measured the time difference between this call and the next call in the track and saved this value as the ICI. Only tracks or segments of tracks that were within the focal area were modeled in the HMMs. For tracks with multiple segments within the focal area, we only kept the longest segment. This segment was required to have at least 4 localizations within the focal area.

Since minke whales in Hawai'i have two calling states, a rapid and nominal calling state, and we hypothesized that the likelihood of being in each is affected by the distance to the closest calling conspecific, HMMs were appropriate for modeling. We modeled the minke whale ICI as HMMs that were functions of distance to the nearest calling neighbor. The ICI was modeled as a gamma distribution with initial values of 5 min for State 1 (representing the nominal calling rate) and 0.5 min for State 2 (representing the rapid calling rate) with standard deviations of 1 min for both. These initial values were chosen based on the observed distribution of data and the calling rates reported by Thompson and Friedl (1982), but the results presented were not sensitive to these initial values as initial values $\pm 25\%$ were tested and the best models did not change. We used the Akaike information criterion (AIC) (Akaike, 1974) to determine which nearest neighbor window size was best (10 min, 20 min, or 30 min). Once the best model was selected, we used the Viterbi algorithm to group each localized call into one of the two calling states (Langrock et al., 2012; McClintock and Michelot, 2018). To calculate the amount of time spent in each state, we added up the ICIs for the calls assigned to each state. HMM analyses for this study were conducted in R (v 4.0.3,

R Core Team, 2020) using the momentuHMM package (McClintock and Michelot, 2018).

3 Results

Between August 2012 and July 2017, 599 days of data were recorded on each hydrophone. During this time, 2,245 individual minke whale tracks were observed and contained 223,732 calls. Of these tracks, 509 were located within the focal area at least part of the time and so were included as “focal tracks”. The subset of focal tracks contained 36,033 localized calls. Although we recorded throughout the year, minke whale boing vocalizations were only present between October and May (Figure 3). The increase in recording effort from collecting long-term data at the 6 kHz sample rate (initiated in August 2014) is evident from the lower cyan bars in Figure 3 starting in September 2014.

Manual review of 5% of the 509 focal tracks (26 tracks) resulted in a mean missed localization rate of 4.6%. We noted that missed calls were almost always detected on 8 or more hydrophones, but were sometimes discarded by the automated localization process because the least square error value exceeded the user-defined threshold. No false localizations were noted in the manual review process. Relaxing the least square error threshold would result in fewer missed localizations, but would come at the expense of false localizations that can confuse the tracking algorithm. The 4.6% missed localization rate was acceptable and did not affect the outcome of determining the behavioral state, as demonstrated by the stress test dataset (details presented with the modeling results).

Minke whale boing ICIs followed a bimodal distribution (gray bars, Figure 4). Two calling states based on ICI were identified by the HMM and their probability density functions followed the observed ICI distribution well (blue and teal curves,

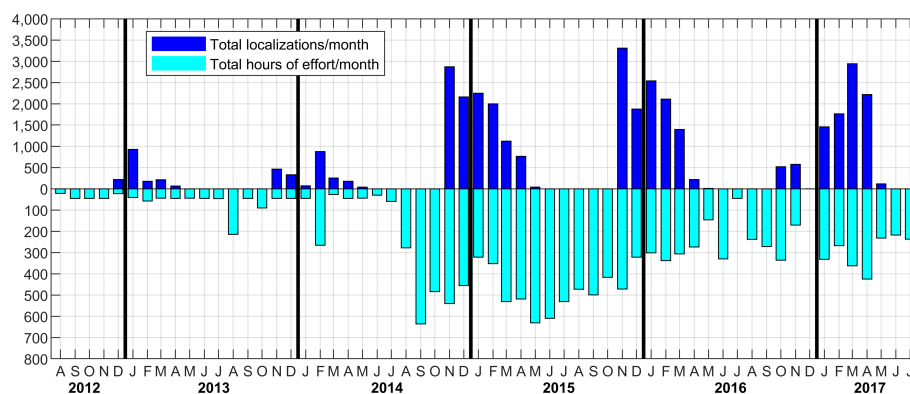


FIGURE 3

The number of localized minke whale calls that were tracked within the focal area per month (upper blue bars), and hours of recording effort per month (lower cyan bars) shown as a function of time from August 2012–July 2017.

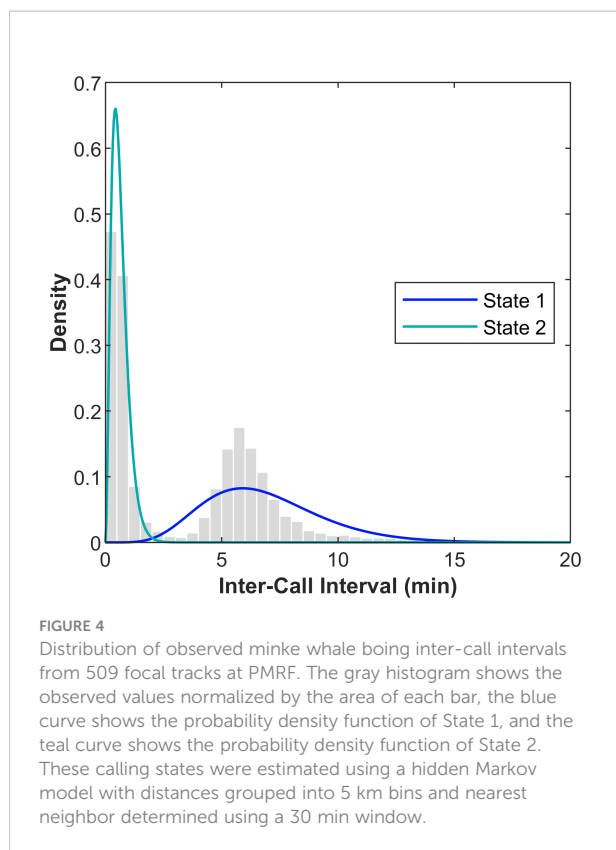


Figure 4). Whales in State 1 had an mean ICI of approximately 6.85 min and whales in State 2 had an mean ICI of approximately 0.63 min (Table 1).

We compared three different time windows to search for the nearest calling conspecific. The 30 min time window performed the best, followed by 20 min, and 10 min, which all performed better than the null model that tested the hypothesis that minke whale inter-call interval was not a function of distance to the nearest neighbor (Table 2). Because the inter-call interval changed by an order of magnitude between State 1 and State 2, these results were not sensitive to occasional missed localizations along a track. In the stress test dataset, 30% of calls were randomly dropped from a track, but the model ranking and stationary state probability trend remained the

TABLE 1 Inter-call interval distribution parameters for hidden Markov model states modeling minke whale calling behavior as a function of distance to the nearest calling conspecific within the past 30 min.

	State 1	State 2
Inter-Call Interval		
Mean	6.85 min	0.63 min
Standard Deviation	2.54 min	0.36 min

TABLE 2 Comparison of models using three different time windows to search for the nearest calling conspecific ranked by the Akaike information criterion (AIC) and AIC weights (Akaike, 1974; Burnham and Anderson, 2002) H_0 represents the null model that calling rate is not a function of nearest calling conspecific.

Time Window	AIC	AIC Weight
30 min	98687	1.0
20 min	98701	1.1×10^{-3}
10 min	98728	1.6×10^{-9}
H_0	98868	5.8×10^{-40}

Distance was modeled as a categorical variable in 5 km bins.

same (although the ICIs for the two states increased, as expected since there were fewer calls).

The probability of a minke whale being in State 1 and calling at a nominal rate increased as its distance to the nearest calling conspecific increased and the probability of a minke whale being in State 2 and calling at a rapid rate increased as its distance to the nearest calling conspecific decreased (Figure 5). Since each observation is a localized call, the plotted probabilities are the probability of a call being in a given state and not the length of time that a whale is in a state (Figure 5 upper). When a whale is calling rapidly, more localizations are available for a given time than when a whale is calling nominally. Of the 36,033 localized calls that were part of focal tracks, 49% were categorized as being in State 1 and 51% were categorized as being in State 2. However, these tracked whales spent a total of 84.7 days calling nominally (State 1) and 8.0 days calling rapidly (State 2), which is equal to 91% of the time in State 1 and 9% of the time in State 2. Therefore, regardless of the distance to the closest calling conspecific, at any given time, minke whales are most likely in State 1 (Figure 5 lower). Calling rapidly has a higher probability when whales are closer together, but it is never more likely than calling nominally.

We selected two interactions between calling minke whales to illustrate these behaviors with individual whales. The first example occurred on 7 Feb 2017 (Figure 6). The minke whale that generated the primary track was calling entirely in State 1 and changed its heading and speed, and ultimately ceased calling during an encounter with a whale that generated the nearest track and was mainly in State 2. At the start of the primary track it was steadily calling and moving east-southeast, and had a distant nearest neighbor that was outside the search area. The whale that generated the track labeled as the “nearest track” in Figure 6 started calling at 18:31 UTC, almost an hour and 15 min after the start of the primary track. When the nearest track started calling it was 11.8 km away from the primary track and it quickly switched into State 2 and traveled southeast. At about the same time, the primary track turned to a south-southeast heading and increased its median speed before it stopped calling. While both animals were calling, the distance between the primary track and the nearest track varied between 10.8–11.8 km.

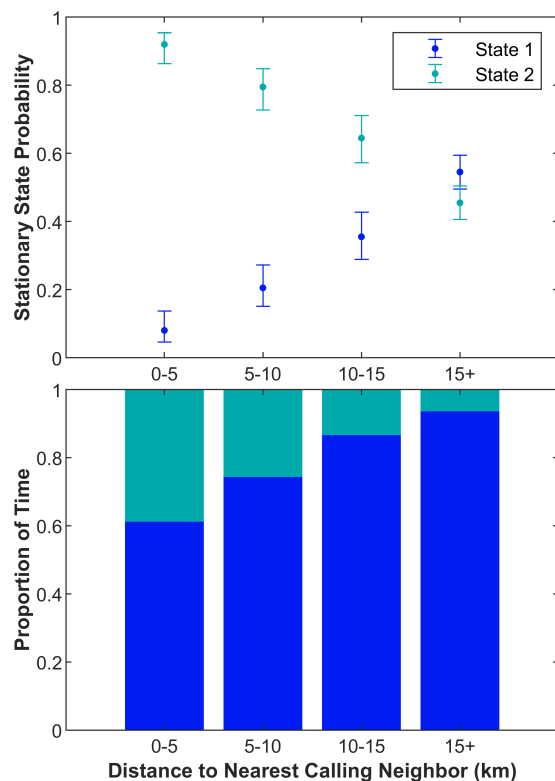


FIGURE 5
The probability of a minke whale call being a part of State 1 or 2 as a function of its distance to the nearest calling minke whale (upper plot) and the proportion of time in each of the states (lower plot). The blue and teal points show the stationary state probabilities of State 1 and State 2, respectively. The error bounds show the 95% confidence intervals. The blue and teal bars show the proportion of time that the focal animals were calling in State 1 and 2, respectively. The nearest neighbor distance is binned in 5 km intervals. The distances to the nearest neighbor are the distances to the closest calling whale within the past 30 min.

The second example of an interaction between two calling minke whales occurred on 8 Nov 2013 (Figure 7). During this encounter, the minke whale that generated the primary track switched to a rapid calling behavioral state when the whale that generated the nearest track and was also calling rapidly headed towards it. At the start of these tracks, the primary track was traveling southwest and the nearest track was traveling northeast and then north, with the distance between the two tracks decreasing. The primary track switched to calling mainly in State 2 at 6:27 UTC (indicated by arrow in Figure 7) when the whales were about 6.9 km apart. At the same time, the nearest track's heading became more northeast, a reciprocal heading of the primary track. Before the tracks intersected, the whales paused calling for 36 min (primary track) and 15 min (nearest track). The nearest track started calling again first and was traveling northwest. When the primary track started calling it

was about 2.7 km southwest of the nearest track and milled in that area while still calling in State 2. The nearest track then turned and headed south towards the primary track. The whale generating the primary track ceased calling when the nearest track was 900 m away.

4 Discussion

Minke whales were more likely to call at an increased calling rate when in close proximity to another calling minke whale. They increased their calling rate by an order of magnitude between State 1 and State 2. Converting the ICIs reported in the Results section, the mean calling rate for State 1 was 8.7 calls/whale/hour and the mean calling rate for State 2 was 95.2 calls/whale/hour. The overall mean calling rate for minke whales on PMRF was 15.7 calls/whales/hour. Since calling rate is dependent on distance to the nearest neighbor, calling rate would be expected to be higher in areas where minke whale density is higher and lower in areas where minke whale density is lower.

The findings in this paper add complication to PAM cue-rate-based density estimation since calling rate is needed and is dependent on the number of animals in an area. In contrast, using PAM tracks of localized calls for a census-type density estimation (counting the number of tracks) is less complicated than density estimation methods using only calling rate, but is only available in places where the number and spacing of hydrophones allow for tracking (requirements for tracking are discussed in detail in Nosal, 2013; Helble et al., 2015). For researchers that are unable to localize and track calls, this work provides information on minke whale calling dynamics that are important to consider when studying calling behavior and density estimation. Although we present a cue rate for minke whale being calls in this paper, this rate should be applied with caution to density estimation equations because we also found that calling rate is density dependent. In addition, this calling rate is based only on regularly vocalizing animals and we do not know the proportion of silent minke whales. Due to the complicated use of vocalizations by mysticetes, deploying multiple hydrophones to track animals may allow for more accurate PAM-based density estimation. Then the “cue” would be a track and the “cue rate” would be related to the probability of tracking a whale, which could be estimated with passive acoustic tagging studies. However, these tagging studies might show that the probability of acoustically tracking whales is also density dependent, which was shown with humpback whales migrating off the coast of Australia by Noad et al. (2017). Even so, deploying multiple hydrophones to localize and track whales is likely more stable for density estimation because it is easier to define a study area and tracking is less impacted by changes in calling rate.

Martin et al. (2015) hypothesized that the minke whale being call is a mating call. Since minke whales increase their calling rate when in close proximity to other calling minke whales, we are

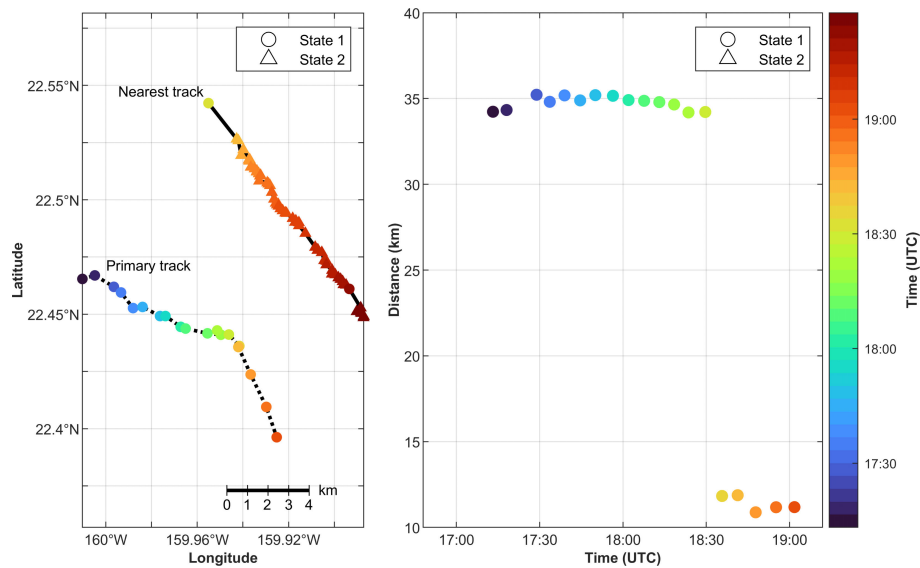


FIGURE 6

Example minke whale being tracks at PMRF on 7 Feb 2017. The left panel shows a map of the interaction between two whales. Marker color indicates time and shape indicates calling state, with circles representing the nominal calling state (State 1) and triangles representing the rapid calling state (State 2). The dotted and solid lines connect the localized calls for the primary and nearest track, respectively. The right panel shows the distance to the primary track's nearest neighbor. Time and calling state are again indicated by color and shape of the markers, respectively. Note that the nearest track between 17:00 and 18:30 UTC was outside of the 15 km search area and is a different track than the "nearest track" depicted in the map. This earlier track is not depicted in the left panel.

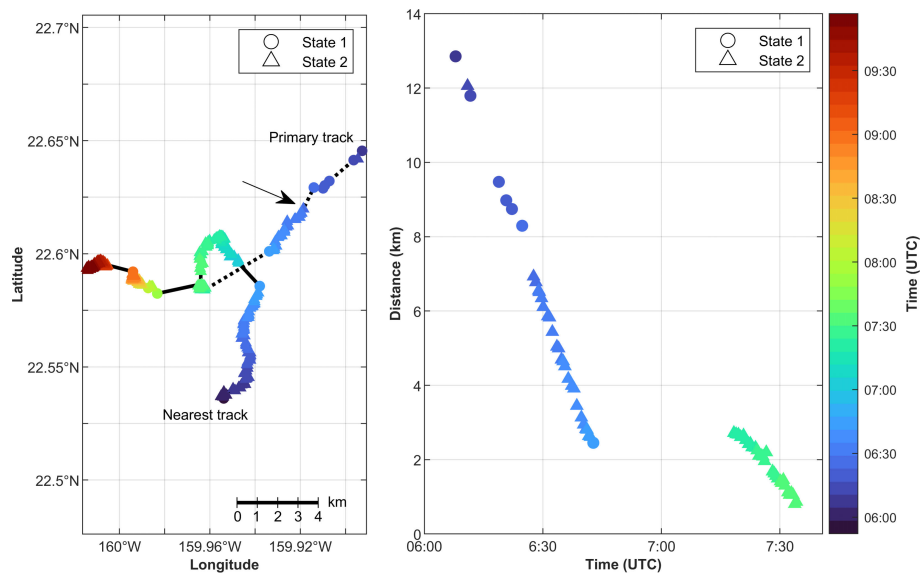


FIGURE 7

Example minke whale being tracks at PMRF on 8 Nov 2013. The left panel shows a map of the interaction between two whales. Marker color indicates time and shape indicates calling state, with circles representing the nominal calling state (State 1) and triangles representing the rapid calling state (State 2). The arrow indicates when the primary track's state changed from mainly State 1 to mainly State 2. The dotted and solid lines connect the localized calls for the primary and nearest track, respectively. The right panel shows the distance to the primary track's nearest neighbor. The time and calling state are again indicated by the color and shape of the markers, respectively.

hypothesizing that the boing call also communicates territoriality when the calling rate increases. Minke whales might call slowly to advertise their position and keep space between other vocalizing whales. When another whale gets too close, they begin to call rapidly, possibly as a sign of aggression. Territoriality is expressed acoustically in many other animal taxa. For example, territorial male Galápagos sea lions (*Zalophus worrellbaeki*) and greater sac-winged bats (*Saccopteryx bilineata*) both increased their vocalization rates as the density of conspecifics around them increased (Kunc and Wolf, 2008; Eckenweber and Knörnschild, 2013). Other species including male green frogs (*Rana clamitans*) and ring-billed gulls (*Larus delawarensis*) use a specific call type to signal aggression and produced those calls when intruders entered their territory (Wells, 1978; Southern, 1981).

The minke whale boing call might have a dual purpose of being a mating call and a territorial call. Other species also use the same calls for both aggression and mating. Anurans, birds, and even fish species have been observed to produce the same calls while defending their territory from an intruder as they would if they were trying to attract a mate, although their calling rate may help signify the intent in these different scenarios (e.g. Wiewandt, 1969; Wingfield, 1994; Borgia and Coleman, 2000; Vasconcelos et al., 2010; Baker et al., 2012). However, aggression and mating may not be independent events. Species that use vocalizations to simultaneously deter competitors and attract mates include male midwife toads (*Alytes obstetricans* and *Alytes cisternasii*), red deer (*Cervus elaphus*), and fallow bucks (*Dama dama*) (McComb, 1991; Bosch and Márquez, 1996; McElligott and Hayden, 1999). These previous studies have used the proximity of non-calling conspecifics (specifically female conspecifics) to help determine the significance of calls, but in our study, we only know the positions of vocal whales and do not know how non-vocal whales are behaving and whether they are attracted or repelled from the boing calls.

Even if vocalizations are associated with mating behavior, their purpose may not be to attract mates. Sometimes other humpback whale males have approached singers, but singers have also been observed to sing when alone and when escorting mother-calf pairs (e.g. Darling and Bérubé, 2001; Smith et al., 2008). Male-male interactions were not always agonistic and Darling and Bérubé (2001) suggested that they might help in social ordering. Similar to minke whales, singing humpbacks might also change their singing behavior when in close proximity to another singing male and often stop singing if the approach gets very close, regardless of whether or not the other male is singing (Darling and Bérubé, 2001; Smith et al., 2008; Cholewiak et al., 2018). Our understanding of baleen whale behavior has advanced more slowly than other taxa due to their vast communication space and difficulties with visual observations, but studies like these can help to increase our knowledge of these protected species.

Although the seasonality of the minke whale boing in Hawaiian waters is similar to that of male songs from

humpback whales and fin whales (*Balaenoptera physalus*) (e.g. Guazzo et al., 2020; Helble et al., 2020a), no biopsies have been collected from calling minke whales to provide evidence of their sex (unlike with humpback and fin whales, e.g. Darling and Bérubé, 2001; Croll et al., 2002; Smith et al., 2008). In other taxa, both males and females have been observed producing territorial calls, so our hypothesis that the minke whale call is used to signal aggression does not also imply the sex of the calling animals. For example, both male and female little blue penguins (*Eudyptula minor*) defended nest sites by vocalizing and/or moving toward intruders and these vocalizations may help them to signal their aggression in the low-visibility nighttime conditions when they are most active (Waas, 1991). Minke whales also live in low-visibility conditions, so vocalizations are more effective than visual signals to communicate a message over long distances. Since territoriality and aggression are associated with mating in many taxa, it is possible that the minke whale boing functions as a mating call when emitted at the lower calling rate and as a territorial or aggressive call at the higher calling rate.

An alternative hypothesis for the minke whale boing call is that this call is a social call not used for mating, and whales are increasing their calling rate to better communicate location and maintain cohesion with another nearby minke whale. The rarity of boing calls reported at higher latitudes during the summer and fall (Delarue et al., 2012) in potential feeding areas suggests that if the boing call is a social call, it seems to be used primarily in tropical waters from fall to spring. More information about the sex of calling minke whales and the reaction of conspecifics to the boing call would help differentiate between hypotheses.

Minke whale vocal activity is likely influenced by other factors not tested in this analysis. If the boing call is part of mating behavior, then calling behavior may be influenced by hormone levels and time of year (proposed for humpback whales by Clark and Clapham, 2004; Vu et al., 2012; Vu et al., 2014). The time of day can also affect whale behavior, including vocalization behavior (observed in gray whales (*Eschrichtius robustus*) by Guazzo et al., 2017). In addition, background noise level might affect the vocalization rate (Helble et al., 2020b; Guazzo et al., 2020). Minke whales might call more if noise levels are higher due to other calling conspecifics in the area or they might call more out of a defensive posture due to reduced communication space. Conversely, minke whales might call less if the communication space is reduced and they cannot hear nearby conspecifics (various responses to increased noise level are reviewed in Brumm and Zollinger, 2011). These variables should be tested with future research.

Ideally, similar studies should be performed in other locations to assess how minke whales and other species vocalize as a function of density. However, very few hydrophone set-ups currently available would be able to replicate the study described in this paper. PMRF is a unique area in that we were able to guarantee detection and localization of calling minke whales within a large (over 3,100 km²) search

area. A large search area is required to be able to test for behavioral responses based on distance to a conspecific when conspecifics are spread out on the order of multiple kilometers.

In conclusion, minke whales producing boing calls in Hawaiian waters are more likely to call at a rapid rate when they are closer to other vocalizing conspecifics. Many questions still remain about the function of these boing calls, but the unique hydrophone array set-up at PMRF combined with the statistical tools applied here allowed for the analysis of more than 500 minke whale tracks containing tens of thousands of calls. Since the calling rate is dependent on the distance to the nearest neighbor, the calling rate would be expected to be higher in areas where the density of minke whales is higher and lower in areas where the density of minke whales is lower, adding complication to density estimation using passive acoustic monitoring. Despite this added difficulty when estimating abundance, these findings provide new information about minke whale calling behavior on what is probably a breeding area.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: <https://seamap.env.duke.edu/dataset/2190>.

Ethics statement

Ethical review and approval was not required for the animal study because this study was conducted using passive acoustic monitoring of wild animals with underwater microphones (i.e. hydrophones) and has no impact on animals' lifecycle.

Author contributions

CM and SM formulated the idea for this study and CM performed the initial analysis. CM, SM, BM, and EH collected the

data. GA and BM programmed the detection, classification, and localization algorithms. GA managed and post-processed the data. SM developed the initial tracking algorithm and CM, GA, and SM tuned the tracking algorithm for minke whale boings. ID assisted with the HMM statistical analysis. CM, RG, and TH validated and analyzed the data and wrote the draft manuscript. All authors discussed the results and contributed to the final manuscript.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Ocean highways in the Western Mediterranean: Which are the areas with increased exposure to maritime traffic for loggerhead turtles?

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Many marine megafauna taxa are tied to the sea surface for breathing which makes them vulnerable to vessel collisions. Sea turtles have developed efficient mechanisms to reduce surface time for breathing to a few seconds, but they can extend their surface periods to rest or to rewarm after diving into deep and colder waters. However, knowledge of collision occurrences is limited to data of turtles stranded along the coastline worldwide, whereas events occurring offshore go likely underestimated due to the sinking of carcasses. Here we performed a spatially explicit assessment to identify, for the first time, oceanic areas of higher exposure for sea turtles from maritime traffic in the Tyrrhenian Sea, Western Mediterranean. Satellite-tracking data were used to estimate utilization distributions of loggerhead turtles using Brownian bridge kernel density estimation. Maritime traffic density maps based on Automatic Identification System (AIS) data were extracted from open-access data layers, provided by the European Maritime Safety Agency, summarized, and used for the exposure analysis. Turtle occurrences were also investigated in response to vessel densities and seasonal patterns by fitting a generalized additive model to the data. Our results demonstrated that loggerhead turtles are potentially exposed to maritime traffic across the entire basin, especially in the easternmost part. The exposure varies among spring/summer and autumn/winter months. Highest turtle occurrences were found in regions primarily subjected to cargo, tanker, and passenger transportation. This study represents the first-ever effort to characterize the exposure of oceanic loggerhead turtles to maritime traffic and highlights oceanic areas of higher exposure where

research and conservation efforts should be directed to understand the effective impact of this stressor on the species.

KEYWORDS

Sea turtle, vessel collisions, Mediterranean Sea, satellite tracking, marine traffic, home range, exposure analysis

Introduction

The Mediterranean Sea is among the world's busiest waterways. It accounts for 15% of the world's maritime activity and 20% of seaborne trade, with approximately 200,000 merchant vessels of more than 100 t crossing the Mediterranean Sea each year (Leone, 2017). Maritime activity has steadily increased since the end of the 1990s and during the 2000s in the Mediterranean Sea (Plan Bleu, 2014) and is expected to increase in the coming years in the number of routes, traffic intensity, and vessel size, according to the global seaborne trade growth (Union for the Mediterranean, 2021). The expansion of the maritime transport sector will result in the intensification of several associated impacts on marine biodiversity such as chemical and noise pollution, accidental oil spills, marine litter, the introduction of non-indigenous species, and collisions between ships and marine fauna (di Pepe and Tribe, 2009; Piante and Ody, 2015; Randone et al., 2019).

Vessel collision is a recognized significant threat for large whales (Laist et al., 2001; Panigada et al., 2006; David et al., 2011; Campana et al., 2015; Campana et al., 2017; Cates et al., 2017; Pennino et al., 2017; Winkler et al., 2020; Grossi et al., 2021), but there is increasing evidence that other marine species are affected as well, including dolphins, porpoises, dugongs, manatees, sharks, seals, sea otters, fish, penguins, and sea turtles (Schoeman et al., 2020). Like cetaceans, sea turtles surface or stay close to the surface to breathe, bask, forage, rest, and, in the case of shallow waters, mate; they may also remain at the surface for a prolonged time to reoxygenate and rewarm after deep dives below the thermocline (Hochscheid et al., 2010; Hochscheid 2014), hence becoming exposed to the risk of vessel collisions. When the ship hull or propeller hits a sea turtle, the collisions usually cause major, life-threatening injuries such as massive carapace fractures or deep cuts on the head, flippers, and carapace (Hazel and Gyuris, 2006; Work et al., 2010).

To date, information regarding the impact of vessel collisions on sea turtles is restricted to data derived from stranding events (Cannon, 1998; Jepson, 2005; Orós et al., 2005; Hazel and Gyuris, 2006; Chaloupka et al., 2008; Tomás et al., 2008; Work et al., 2015; Meager, 2016; Foley et al., 2019; Belmahi et al., 2020). In the Mediterranean Sea, a study based on

30-year stranding records reported injuries possibly due to vessel collisions in 6.4% of turtles recovered/stranded along the Italian coast (Casale et al., 2010a). Furthermore, according to the mentioned study, this trend increases during warm seasons when traffic is generally higher, and sea turtles spend more time at the surface and are more susceptible to vessel encounters. However, stranding data are potentially biased. The probability that a dead or distressed sea turtle will drift ashore and become reported is influenced by several factors such as decomposition and scavenging rates, carcass buoyancy, oceanographic and atmospheric conditions, shoreline characteristics, and detection probability, which are highly variable by location and time of year (Cook et al., 2021; Dimitriadis et al., 2022). In this respect, the number of reported onshore strandings may only represent a minimum measure of the overall mortality and, most importantly, may not reflect events occurring in oceanic areas (Hart et al., 2006), where fatal collisions likely go unnoticed due to the sinking of the carcasses. Consequently, the vessel-related impact in oceanic habitats, where turtles are likely to spend more time near the surface (Hochscheid et al., 2010), is largely unknown. Furthermore, large vessels (i.e., cargo, passenger, tanker, cruise ships, etc.) transit the open sea generally at high speeds increasing the probability of collisions and lethal injuries on animals. Indeed, higher speeds may result in a decreased probability that an approaching vessel is perceived by the animal, and in a higher impact force (Schoeman et al., 2020). During systematic monitoring of marine megafauna on board of passenger vessels performed in the open waters of the Mediterranean Sea within the **Fixed Line Transect Mediterranean Monitoring Network**, sea turtles were observed vanishing under the ship's hull without reemerging behind, or apparently being taken by the water vortex (A. Arcangeli, Pers. Com., April 15, 2022), indicating a likelihood for collision events in these areas due to high-speed traffic.

In summary, given the intrinsic difficulty of quantifying the mortality rate due to vessel collisions on turtles, especially in oceanic environments, the extent of this human pressure on sea turtles likely goes underestimated. Risk assessment approaches, such as those already implemented in the study of collision events between vessels and large cetaceans (Williams and O'Hara, 2010; Nichol et al., 2017; Pennino et al., 2017; Blondin et al., 2020; Smith et al., 2020; Grossi et al., 2021;

Silber et al., 2021; Awbery et al., 2022), or more recently on the study of multiple anthropogenic pressures that potentially impact sea turtles (Dimitriadis et al., 2022), may improve our understanding of maritime traffic consequences in oceanic areas. However, the assessment of collision risk requires preliminary information on animal and vessel distribution patterns and vessel- and animal-related factors, which in the case of Mediterranean sea turtles are still unknown and require targeted research. In this process, one of the key steps is the identification of high-exposure areas, where a high number of vessels and a relatively high number of animals overlap (Cates et al., 2017).

The loggerhead turtle (*Caretta caretta*) is the most common sea turtle species in the Mediterranean Sea. This species is widely distributed in all the areas of the basin (Casale et al., 2018; Luschi et al., 2018; Almpandou et al., 2021; Loisier et al., 2021), including the northernmost ones (Hochscheid et al., 2010), and frequents a wide range of habitats throughout its life cycle (Luschi and Casale, 2014). Although the Mediterranean loggerhead population was categorized as “Least Concern” by the last IUCN Red List assessment (Casale, 2015), several rigorous conservation measures are needed to maintain this status and ensure their protection from human activities (Camiñas et al., 2020). Marine turtle populations are acknowledged as a conservation concern in the Mediterranean and have been the subject of Action Plans for their protection, compiled under the direction of the Barcelona Convention, since 1989. According to the updated UNEP MAP Action Plan for the Conservation of Mediterranean Marine Turtles (UNEP/MAP-SPA/RAC, 2019), the most critical threats to sea turtles include the deterioration of critical habitats, incidental captures in fisheries, intentional killing, consumption, egg exploitation, pollution, and vessel collisions (Casale and Margaritoulis, 2010b). Therefore, identifying the spatial and temporal use of the Mediterranean Sea by loggerhead turtles (Casale et al., 2012a) and its overlap with anthropogenic pressures could be crucial to set up proper conservation-related management interventions. In this context, satellite tracking is a promising approach for acquiring detailed knowledge of habitat utilization and supporting conservation measures of these highly migratory species. Thanks to many technological advances in satellite telemetry, our knowledge of loggerhead turtles’ spatial patterns has considerably improved (Casale et al., 2018), and key oceanic and neritic areas for sea turtles have been identified in the Algerian Sea, the Sicilian Strait, the Western and Central Ionian Sea, the Aeolian Archipelago, the North Adriatic, Southeast Turkey, and Egypt (Bentivegna, 2002; Margaritoulis and Demetropoulos, 2003; Zbinden et al., 2008; Schofield et al., 2010; Zbinden et al., 2011; Hays et al., 2014; Blasi et al., 2016; Mingozzi et al., 2016; Blasi and Mattei, 2017; Casale et al., 2018). Furthermore, the Tyrrhenian Sea (Western Mediterranean) has recently been recognized as an important foraging and overwintering area for Mediterranean loggerhead turtles

(Luschi et al., 2018; Chimienti et al., 2020; Chatzimentor et al., 2021). In these studies, turtles were tracked while moving in the oceanic waters for extended periods, often close to seamounts and volcanic islands (Fiori et al., 2016) or in the proximity of fishing areas (Blasi et al., 2016; Blasi and Mattei, 2017).

In the current study, we analyzed satellite tracking data collected over a 15-year period on loggerhead turtles primarily moving within the oceanic habitats of the Tyrrhenian Sea to determine their main patterns of movement in the oceanic realm. Then, we performed a spatially explicit assessment of exposure for the species to maritime traffic by using published vessel density data. Our main goals were i) to identify and map high-use oceanic areas frequented by loggerhead turtles in the Tyrrhenian Sea; ii) to investigate vessel density distributions in the basin according to different vessel categories; and iii) to assess the exposure to the risk of collision for sea turtles from maritime traffic and identify high-exposure areas.

Materials and methods

Study area

The geographical area considered in this study is the Tyrrhenian Sea (TYS hereafter), in the Western Mediterranean Sea, from 8.6° to 16.2° E and from 37.8° to 44.1° N. This triangular basin has a surface of 275,000 km² (or 182,000 km² if we exclude the neritic zones from 0- to 200-m depth). It has a complex structure and bathymetry, with a mean and a maximum depth of 2,000 and 3,780 m, respectively. The YYS large-scale circulation is strongly affected by the complex exchanges which take place through the three main openings: the Corsica and Sardinia channels (to the north and southwest, respectively), connecting the YYS to the westernmost part of the Mediterranean Sea, and the Sicily Strait (to the south), through which the YYS communicates with the eastern basin (Danovaro and Boero, 2018).

Turtle tracking

Tracking data of 22 loggerhead sea turtles were collected over 15 years, from 2006 to 2021 (T1 to T22, Table 1) using both ARGOS- and GPS-derived locations. Turtles with IDs T1 to T4 corresponded to individuals published in Luschi et al. (2018), T5 to individuals in Uçar et al. (2018), and T6 to T16 to individuals in Chimienti et al. (2020) and Hochscheid (2010). Turtles from T17 to T22 were presented here for the first time. Some turtles considered in this study (n = 7) were recovered from various YYS areas after being accidentally caught by bottom trawlers, found floating or entangled in nets, kept in captivity for a variable period to be rehabilitated, and then released at different locations. Other turtles (n = 15) were deliberately

TABLE 1 Turtle ID, sex, curved carapace length (CCL) and weight, and total days of tracking and number of days tracked in the Tyrrhenian basin.

ID	Sex	CCL (cm)	Weight (kg)	Date of release	Site of release	History prior to release	Days in rehabilitation	Total days of tracking	Days in TYS
T1	n.a.	67.7	37.16	20/10/2006	Capri (NA)	Rehabilitated	60	192	192
T2	n.a.	69.8	34.71	17/10/2009	Capri (NA)	Rehabilitated	463	312	165
T3	n.a.	*75.3	59.10	23/09/2011	Pisciotta (SA)	Rehabilitated	109	190	190
T4	Male	*81.0	58.10	17/06/2011	Agropoli (SA)	Rehabilitated	119	120	120
T5	n.a.	58.8	24.90	09/10/2014	Ventotene (LT)	Rehabilitated	23	813	84
T6	n.a.	64.5	30.92	13/10/2016	Procida (NA)	Caught at sea	–	194	194
T7	n.a.	59.5	n.a.	04/11/2016	Filicudi Island (ME)	Caught at sea	–	173	173
T8	Female	65.5	n.a.	04/11/2016	Filicudi Island (ME)	Caught at sea	–	265	22
T9	n.a.	62.0	n.a.	04/11/2016	Filicudi Island (ME)	Caught at sea	–	216	194
T10	Male	*70.5	n.a.	04/11/2016	Filicudi Island (ME)	Caught at sea	–	195	27
T11	n.a.	61.0	n.a.	09/06/2017	Filicudi Island (ME)	Caught at sea	–	22	6
T12	n.a.	59.0	n.a.	09/06/2017	Filicudi Island (ME)	Caught at sea	–	35	15
T13	n.a.	55.0	n.a.	09/06/2017	Filicudi Island (ME)	Caught at sea	–	6	6
T14	n.a.	58.0	n.a.	09/06/2017	Filicudi Island (ME)	Caught at sea	–	48	48
T15	Female	*75.0	n.a.	09/06/2017	Filicudi Island (ME)	Caught at sea	–	36	36
T16	n.a.	62.0	28.60	08/07/2018	Filicudi Island (ME)	Caught at sea	–	116	116
T17	n.a.	57.0	54.50	07/08/2019	Ventotene (LT)	Caught at sea	–	74	74
T18	Male	*71.5	n.a.	23/07/2020	Ventotene (LT)	Caught at sea	–	124	124
T19	n.a.	65.0	n.a.	23/07/2020	Ventotene (LT)	Caught at sea	–	65	65
T20	Female	*78.0	58.45	10/07/2020	Eboli (SA)	Caught at sea	–	198	87
T21	n.a.	*72.9	41.60	06/06/2016	Battipaglia (SA)	Rehabilitated	105	306	306
T22	n.a.	63.8	23.45	04/10/2019	Marina di Ascea (SA)	Rehabilitated	328	507	507

*Possibly adult. n.a., not available.

caught, equipped with satellite tags, and then released immediately at the same location where they were caught. The overall mean curved carapace length (CCL) was 66 ± 7.2 cm (range 55–81 cm). According to the approximate size at maturity reported for loggerhead turtles in the Mediterranean, which is >70 cm CCL (Margaritoulis and Demetropoulos, 2003; Casale, 2005), our turtles can be assumed to be primarily large juveniles with some adults ($n = 7$) (Table 1). All turtles were equipped with satellite tags just before their release, by gluing the tag directly on the second vertebral scute of the carapace, as described in detail by Chimienti et al. (2020). Over the years that the data for this study were collected, various models of telemetry tags operating with different data relay platforms and geolocation methods were used (see Table S1). Depending on the platform and method used, location data were subject to different measurement errors, temporal irregularity, and space–time resolutions. ARGOS error estimates are assigned to one of seven location classes (LC 3, 2, 1, 0, A, B, Z in descending order of quality) or characterized by ellipsis errors (semi-major axis, semi-minor axis, and orientation). The accuracy of Fastloc GPS positioning depends on the number of receiving satellites, ranging from 10 to 70 m when more than five satellites are used to calculate the location (Dujon et al., 2014). The QFP (Quick

Fix Pseudorange) error estimate is virtually the same as standard GPS (typically better than 25 m). It varies according to number and spatial arrangements of GPS satellites and is assigned to four quality classes (“Succeeded,” “Resolved QFP,” “Resolved QFP-Uncertain,” and “Unresolved QFP”). The data analysis presented in this study was performed in both R statistical computing software (version 4.0.4, R Development Core Team, 2009) and QGIS (version 3.10.11).

Preparing tracking data and standardizing locations

Prior to any analysis, locations were visually inspected and the first 24 h after the release of the turtle was omitted. For ARGOS tags, locations with no estimable location accuracy (i.e., location class Z) were excluded. In order to also eliminate the low-accuracy locations (location classes A and B) associated with unrealistic speeds, a 200-km/day speed filter (Dujon et al., 2017) was also applied to raw ARGOS datasets. Filtering was performed by using the function “vmask” (algorithm by McConnell et al., 1992) within the “argosfilter” package (Freitas, 2012). For QFP positioning, only the quality classes

“Succeeded” and “Resolved QFP” were considered. Finally, for Fastloc-GPS, only positions calculated with more than five satellites were included in the analysis. The “CrawlWrap” function from the *momentuHMM* R package (McClintock and Michelot, 2018) was then applied to speed-filtered data to fit continuous-time-correlated random walk models (CTCRW), predict temporally regular locations at 12-h steps, and improve location estimates considering location errors. The function was called separately for locations including the ARGOS location quality classes, or ARGOS location ellipse errors, or GPS errors, in order to incorporate different measurement errors into the analysis. For ARGOS data, we referred to the “bearded seal” or “harbor seal” examples of Johnson et al. (2008) assuming a bivariate normal measurement error model that accounts for ARGOS estimated error ellipses or the errors associated with ARGOS location quality classes. On the other hand, for Fastloc GPS and QFP-GPS, we followed the “harbor seal” example of McClintock et al. (2013) by assuming an isotropic error ellipse with a 50-m semi-major error and including it in the function. Turtle positions were then merged into a single data frame with turtle IDs, relocations, and errors associated with the estimates. Loggerhead turtles showing a marked preference for coastal habitats and with a tracking duration of less than 28 consecutive tracking days in the TYS ($n = 6$) were discarded and not included in the following analysis.

Utilization distribution estimates

Animals’ utilization distributions (UDs) were estimated using the Brownian bridge approach of the Kernel method for auto-correlated relocations (Bullard, 1991; Horne et al., 2007) applying the function “kernelbb” within the *AdehabitatHR* R package (Calenge, 2006; Calenge, 2019). Instead of simply smoothing the relocation pattern as the classic kernel function does, the method considers that the animal has moved through a continuous path, which is not necessarily linear, between two successive relocations. The Brownian bridge model estimates the probability density that this path passed through any point of the study area, given that the animal was located at the point r_1 at time t_1 and at the point r_2 at time t_2 , with a certain amount of inaccuracy. The estimation relies on two smoothing parameters, sig1 and sig2 : the first measure is based on the inaccuracy of the relocations, and the second was computed following the maximum likelihood approach described in Horne et al. (2007) by using the function “liker” of the package. The function’s output is the probability density to relocate the animal at a given place (UD) which was then multiplied by cell area (1 km^2) to standardize it over the area of interest, so that the volume under the UD is equal to 1. The function “getvolumeUD” was then used to estimate the home range distributions (HRs) of individuals and function “rasterize” of the raster package to compute the mean HR and the mean UD for all animals.

The same procedure was followed to estimate densities over different periods of the year, partitioning data in two semesters in order to allow the comparison with ship density data: from October to March (autumn/winter, n relocations: 2,904) and from April to September (spring/summer, n relocations: 1,781). It is worth clarifying that such a division of the year was done to be able to compare turtles’ distribution with vessel density data; hence, by using the term “season” here onward, we refer essentially to the seasonality based on dynamics of human activity and not of turtles. The seasonal kernel analysis excluded turtles with a tracking duration of less than 28 days for season. We were obligated to consider turtle T22 monitored for two successive semesters as two different animals since the kernel function does not permit the partitioning of an animal trajectory into sub-tracks.

To exclude potential differences in spatial use between rehabilitated turtles ($n = 6$) and those caught at sea (renamed as “wild” from now onward, $n = 10$), we used Bhattacharyya’s affinity (BA) (Bhattacharyya, 1943). The affinity index ranges from 0, meaning no overlap, to 1, meaning identical UD. This was done using the “kerneloverlap” function in the R package “adehabitatHR” (Calenge, 2006) to measure the overlap of the two populations (wild versus rehabilitated) in both core (50% kernel) and general use (95% kernel) areas. Due to the different sample sizes between the two subgroups, we considered all the six rehabilitated turtles and randomly selected six out of ten wild turtles and repeated this procedure 10 times. According to our results for randomized samples (BA index 95% = 0.82 ± 0.03 ; BA index 50% = 0.33 ± 0.02) and for observed samples (BA index 95%: 0.84, BA index 50%: 0.33), we concluded that there is no evidence of spatial segregation between rehabilitated/wild turtles in our sample (see [Supplementary Material](#) for more details, [Figures S1, S2](#)). Therefore, we decided to include them all in our exposure analysis.

To display in a map the overall utilization distribution of turtles with respect to the presence of Tyrrhenian seamounts, the shapefile of these submerged structures was retrieved at the EMODnet Geology website (Geology Submerged Landscapes, <https://www.emodnet-geology.eu/>) and used in GIS environment.

Summarizing maritime traffic AIS-based data

Vessel density maps were provided by the European Maritime Safety Agency (EMSA) and retrieved at the [EMODnet Human Activities](#) website. Here, data are provided as the density (h/km^2) of vessels of certain type (cargo, passenger, fishing, etc.) in a given period (month or year) within a grid cell of 1-km^2 resolution, from January 2017 to 2020. Vessel density maps were based on Automatic Identification Systems (AIS) data. AIS is an automatic tracking

system that uses transceivers installed on vessels by automatically broadcasting critical information, including the vessel's identity and real-time position, course, and speed, using VHF frequencies. European law requires AIS to be fitted aboard all ships of 300 gross tonnage and upward engaged on international voyages, cargo ships of 500 gross tonnage and upward not engaged on international voyages, and all passenger ships irrespective of size. Furthermore, since May 2014, all European fishing vessels exceeding 15-m length overall are required to carry and operate an AIS device (EU Dir 2011/15/EU).

Traffic densities were gathered and manipulated with the “raster” package to obtain both total and seasonal (October–March and April–September) average maps for the period 2017–2020 sorted by four selected vessel types (Cargo, Fishing, Passenger, Tanker, and an additional category combining “All traffic”). Due to the lack of data anterior to 2017, it was not possible to match the entire tracking period (2006–2021). Yearly vessel densities were compared to understand the degree of the yearly variation. Kruskal–Wallis tests were performed to identify significant differences in (i) total ship density among subareas, (ii) total ship density among two seasons, and (iii) total densities among ship categories. In case of statistical significance in group medians, *post-hoc* testing was conducted using the “Bonferroni” p-adjusted method to determine which groups are different from others and avoid potential errors.

Maritime traffic exposure analysis

In order to identify oceanic areas with relatively high exposure to maritime traffic, we estimated separately both the probability of turtle occurrence and the probability of vessel occurrence across all grid cells of 1 km² and relatively to the oceanic TYS (>200-m depth) utilizing the above-described yearly and seasonally averaged maps. The assessment was performed adapting the approach followed by Vanderlaan et al. (2008) and Nichol et al. (2017). For the estimate of the relative turtle occurrence probability [Prel(Turtle)], we used the output from the Kernel analysis (UD) and standardized it over the area of interest (oceanic area), so that the volume under the UD and over the area is equal to 1. We likewise standardized the ship traffic intensity values to determine the relative probability of vessel occurrence [Prel(Vessel)] in the area. All the computations were executed on raster layers using the Raster Calculator tool in QGIS for all the considered vessel and seasonal categories on a grid of 1 × 1 km² and then rescaled to 15 × 15-km² resolution using the “r.resamp.stats” function in QGIS and setting the new values as the sum of the values in the original cells. Finally, we multiplied Prel(Turtle) by Prel(Vessel) and standardized the resulting value over the area to estimate the probability of a turtle being exposed to maritime traffic [Prel(Exposure)]. High-exposure thresholds

were defined as the 90th percentiles of the Prel(Exposure) distributions and used to identify most exposed areas.

Generalized Additive Model (GAM) analysis

The aim of the GAM was to investigate relationships between loggerhead turtles and vessel occurrence in the oceanic TYS. In this regard, we fit the GAM to our data using the “mgcv” package (Wood, 2011). The dataset was obtained by rescaling from 1- to 15-km² resolution the raster of turtles' seasonal UD and vessel densities and setting the new values as the sum of the values in the original cells using the “r.resamp.stat” function. A grid of points of 15 km² was then used to sample raster values using the “Point Sampling Tool” in QGIS. This grid size was chosen among other resolutions (5 km², 10 km², and 30 km²) as the best option to reduce spatial autocorrelation effects to acceptable level and maintaining the finest possible scale. The model used the seasonal UD as the response variable (UD_season) and the log-transformed vessel density (logVD_season) as the explanatory variable. To test whether Season had an effect on the shape of the relationship, we modeled the log-transformed vessel density with and without the “by” term within the spline. Location data (latitude and longitude) were added to account for spatial autocorrelation and season ID (spring/summer vs. autumn/winter) as fixed effect (Season).

We also considered the null model and selected the best model using the model.sel() function of the “MuMIn” package. The formula used for each model is reported below.

$$mod_null = UD_season \sim 1$$

$$mod0 = UD_season \sim s(logVD_season) + s(lon, lat) + Season$$

$$mod1 = UD_season \sim s(logVD_season, by = Season) + s(lon, lat) + Season$$

Models were run using the gamma distribution family and checked for violations of model assumptions in terms of residual autocorrelation, heterogeneity, and normality using the gam.check(), acf(), and pacf() functions. The model with the lowest Akaike information criterion (AIC) was selected as best.

Results

Turtle utilization distribution analysis

The majority of turtles (n = 14) remained in the TYS or its adjacent waters throughout transmission (range: 6–507 days) (Table 1; Figure 1). Only eight turtles moved to other areas of the Mediterranean Sea, such as Northern Tunisia (T9), the Balearic

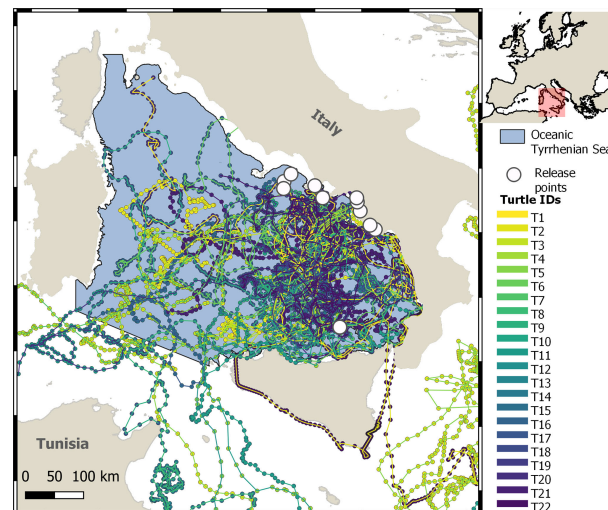


FIGURE 1

Overview of the fixed-time trajectories of 22 large juvenile and adult loggerhead turtles in the Tyrrhenian Sea, obtained by fitting the CTCRW model to satellite location data.

Sea (T20), or the central and eastern parts of the basin (T2, T5, T8, T10, T11, T12, T5). The overall UD analysis was performed on 16 out of the 22 loggerhead turtles monitored (4,979 location data), as six turtles (T2, T8, T10, T11, T12, T13) were excluded (see Section 2.3). Similarly, the seasonal UD analysis was performed on 11 turtles for the spring/summer (1,781 locations) and 12 for the autumn/winter (2,904 locations), excluding turtles with less than 28 consecutive tracking days

per season. As a result, the period of tracking in the TYS was on average 152 (± 116 std. dev.) days in total or 74 (± 41 std. dev.) days during the spring/summer and 132 (± 51 std. dev.) during the autumn/winter season. The average home range distribution referring to the overall dataset indicated three main core areas (75% HR) in the southeastern and partially the central-eastern parts of the TYS (Figure 2) sized 909, 488, and 261 km². Seasonal mean home ranges indicated that the overall area used is greater

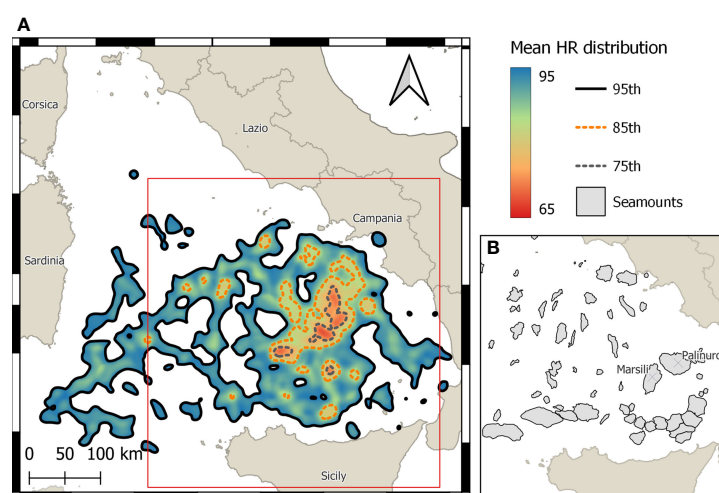


FIGURE 2

(A) Average home range distribution of 16 loggerhead turtles during the whole period of tracking (4,979 observations) and (B) location of major seamounts in the Tyrrhenian Sea (right panel referring to the area confined by the red rectangular in the left panel).

over autumn/winter, with core areas identified again in the eastern TYS (the largest sized 1,247 km²), whereas during the spring/summer (Figure 3A) turtles seem to use smaller patches and disperse more widely over the basin, without a common core area (Figure 3B).

Maritime traffic distributions and composition

No large variations in vessel density were observed in the TYS over 4 years (mean values \pm SD for 2017: 0.34 ± 1.98 h/km²/month; 2018: 0.34 ± 1.71 h/km²/month; 2019: 0.40 ± 4.05 h/km²/month; 2020: 0.33 ± 2.79 h/km²/month). Densities varied significantly among sectors (Kruskal–Wallis chi-squared, $H = 27,708$, $df = 4$, p -value <0.001), and all of the pairwise tests of mean rank difference were statistically significant after controlling for multiple tests (adjusted p -value <0.001). The northern Tyrrhenian Sea and the central-eastern and south-eastern Tyrrhenian (N-TYS, CE-TYS, and SE-TYS, respectively, hereafter) were the sectors with the higher mean values of total traffic densities (Figure S3; Table S2). Seasonal average vessel densities were significantly higher during spring/summer than during autumn/winter months (Kruskal–Wallis chi-squared, $H = 44,796$, $df = 1$, p -value <0.001). Density also significantly differed with respect to the vessel type (Kruskal–Wallis chi-squared, $H = 95,595$, $df = 3$, p -value <0.001) in all pairwise comparisons (adjusted p -value <0.001). Mean densities in the basin were 0.10 ± 0.23 , 0.08 ± 0.52 , 0.06 ± 0.42 , and 0.03 ± 0.23 h/month/km² for Cargo, Fishing, Passenger, and Tanker vessels, respectively. Mean vessel densities were also reported according to vessel type and different TYS sectors (Figure S4).

High-exposure areas

The SE-TYS and CE-TYS presented the highest mean values of relative probability of turtle-vessel co-occurrence (exposure) (Table S3). The overall cumulative probability of exposure over the entire TYS was approximately 60% for the SE-TYS alone (Figure 4). Notably, during the spring/summer semester, three main high-exposure areas were identified: off the Campanian continental shelf, at the center of the eastern basin, and off the continental shelf of Sicily (north of Palermo) (Figure 5, at the bottom center). During autumn/winter, in contrast, a main area of high exposure extends from the Strait of Messina (Figure 5, at the bottom right) up to the central part of the eastern TYS. Probabilities of turtle exposure to specific vessel categories (passenger, cargo, tanker, fishing) were also computed (Figure 6). In particular, we found areas of relatively high exposure to passenger ships along the route connecting Naples (Campania) and Palermo. In contrast, the exposure distributions for cargo and tankers were spatially similar, with the highest values along the corridors connecting northern and southern parts of the TYS, and in the proximity of the Port of Gioia Tauro. Finally, oceanic areas with relatively high exposure to fishing vessels were in the proximities of Ustica Island, off the northwest coast of Sicily and off the Gulf of Salerno.

GAM output

The best model selected the formula accounting for seasonal differences within the spline (see Table S4). The seasonality had a significant effect on turtle distribution (R -adj sq = 0.474, p -value <0.001 , Table 2). The higher probability of turtle occurrences

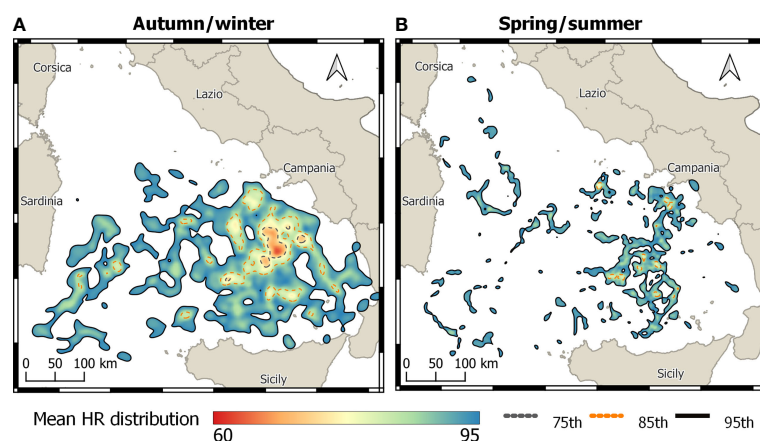


FIGURE 3
Seasonal average home range distributions of loggerhead turtles during (A) autumn/winter ($n = 11$) and (B) spring/summer ($n = 12$) semesters (number of observations of 2,904 and 1,781, respectively).

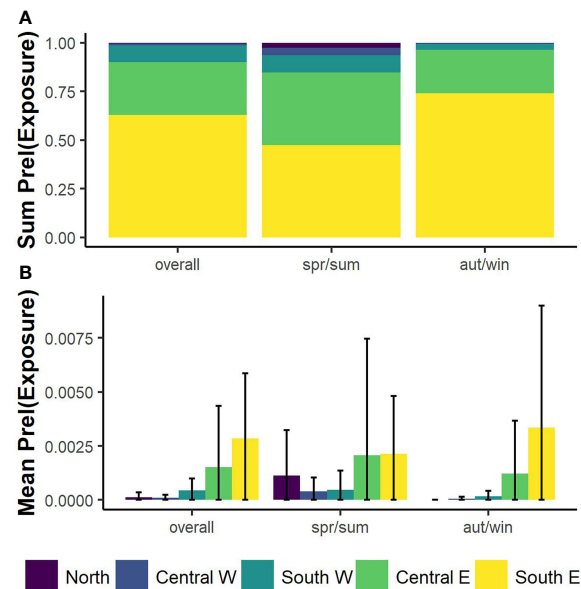


FIGURE 4

Bar plots of summed values (A) and mean values with error bars (B) of relative probabilities of vessel-turtle co-occurrences (prel(Exposure)) according to TYS subareas; N-TYS, northern Tyrrhenian Sea; CW-TYS, central-western Tyrrhenian Sea; CE-TYS, central eastern Tyrrhenian Sea; SW-TYS, southwestern Tyrrhenian Sea; SE-TYS, south Eastern Tyrrhenian Sea.

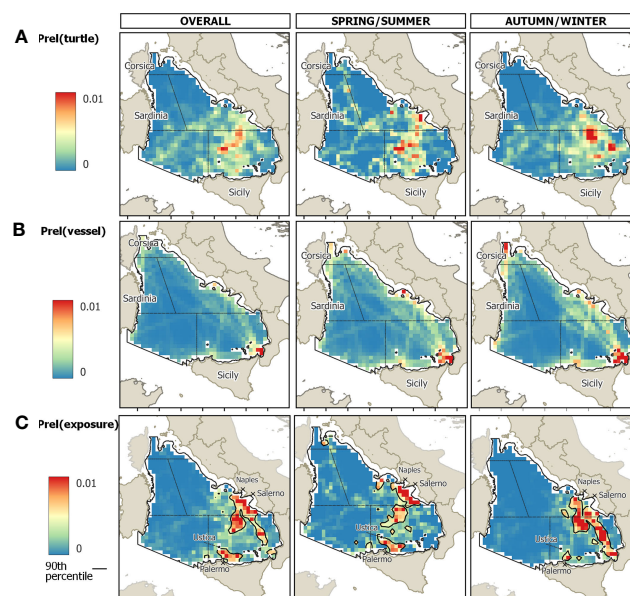


FIGURE 5

The oceanic TYS study area divided into cells of 15 km² (688 cells); colors indicate the relative probability of (A) loggerhead turtle occurrence (obtained through the application of the Brownian bridge kernel method to satellite data, see methods for details), (B) vessel occurrence, (C) and total vessel and turtle co-occurrence (exposure), calculated over the yearly average (1) or according to spring/summer (2) or autumn/winter (3) averages.

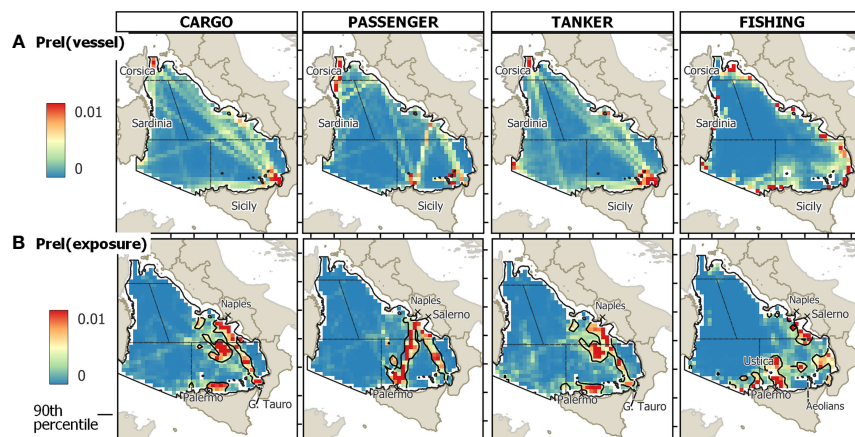


FIGURE 6

The oceanic TYS study area divided into cells of 15 km² (688 cells); colors indicate the relative probability (A) vessel occurrence, (B) total vessel and turtle co-occurrence, calculated over the yearly average sorted by the type of vessel (Cargo, Passenger, Tanker, and Fishing). The loggerhead turtle occurrences included in the risk analysis correspond to that already reported in Figure 5 and referred to the whole year.

was also associated with higher vessel density for the spring/summer period (Figure 7A), up to values of 100 h/cell/month. Within the same range, the probability of turtle occurrences was lower for the autumn/winter period at increasing vessel densities (Figure 7B). Most of the data points are within 200 h/cell/month value; hence, prediction above these values is highly uncertain. Outliers (>200 h/cell/month) were associated with vessel density hotspots in the oceanic proximity of both mainland and islands, particularly off the Messina Strait, the Aeolian Islands, and Campania. Diagnostic and autocorrelation plots of the fitted GAM are reported in Figures S5 and S6. The model with the lowest AIC was selected as best.

Discussion

Maritime activity poses serious threats to sea turtles by potentially killing or injuring them in case of vessel collision. Our study shows that loggerhead turtles are extensively exposed to maritime traffic in the oceanic areas of the TYS, particularly in

its eastern side, where we identified the main high-exposure areas. We also found that the exposure (co-occurrence) varies spatially according to different periods of the year and that it is mainly due to passenger ships, cargo, and tanker traffic. These vessel categories, due to their large size and high traveling speeds, are indeed worthy of particular concern in the area.

Movement patterns of sea turtles

The data presented in this paper confirmed that loggerhead turtles are regular inhabitants in the TYS, because tracked turtles spent a significant amount of time in the area across different seasons and years. In fact, most of them (>70%) remained in the TYS for the whole tracking period comprising even 2 consecutive years for one individual, which thus highlights the importance of TYS as foraging and overwintering area. This result is coherent with previous findings, already indicating the presence of sea turtles in the eastern TYS, which emerged in our study as the most frequented sector (Figure 2). Chimienti et al.

TABLE 2 Summary of the selected GAM model; edf=estimated degrees of freedom. Results -> log scale.

Coefficients of parametric terms			
	Estimate	Std. error	P-value
Intercept (SeasonSummer)	265.06	51.90	< 0.001
SeasonWinter	147.54	53.16	< 0.01
Approximate significance of smooth terms			
	edf		P-value
s(VD_summer): SeasonSummer	2.833		< 0.05
s(VD_winter): SeasonWinter	1.344		< 0.001
s(lon,lat)	27.359		< 0.001

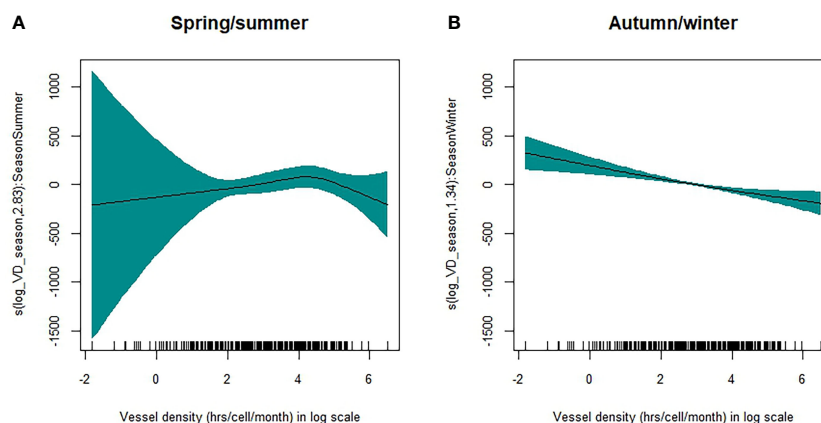


FIGURE 7

GAM plots show the effect of the smooth terms (vessel densities) and linear terms (seasonality) in the model, with reference to Spring/summer (A) and Autumn/winter (B) seasons. Results are in log scale. The blue shades show the 95% confidence interval for the mean shape of the effect. Data points are represented by the black vertical lines at the bottom of the plot.

(2020) reported high-intensity diving and movement patterns characteristic of “area-restricted search” for loggerhead turtles in the same area evidenced also by our kernel analysis, suggesting that the utilization of this site is likely linked to foraging activities. Loggerhead occurrences within the oceanic TYS significantly differed according to the two semesters of the year. Indeed, during spring/summer small patches are used by sea turtles over a wider area, without a main identifiable spatial pattern, whereas during the autumn/winter turtles mainly frequent the eastern TYS. The strong seasonality of the TYS circulation, and the formation of more active anticyclonic eddies during summer months (Iacono et al., 2021), could play a role in determining loggerhead movements by influencing the availability and distribution of prey in different TYS sectors.

Intriguingly, in our study, the areas with the higher mean values of turtle occurrences were in the northwestern surroundings within 50 km from the peak of the Marsili volcano (Figure 2), the biggest seamount of the TYS characterized by active hydrothermal activity (Italiano et al., 2011). Frequent occurrences of sea turtles in the proximity of Tyrrhenian seamounts were also reported by other previous studies (Luschi et al., 2018; Sparks and DiMatteo, 2020). Seamounts have been recognized as possible biodiversity hotspots for pelagic predators (Morato et al., 2008; Morato et al., 2010), including cetaceans and sea turtles. The attraction exerted by seamounts may be associated with their possible role in shaping local or mesoscale water circulation through eddy formation, local upwelling or downwelling, or closed circulation patterns called Taylor columns which form when water is trapped over the crest of a seamount, creating turbulence and mixing the upper layers of water. All these oceanic features, in turn, may determine the accumulation or flow of nutrients and

increase offshore ecosystems’ overall productivity (Boehlert and Genin, 1987). Improving our understanding of how seamounts influence sea turtle movements may be critical for successful conservation plans. Therefore, further research is urgently needed in the area.

We acknowledge that the analysis of loggerhead turtle distribution implemented in this study did not account for the interannual environmental variability. Other approaches such as ecological niche and spatial distribution modeling (Melo-Merino et al., 2020; Smith et al., 2020; Chatzimentor et al., 2021; Zampollo et al., 2022) should be enhanced to further investigate the distribution of this species in the area in response to environmental variables (i.e., sea surface temperatures, chlorophyll-a concentration, distance to seamounts, bathymetry, etc.), in order to identify mechanisms and variability in habitat utilization, and to predict future distribution patterns.

Maritime traffic and its composition

Our study provided evidence that the TYS is a busy waterway with maximum vessel densities in the oceanic proximity of both mainland and islands. Overall traffic densities were greater than 0 across almost every cell in the study domain and seasons, indicating that the whole area was intensively used by vessels of all kinds. Contrary to the global trend toward increasing vessel traffic (Union for the Mediterranean, 2021), mean total vessel densities did not vary significantly between 2017 and 2020, possibly due to the short time window considered. The higher densities in spring/summer across all the subareas of the basin are consistent with the seasonal trend observed in the Western Mediterranean Sea

(Campana et al., 2015). The fact that the eastern TYS emerged as the busiest sector is not so surprising considering the presence of some of the major landing harbors for cargo and passenger transportation in the area, such as Naples, Salerno, and particularly Gioia Tauro, the largest transshipment terminal in Italy and one of the most crucial cargo container traffic hubs in the whole Mediterranean basin (Lloyd's Marine Intelligence Unit, 2008). Indeed, looking at the detailed traffic composition (Figure S4), cargo was the vessel type contributing most (38%) to all-traffic densities, presenting the highest values in the northern and southeastern parts of the basin due to the important global route passing through the Messina Strait that connects the western and eastern areas of the Mediterranean. Fishing can also contribute considerably to the overall traffic in the oceanic TYS (28%, in our dataset) (Coomber et al., 2016). However, we acknowledge that fishing activity is not represented completely in our analysis, as we excluded areas on the continental shelf where most of the fishing activity, including artisanal fishery, is expected to occur (Mangano et al., 2014).

High-exposure areas

Relatively high-exposure areas for loggerhead turtles to maritime activity are concentrated in the SE and CE TYS, along main shipping routes for cargo, tanker, and passenger transportation. Higher loggerhead turtle occurrences are associated with higher vessel densities during the spring/summer semester with high-exposure areas localized along the passenger transport linking the Campania Region to Sicily (Figure 5). This is likely due to the general increase in marine traffic and the fact that many passenger companies double their runs during the spring and summer months. In autumn/winter, turtles use areas with lower associated traffic, being mostly exposed to cargo and tanker transportation.

Hence, passenger, cargo, and tankers are vessel types of particular concern as they generally travel at high speeds, especially when moving in the open sea. Indeed, higher speeds potentially reduce the chance for the animal to notice the approaching vessel and dive or move away from its course and imply heavier consequences in case of collision (Schoeman et al., 2020). Studies in coastal regions suggested that green turtles are unlikely to take effective evasive action when approached by small-medium vessels at speeds exceeding 4 km/h (Hazel et al., 2007), and that vessels had to slow down to decrease the probability of severe injuries also on loggerhead turtles (Work et al., 2010). It is possible to expect that passenger ships, cargo, and tankers, which travel approximately around 28, 21, and 16 km/h, respectively (Coomber et al., 2016), have a greater likelihood for collision events compared to other vessels. Additionally, larger vessels have deeper drafts which may exceed 10 m (for cargo vessels, data from Marine Traffic–

Global Ship Tracking Intelligence), implying a large potential collision zone for turtles, which might be easily pulled underneath the vessel by the suction of the huge propeller. A study based on whale vessel collisions indicated a drawing of the animal toward the hull and an increased probability of propeller strikes when the animal is below the surface at one to two times the ship's draft at the time of the encounter (Silber et al., 2010). These forces are likely of more significance for small and slow-moving species, such as sea turtles, although details of these interactions with sea turtle species were poorly investigated, and to our knowledge reported only the study by Work et al. (2010).

Important knowledge is still missing to be able to complete a collision risk assessment of sea turtles in the Mediterranean Sea. Our seasonal exposure maps are aggregated over several years not taking into account interannual variability. Therefore, it would be appropriate to gather further long-term tracking data on sea turtle distributions to enhance the spatiotemporal analysis. Our exposure analysis illustrated where loggerhead turtles are most likely to be exposed to maritime traffic. However, it did not consider the probability that loggerhead turtles are at the surface when a vessel passes and that they are injured or killed by the collision. The dynamics of surfacing behavior in sea turtles are influenced by several factors such as life stages, habitats, and feeding strategies. Oceanic turtles which sometimes use the surface for extended periods (Hochscheid et al., 2010), may be more prone to vessel collision risk compared to turtles foraging on benthic prey in shallow waters. Interestingly, turtle C06 in Hochscheid et al., (2010), i.e., turtle T1 in this study, showed an extended surface behavior in many areas we identified as highly frequented by turtles and more exposed to vessel traffic. In this regard, a detailed surface interval assessment on a vast number of oceanic loggerhead turtles is required to investigate whether there are periods and areas of increased surface activity that might lead to a greater collision risk assessment.

Conclusions and final remarks

Our study represented a first important step to increase our knowledge of the consequences of maritime activity on oceanic loggerhead turtles in the Mediterranean Sea. Further research is urgently needed to characterize the risk of collision and the probability that collision results in lethal injuries in the high-exposure areas evidenced by our analysis.

The novelty of our study resides on the estimates of vessel exposure for sea turtles in oceanic areas where the problem has not been addressed before. In contrast, for some Mediterranean coastal areas, vessel collision incidence was already assessed by analyzing stranding data (Casale et al., 2010a), which however may contain certain biases as already explored in the introduction. Therefore, a similar approach based on tracking data could be very useful if extended to coastal areas. Indeed,

coastal areas are crossed by many vessels (e.g., recreational boats and artisanal fishing boats <15 m), which are not required to carry AIS. Therefore, AIS data alone would not be adequate to describe coastal marine traffic data.

The core areas highlighted by our KDE analysis may be suitable candidates as Important Marine Turtle Areas (IMTAs) due to its role as oceanic foraging area for both large juveniles and adults, which are considered a priority conservation target for their high reproductive value (Casale et al., 2012b). Indeed, IMTAs were defined by the IUCN Marine Turtle Specialist Group as “discrete areas within existing marine turtle regional management units that are of particular biological significance for the persistence of sea turtles” (Bandimere et al., 2021).

Finally, our study also outlined the remarkable power of bio-logging technology and animal movement modeling in identifying high-use areas and potential risks for their conservation. By combining further knowledge of individual behavior and energetics, with higher-resolution environmental data (both biological and human derived), these types of modeling techniques can be used to detect individual responses to environmental disturbance and their consequences at the population level. Indeed, quantifying how, where, when, and why marine megafauna are exposed to potential threats from anthropogenic activities is considered a key goal for research to optimize management and conservation strategies (Hays et al., 2016).

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: <https://www.datarepository.movebank.org/handle/10255/move.1099> <https://www.emodnet-humanactivities.eu/view-data.php> Some raw data from satellite tracking of turtles are not included in the public database but can be made available upon request.

Ethics statement

This study was carried out under the authorizations notwithstanding the regulation 357/97 implementing the European Habitats Directive (92/43/EEC): Prot. 0042848/PNM of 09/08/2013, Prot. 0024471/PNM of 22/11/2016, Prot. 9033 of 03/05/2017, Prot. 0012046.05-06-2018, and Prot. 0000992.22-01-2020 of the “Ministero della Transizione Ecologica” (Ministry of the Environment) which were issued to SH for the handling and tagging of sea turtles, and was performed in accordance with the national “Guidelines for the recovery, rescue, custody and management of sea turtles for the purposes of rehabilitation and for manipulation for scientific purposes” (ISPRA MLG 89/2013).

Author contributions

EP, MC, SH conceived the study. EP organized the database, wrote the first draft of the manuscript and produced the tables and figures. EP and MC conducted statistical analysis. SH, FM and MB conducted fieldwork. FM, MC and SH wrote sections of the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.924532/full#supplementary-material>

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Exposure to whale watching vessels affects dive ascents and resting behavior in sperm whales

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Disturbance from whale watching can induce a wide range of behavioral responses in cetaceans, some of which can affect their energetic balance and, ultimately, their long-term fitness. However, assessing disturbance effects on deep-diving cetaceans remains challenging, as the majority of their activities occurs underwater and are difficult to monitor from surface observations. To surpass this limitation, we attached high-resolution multi-sensor tags (DTAGs) on 24 sperm whales (*Physeter macrocephalus*) off the Azores, an area of intense whale watching, to evaluate changes in movement and acoustic parameters related to foraging effort and dives, locomotion effort, and non-foraging behavior. These parameters were compared between periods of exposure and non-exposure to whale watching vessels, using linear mixed-effect models to assess the presence of short-term effects, accounting for individual differences in behavior. We found no significant changes in foraging effort (number of buzzes, bottom phase depth, proportion of search and foraging phases) and overall dive behavior (dive duration, proportion of dive phases, and descending or ascending pitch) between non-exposure and exposure periods. In contrast, variation in body pitch during non-foraging periods increased during exposure but not variation in body roll. Taken together, these results suggest increased movements during resting activity, which may carry energetic costs to whales and impact their health. Vertical velocity during ascents was also significantly higher in response to vessel exposure, suggesting that sperm whales increased the frequency of fluke strokes, which was consistent with a higher Overall Dynamic Body Acceleration (ODBA) during ascents, incurring in higher energy expenditure. If the detected changes are repeated across multiple exposures, they might affect the individual's energetic budget, and consequently their fitness. Our

study contributes to a better understanding of the short-term behavioral responses of sperm whales to whale watching vessels and highlights the need for further studies examining the potential consequences from repeated disturbance to individuals.

KEYWORDS

Physeter macrocephalus, disturbance, whale watching, foraging and diving effort, locomotion effort, resting and socializing

Introduction

Effects of non-lethal disturbance from anthropogenic activities are increasingly recognized as a severe threat to marine wildlife, especially due to their potential for repercussions at the population level (Lima, 1998; Hazel et al., 2007; Christiansen et al., 2014; Avila et al., 2018; Pirotta et al., 2018; Montero-Quintana et al., 2020). Human-related disturbance stimuli (*sensu* Frid and Dill, 2002) may elicit costly avoidance behaviors (Kvadsheim et al., 2017; Onoufriou et al., 2021), reduce time for, or disrupt, critical activities such as foraging, resting, nursing or socializing (Visser et al., 2011; Christiansen et al., 2013; Wisniewska et al., 2018; Sprogis et al., 2020; Arranz et al., 2021), increase stress levels (Rolland et al., 2012), or induce temporary hearing loss (Finneran, 2015). The effects of such behavioral and physiological responses may accumulate with repeated exposure to disturbance, impacting the health and vital rates (survival, reproductive success) of individuals and, ultimately, their fitness (New et al., 2014; Pirotta et al., 2018; Wilson et al., 2020a). Depending on the proportion of individuals affected in the population, changes in individual fitness can scale up to influence population dynamics (Pirotta et al., 2018).

Despite being often hailed as a “green” or “sustainable” touristic activity, whale watching may disturb marine mammals through increased underwater noise and the physical presence of vessels near individuals (Bearzi, 2017). The presence of whale watching vessels often induce changes to cetacean behavioral budgets, with social, energetic and physiological consequences (Senigaglia et al., 2016). The observed behavior responses of cetaceans to whale watching vessels include alteration of blow rates, increased surface swim speed and frequency of aerial displays, and decreased dive durations, nursing and resting periods (Avila et al., 2015; Senigaglia et al., 2016; Schuler et al., 2019; Arranz et al., 2021; Currie et al., 2021). Studies have also reported disruption of foraging (Christiansen et al., 2013), shifts in acoustic behavior (Heiler et al., 2016; Burnham et al., 2021), and reduction of communication ranges (Erbe, 2002; Jensen et al., 2009). Although more difficult to document, an increasing body of

evidence suggests long-term detrimental effects of whale watching activities on some cetacean populations, ranging from displacement to population decline (Bejder et al., 2006; Lusseau et al., 2006a; Bain et al., 2014; Christiansen and Lusseau, 2014). Thus, in order to implement management measures to ensure the sustainability of whale watching activity, it is essential to assess both short- and long-term effects on cetaceans (Lusseau and Bejder, 2007; Bearzi, 2017). This is even more critical, as these effects may interact and add up with effects from other anthropogenic stressors (e.g., global warming, marine debris and ocean noise) (Pirotta et al., 2022).

The sperm whale (*Physeter macrocephalus*) is classified as a vulnerable species according to the International Union for Conservation of Nature’s Red List of Threatened Species (Taylor et al., 2019). At lower latitudes, female and juvenile sperm whales live in social groups and spend about 70% of their time in foraging behavior (Amano and Yoshioka, 2003; Watwood et al., 2006). After each foraging dive, they remain about 8–10 minutes at the surface to recover and replenish their oxygen stores for the next foraging dive (Watwood et al., 2006). The remaining time is allocated to nursing, breeding, social interactions, resting and sleeping, often taking place at or near the surface (Whitehead, 2003; Miller et al., 2008). Sperm whales produce two types of echolocation sounds during foraging dives, thought to be involved in navigation and prey detection (usual clicks), and in prey capture attempts (buzzes) (Madsen et al., 2002b; Miller et al., 2004a).

In the presence of vessels, sperm whales often change behavior, either while foraging or when engaged in near-surface behaviors, which may be indirectly detrimental to their fitness, survival and reproductive success. For example, sperm whales produced less clicks while ships were approaching and after their passage compared to control periods (Azzara et al., 2013). During interactions with whale watching vessels, sperm whales changed their blow interval, surface period duration, heading and speed while at the surface, and number of aerial displays (Gordon et al., 1992; Magalhães et al., 2002; Richter et al., 2003). In addition, the presence of whale watching vessels increased the probability of sperm whales performing shallow dives (Cosentino, 2016). All these studies were based on surface

observations or acoustic data collected from bottom moored hydrophones, and could not quantify the energetic costs of surface and near-surface responses of individual whales, or how such responses affected biologically important activities that occur underwater, such as feeding. Using hand-held hydrophones and towed arrays [Isojunno et al. \(2011\)](#) tracked individual whales through several dives before, during and after exposure to whale watching vessels. While there was no evidence that whale watching vessels significantly changed sperm whale foraging effort and feeding success, these authors stress that their results may have been affected by a small sample size ([Isojunno et al., 2011](#)). Hence, it remains unclear if and to what extent sperm whale responses to whale watching vessels impact their energy budget.

The aim of this study was to investigate if the presence of whale watching vessels affects sperm whale foraging effort and foraging dive behavior, locomotion activity, and non-foraging behavior. Whale watching vessels may indirectly affect dive and foraging effort by interfering with the individual's recovery and oxygen replenishment from the previous dive, resulting in shorter or shallower dives, and/or in less time spent searching and foraging at the bottom phase, and ultimately reducing the number of prey capture attempts. Whale watching vessels may also elicit avoidance responses by sperm whales, leading to steeper or faster dive descents and increased locomotion activity (as measured by the overall dynamic body acceleration, ODBA), with potential implications for the remaining dive phases. As we expected short-term responses to whale watching vessels to be stronger immediately after the exposure, changes in parameters linked to foraging effort, dive behavior, and locomotion activity were investigated by comparing the first dive following exposure with non-exposure periods. Finally, we hypothesized that presence of whale watching vessels would interfere with the near-surface activities of sperm whales and elicit avoidance behavior, through increased movement and number of shallow dives. To address these hypotheses, we instrumented sperm whales with multi-sensor digital acoustic recording tags [DTAGs; [Johnson and Tyack \(2003\)](#)] in the Azores archipelago, where there is a seasonal whale watching activity targeting sperm whales, as one of the most important species ([Oliveira et al., 2007](#)).

Materials and methods

Field data collection

Fieldwork was conducted off the Azores archipelago (38.5°N, 28.5°W), between July 2017 and June 2019, where a regulated whale watching industry exists (Regional Law Decrees 10/2003/A and 13/2004/A and Ordinances 70/2005 and 17/2007). Within the study area, there are 10 whale watching companies that operate 23 vessels, all engine driven. The activity is seasonal

(March to October) but during the summer peak each vessel can carry out 2-3 trips a day. Prior to the fieldwork season, whale watching companies working in the study area were informed about the project goals and protocol and they were asked to collaborate both on land and at sea.

Sperm whales were located by land-based spotters working for the whale watching operators or by hand-held directional hydrophone in the research boat. The intention was to work within a whale watching area and to tag individuals before the arrival of whale watching vessels. However, that was not always possible and, on several occasions, tagging occurred when whale watching vessels were already in the area, although we only approached whales for tagging when vessels were at >800 m from the target whale. Tagging was performed from either a 9 m or a 5 m rigid-hulled inflatable boat (RHIB), using a 11 m cantilevered pole or a 6 m hand pole. Audio and movement recording tags [DTAG-3 or DTAG-4; [Johnson and Tyack \(2003\)](#)] were attached to the whales using suction cups and programmed to release after 24 hours. At the surface, whales showed no reaction or only a mild behavioral response to tagging (e.g., typically a dorsal flex and occasional defecation with or without fluking). Size class of tagged whales was visually estimated by the research boat crew.

Whale watching vessels were informed about the tagging event over VHF radio, but there was no control on their approach to the animals, nor did we interfere in their maneuvers while observing the tagged whales. Although our aim was to let vessels behave “naturally”, we cannot assess if the way they operated was representative of their usual behavior towards sperm whales. Whenever possible, the number and distance of whale watching vessels to tagged individuals was also estimated by the research boat. However, as tagged whales were tracked (visually or using the VHF beacon on the tag) from a distance (i.e., >500 m, which corresponds to the limit of the observation area defined by the regional whale watching regulations), to avoid interfering with whale's behavior ([Isojunno and Miller, 2015](#)), distances were only roughly estimated.

Data processing

The DTAG-3 recorded two channels of acoustic data at a sampling rate of 120 kHz, and sampled pressure, temperature, and tri-axial accelerometers and magnetometers at 20 Hz or 25 Hz. DTAG-4 recorded one acoustic channel at 192 kHz and sampled all other data at 25 Hz. DTAG data were calibrated and analyzed in Matlab 2007b, 2016b (Mathworks ©) with custom tools developed specifically for these data-loggers (<https://www.soundtags.org/dtags/dtag-toolbox/>). Whale orientation was determined from the accelerometer and magnetometer data, and whale depth from pressure and temperature, using established methods ([Johnson and Tyack, 2003](#)). An audit tool

was used to analyze the audio files to identify and mark the periods with clicks associated with foraging, i.e., long-range echolocation search clicks (hereafter “usual clicks”), and foraging buzzes, i.e., short-range fast echolocation click trains which likely indicate prey capture attempts (Miller et al., 2004a). Clicks were assigned to the tagged or other non-tagged whales based on their angle-of-arrival [only for DTAGs-3; (Johnson et al., 2006)], their received levels and the depth of the tagged individual (for all DTAGs). The audit tool was also used to identify vessel noise of the research boat and whale watching vessels in the tag data.

Foraging dives were defined as dives with usual click and buzz production (Isojunno and Miller, 2015) and were divided into descent, bottom, ascent and surface phases [Figure 1; Miller et al. (2004b); Watwood et al. (2006)]. The descent phase refers to the period from the surface until the pitch of the whale exceeded 0 degrees. The ascent phase started when the pitch was consistently greater than 0 degrees until surfacing (Miller et al., 2004b). The bottom phase was the period between descent and ascent phases, and the surface phase was the interval between consecutive foraging dives (Watwood et al., 2006). To distinguish surfacing (i.e., oxygen replenishment and physiological recovery at the surface; Isojunno et al., 2016) from longer periods spent at and near the surface (hereafter termed “non-foraging”) we used an upper threshold of 18.2-minute duration, which corresponded to the 97.5th percentile of the durations between consecutive foraging dives (Supplementary Figure 1). Non-foraging periods likely include socializing and resting but may also include travelling. This category also contained periods of vertical resting and sleep underwater, when whales vertically drifted with their heads up or

down (Miller et al., 2008). Finally, the search phase was defined as the period between the first and last usual clicks within a dive and the foraging phase as the period between the first and last buzzes (Watwood et al., 2006).

Data collected during night time (calculated from the sunrise and sunset times NOAA Solar Calculator; <https://www.esrl.noaa.gov/gmd/grad/solcalc/>) were removed from the analyses because there was no whale watching activity at night and there is some evidence that sperm whale behavior exhibits diel variation (Aoki et al., 2007; André et al., 2017; Isojunno et al., 2020). To minimize potential effects of tagging on sperm whale behavior, the first foraging dive cycle (i.e., descent, bottom, ascent, and surface phases) after tagging was removed (Miller et al., 2009). For whales that remained at the surface after being tagged, we excluded the first 1 hour of data (i.e., approximate duration of a dive cycle). In addition, all dives and near-surface periods that had vessel noise that could have been produced by the research boat were removed. Vessel noise was attributed to the research boat whenever the boat was close to tagged individuals and there were no other vessels nearby. To determine the distance at which noise from the research boat could be detected on the tag, we used the GPS positions of the research boat and of 4 individuals that had a FastLoc GPS incorporated on the tag (sw18_170a, sw18_172a, sw18_173a and sw18_177a). The research boat was acoustically detected in 3% of the times it was < 500 m from the whale, in 1% of the times it was 501–1000 m from the tagged whale, and there were no detections at distances > 1000 m.

According to the whale watching regulations in the Azores, whale watching vessels cannot be at less than 50 m from a sperm whale (100 m for individuals/groups with calves) and a

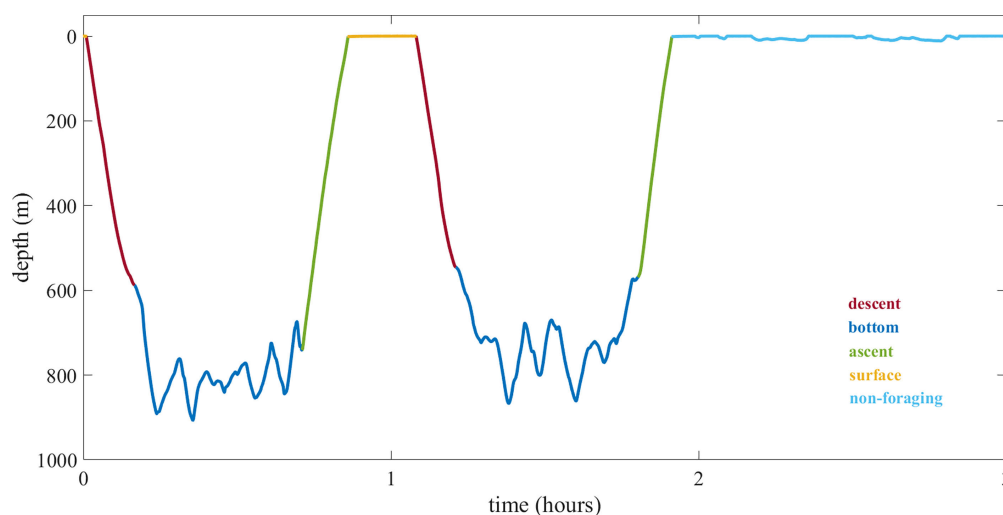


FIGURE 1

Example of foraging dive phases and a non-foraging period: descent (dark red), bottom (dark blue), ascent (green) and surface (orange) phases, and a non-foraging period (light blue).

maximum of three vessels is allowed simultaneously within a 50–500 m radius of a whale. Each vessel cannot stay more than 15 minutes within this radius. Vessels need to approach whales from behind, navigate with a constant speed of a maximum 2 knots above the animal's speed, and are not allowed to overtake the animal (Law Decrees 10/2003/A and 13/2004/A). While observing sperm whales at the surface, whale watching vessels typically remain in engine neutral mode, with occasional gear shifts to adjust the distance to the animals. When sperm whales start foraging, as indicated by a common fluke up, whale watching vessels usually wait for a minute or so and then gradually accelerate to move away from the diving whale. Based on this, we expected to detect whale watching vessel noise in tag sound recordings when vessels were observed near the tagged individuals. Indeed, a type I and II error analysis showed very good accordance between visual and acoustic detections of whale watching vessels during whale dives (0% of probability of making a type I error for all dive phases, and 50%, 28% and 37% of probability of making a type II error for surface, bottom and ascent phases, respectively). However, agreement between visual and acoustic detections of whale watching vessels was lower during non-foraging periods (43% of probability of making a type I error and 33% of probability of making a type II error), when whales were at or close to the surface (see [Supplementary Material](#) and [Supplementary Table 1](#)). Based on this analysis, the typical behavior of whale watching vessels around sperm whales, and the distances set by the whale watching regulations, we defined exposure and non-exposure

as follows. Exposed foraging dives were the dives that followed the observation of one or more whale watching vessels within 500 m from the tagged whale while it was at the surface and/or the dives with vessel noise in the first 200 m of the descent phase. Thus, by definition, only the first dive following detection of whale watching vessels was considered to be exposed, when short-term responses of sperm whales are expected to be stronger ([Miller et al., 2009](#)). Non-exposed foraging dives were all dives where whale watching vessels were not observed or acoustically detected during the first 200 m of the descent phase. Exposed non-foraging periods were the ones where whale watching vessels were visually observed within 500 m from the surfacing tagged whale ([Figure 2](#)), while the remaining ones corresponded to non-exposed non-foraging periods. Both foraging and non-foraging non-exposure periods could have been preceded by exposure periods. Therefore, this study focuses on the immediate, short-term effects of whale watching vessels on sperm whale behavior and does not account for cumulative effects. Surfacing periods between foraging dives were excluded from subsequent analyses due to the insufficient number of exposures visually confirmed by the research boat.

Behavioral indicator variables and hypotheses

We hypothesized that exposure to whale watching vessels influenced the foraging effort, foraging dive behavior,

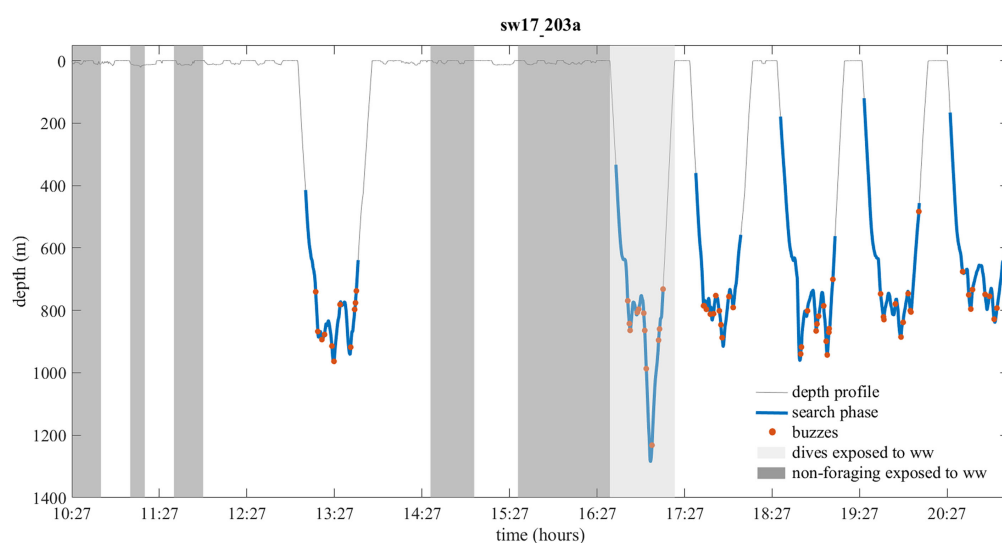


FIGURE 2

Dive profile (thin grey line) of tagged whale sw17_203a with its echolocation behavior (search phase – blue thick segments; buzzes – red circles) superimposed. Dives (light grey shadowing) and non-foraging periods (darker grey shadowing) exposed to whale watching (ww) vessels are indicated.

TABLE 1 Hypotheses, variable names and variable descriptions used in the analysis of the effects of whale watching vessels on sperm whales.

	Variable	Variable description (units)
Foraging effort	Bottom phase depth	Median of bottom phase depth (m)
	Buzzes/minute	N° of buzz starts per minute, during the foraging phase (nr.min ⁻¹)
	Search ratio	Proportion of search phase within a dive
	Foraging ratio	Proportion of foraging phase within a dive
Diving behavior	Dive duration	Duration of dive (min)
	Descent ratio	Proportion of descent phase within a dive
	Bottom phase ratio	Proportion of bottom phase within a dive
	Ascent ratio	Proportion of ascent phase within a dive
	Pitch descent *	Mean pitch during descent phase (rad)
Locomotion effort	Pitch ascent *	Mean pitch during ascent phase (rad)
	Vvelocity descent *	Mean vertical velocity during descent phase (ms ⁻¹)
	Vvelocity ascent *	Mean vertical velocity during ascent phase (ms ⁻¹)
	ODBA descent *	Mean Overall Dynamic Body Acceleration during descent phase (ms ⁻²)
	ODBA bottom *	Mean Overall Dynamic Body Acceleration during bottom phase (ms ⁻²)
Non-foraging behavior	ODBA ascent *	Mean Overall Dynamic Body Acceleration during ascent phase (ms ⁻²)
	Pitch SD non-foraging *	Standard deviation of pitch during non-foraging periods (rad)
	Roll SD non-foraging *	Standard deviation of roll during non-foraging periods (rad)

* Variables that were calculated in 1-min time bins.

locomotion effort, and non-foraging periods in sperm whales. To investigate these hypotheses, we selected a set of variables describing the underwater movement and acoustic behavior of sperm whales. An exploratory analysis showed that several of these variables were correlated (see [Supplementary Table 2](#)) and did not differ significantly between exposure and non-exposure periods. Therefore, to reduce the number of multiple tests based on the same data (see below), we used only those variables that more adequately described the expected changes in sperm whale behavior during exposure to whale watching vessels ([Table 1](#)). Variables related to foraging effort included the median depth of the bottom phase (reflecting the prey depth layer targeted by the whale), the number of buzzes produced per minute within the foraging phase (i.e., buzzes/minute), and the proportion of time in the search and foraging phases within a dive (i.e., search and foraging ratios). Variables used to characterize the foraging dives were the dive duration, the duration of descent, bottom and ascent phases relative to the total dive duration, and the pitch angle in the descent and ascent phases. Variables related to locomotion activity were the vertical velocity (i.e., depth rate in meters per second) of descent and ascent phases, and the overall dynamic body acceleration (ODBA; [Wilson et al., 2006](#); [Halsey et al., 2009](#)) of descent, bottom and ascent phases. ODBA is defined as the sum over a reference interval of the magnitude of the triaxial acceleration after the removal of a running mean, and is considered a proxy of energy expenditure ([Wilson et al., 2006](#)). While at the surface (i.e., during surface phases and non-foraging periods), there is the potential of ODBA estimations being influenced by sea state ([Wilson et al., 2020b](#)). For this

reason, we did not calculate ODBA during non-foraging periods. Instead, we used the standard deviation (SD) of body pitch and roll to characterize changes in body orientation and examine whale maneuvers during non-foraging periods in response to presence of whale watching vessels ([Table 1](#)). To avoid the potential confounding effects of orientation shifts by whales while vertically resting on the values of SD pitch, we identified and removed from the analysis all these periods, i.e., the apparent 180° (3.14 radians) shifts in vertical position ([Miller et al., 2008](#)). These shifts were first detected through a visual inspection of the dive profile and the pitch signal and, later, an automatic detection was defined with shifts occurring in intervals of 2-3 minutes in a range of 103-114° (1.8-2 radians). Additionally, we also calculated the number of shallow dives (depth > 2 m below the surface) per minute during non-foraging periods. Vertical velocity and ODBA were calculated using the previously referred tag tools. The mean of vertical velocity and ODBA, and the standard deviation of pitch and roll were calculated over 1-minute periods. To account for potential effects of variable tag position on ODBA calculations, ODBA values were standardized across in 1-minute intervals, by dividing by the median value of that individual and then multiplied by the median ODBA across all individuals ([Isojunno and Miller, 2015](#)). DTAG-4 had problems in the magnetometer data, thus, to avoid the use of distinct methods to calculate ODBA for the two types of tags used, ODBA was calculated using accelerometer data. For the same reason, fluke strokes could not be calculated for DTAG-4 tags, precluding the calculation of fluking and gliding periods in this study.

TABLE 2 Mean and standard deviation (SD) of variables used during non-exposure and exposure to whale watching (ww) periods and summary of results from the Linear Mixed-Effect Models testing the effects of ww vessel presence on the four sets of variables.

Hypothesis	Variable	Non-exposure to ww		Exposure to ww		Correlation	Transformation	Distribution	p-value	FDR correction
		Mean	SD	Mean	SD					
Foraging effort	Bottom phase depth	730.50	116.98	681.85	92.98	No	No	Gaussian	0.3291	0.4388
	Buzzes/minute	0.53	0.19	0.44	0.15	No	No	Gaussian	0.2483	0.3972
	Search ratio	0.80	0.04	0.81	0.07	No	Sqrt	Gaussian	0.9665	0.9665
	Foraging ratio	0.57	0.11	0.58	0.12	AR1	Log10	Gaussian	0.0203*	0.1624
Diving behavior	Dive duration	46.37	5.32	47.13	6.82	AR1	No	Gaussian	0.7629	0.8719
	Descent ratio	0.21	0.05	0.19	0.04	No	No	Gaussian	0.1524	0.3160
	Bottom phase ratio	0.60	0.09	0.63	0.09	No	No	Gaussian	0.0458*	0.1832
	Ascent ratio	0.19	0.06	0.17	0.06	ARMA	No	Gamma	0.1580	0.3160
	Pitch descent	0.95	0.33	0.89	0.33	ARMA	Log10	Gaussian	0.0960	0.2160
	Pitch ascent	0.96	0.33	0.97	0.36	ARMA	Log10	Gaussian	0.3170	0.4435
Locomotion effort	Vvelocity descent	1.11	0.42	1.12	0.44	ARMA	No	Gaussian	0.2440	0.4392
	Vvelocity ascent	1.25	0.43	1.32	0.45	ARMA	No	Gaussian	0.0097**	0.0390*
	ODBA descent	93.84	47.88	92.49	68.13	AR1	No	Gaussian	0.9830	0.9999
	ODBA bottom	131.51	76.90	128.66	78.81	ARMA	Log10	Gamma	0.3450	0.4438
	ODBA ascent	64.90	40.63	87.71	90.683	ARMA	Log10	Gaussian	0.0130*	0.0390*
Non-foraging behavior	Pitch SD non-foraging	0.11	0.14	0.12	0.12	AR1	Log10	Gaussian	0.0023**	0.0207*
	Roll SD non-foraging	0.37	0.57	0.31	0.46	ARMA	Sqrt	Gamma	0.8850	0.9830

Temporal autocorrelation structures were AR1 and ARMA; p-values before and after the false discovery rate (FDR) correction are presented. Bold variable names and FDR correction values indicate significant effects of whale watching vessel presence. * $p < 0.05$, ** $p < 0.01$.

Statistical analysis

Linear Mixed-Effects Models were used to test the effects of whale watching vessel presence on all the behavioral variables (Table 1). Separate models were built for each variable, always including individual ID as a random effect to account for within-individual correlation. A log or squared root transformation was applied to variables when model assumptions were not met (Table 2). Model assumptions were verified by plotting normalized residuals versus fitted values to check for heterogeneity of variance, and histograms and Q-Q plots to check for normality (Zuur and Ieno, 2016). Additionally, autocorrelation plots (ACF and PACF) were visually inspected for the temporal dependency of the residuals (Zuur and Ieno, 2016). AR1 or ARMA correlation structures were included in the model, if needed, to account for the temporal autocorrelation. Finally, a correction controlling for false discovery rate (FDR) was applied to p-values obtained from the models to adjust for multiple comparisons using the same dataset (Jafari and Ansari-Pour, 2019). All analyses were performed using the R software (R Core Team, 2016) and the package “mgcv” (Wood, 2017). All values reported below are mean values unless otherwise stated.

Results

Between 2017 and 2019, 24 sperm whales were tagged with either the DTAG-3 ($n=16$ whales) or DTAG-4 ($n=8$ whales). Tagged whales ranged approximately 9–11 m in length and all were found in social groups. A total of 93 dives and 1135 minutes of non-foraging periods were analyzed (Table 3). Sixteen out of the 24 tagged sperm whales were exposed to whale watching vessels. Overall, tagged individuals were exposed to whale watching vessels in 34 (37%) dives and 504 (44%) minutes of non-foraging periods (Table 3). In total, 13 premature detachments of DTAGs occurred due to breaches and only two individuals had deployment durations near the pre-programmed period of 24 hours (sw19_088a and sw19_160a). About 42% of tagged individuals were exposed to whale watching vessels prior tagging, 37% may have been exposed because there were whale watching vessels in the area, and 21% were not exposed.

Sperm whales exhibited higher vertical velocity ($p=0.0390$) and ODBA ($p=0.0390$) on the ascent phase of dives exposed to whale watching vessels (predicted vertical velocities: 1.35 ms^{-1} ($SE=0.045$) and 1.23 ms^{-1} ($SE=0.044$) for exposed and non-exposed dives, respectively; predicted ODBA: 1.79 ms^{-2}

TABLE 3 Summary of the data analyzed.

Date	Individual ID	Tag type	N° foraging dives	N° foraging dives exposed to ww	N° min non-foraging periods	N° min non-foraging periods exposed to ww
12/07/2017	sw17_193a	DTAG-4	6	–	–	–
13/07/2017	sw17_194a	DTAG-3	5	2	–	–
16/07/2017	sw17_197a	DTAG-3	–	–	–	–
22/07/2017	sw17_203a	DTAG-3	6	1	288	23
23/07/2017	sw17_204a	DTAG-4	2	2	–	–
24/07/2017	sw17_205a	DTAG-3	–	–	188	87
13/08/2017	sw17_225a	DTAG-4	2	1	8	7
15/08/2017	sw17_227a	DTAG-4	3	2	267	168
23/08/2017	sw17_235a	DTAG-4	3	3	2	–
25/08/2017	sw17_237a	DTAG-4	3	–	–	–
29/08/2017	sw17_241a	DTAG-4	4	3	42	33
08/09/2017	sw17_251a	DTAG-4	2	–	86	–
19/06/2018	sw18_170a	DTAG-3	3	2	–	–
21/06/2018	sw18_172a	DTAG-3	5	1	6	–
22/06/2018	sw18_173a	DTAG-3	2	2	34	34
26/06/2018	sw18_177a	DTAG-3	3	–	18	–
24/09/2018	sw18_267a	DTAG-3	–	–	–	–
08/10/2018	sw18_281a	DTAG-3	1	–	1	–
19/10/2018	sw18_292a	DTAG-3	3	1	176	133
29/03/2019	sw19_088a	DTAG-3	11	3	–	–
17/05/2019	sw19_137a	DTAG-3	6	–	–	–
07/06/2019	sw19_158a	DTAG-3	6	4	–	–
09/06/2019	sw19_160a	DTAG-3	12	5	–	–
12/06/2019	sw19_163a	DTAG-3	5	2	19	19
Total			93	34	1135	504

Table provides deployment date, individual identification, tag type, total number of foraging dives and how many of those were during exposure to whale watching (ww) vessels, and total number of minutes of non-foraging periods and how many of those were during exposure to ww. Grey shaded rows correspond to individuals exposed to whale watching vessels.

(SE=0.028) and 1.72 ms^{-2} (SE=0.044) for exposed and non-exposed dives, respectively) (Table 2 and Figures 3A, B). Dives exposed to whale watching vessels showed slightly shallower bottom phase depth (non-exposure=730.50 m; exposure=681.85 m) and fewer buzzes/minute (non-exposure=0.53; exposure=0.44) than non-exposed dives, but these differences were not statistically significant. The remaining variables related to foraging effort and dive behavior also did not reveal any statistical significance between exposed and non-exposed dives (Table 2).

SD of body pitch during non-foraging periods exposed to whale watching vessels was significantly higher with -1.05 radians (SE: 0.040) compared to -1.17 radians (SE: 0.039) during non-exposure periods ($p=0.0207$) (Table 2, Figure 3C and Supplementary Figure 2). On the other hand, the roll SD during non-foraging periods was not significantly different between exposure and non-exposure periods (non-exposure=0.37 radians; exposure=0.31 radians). In addition, sperm whales made slightly more shallow dives per minute, when exposed to whale watching vessels (median \pm SD of non-

exposure=0.05 \pm 0.29; median \pm SD of exposure=0.06 \pm 0.08), but differences were not statistically significant ($H(1)=0.22$, $p=0.6413$).

Discussion

Previous studies have assessed the impact of whale watching vessels on sperm whale behavior mostly based on their near-surface responses (Gordon et al., 1992; Magalhães et al., 2002; Richter et al., 2003; Richter et al., 2006; Isojunno et al., 2011; Cosentino, 2016); Isojunno et al., 2011; Cosentino, 2016) and they found changes in sperm whale ventilation patterns and surface heading, duration of surface periods between foraging dives, occurrence of aerial displays, increased number of shallow dives and delayed start of first long-range click. To the best of our knowledge, this is the first study investigating changes on the fine-scale underwater movements and acoustic behavior of sperm whales exposed to whale watching vessels, by instrumenting 24 whales with DTAGs in a region with relatively high whale watching pressure. Here, we found that, in the presence of whale

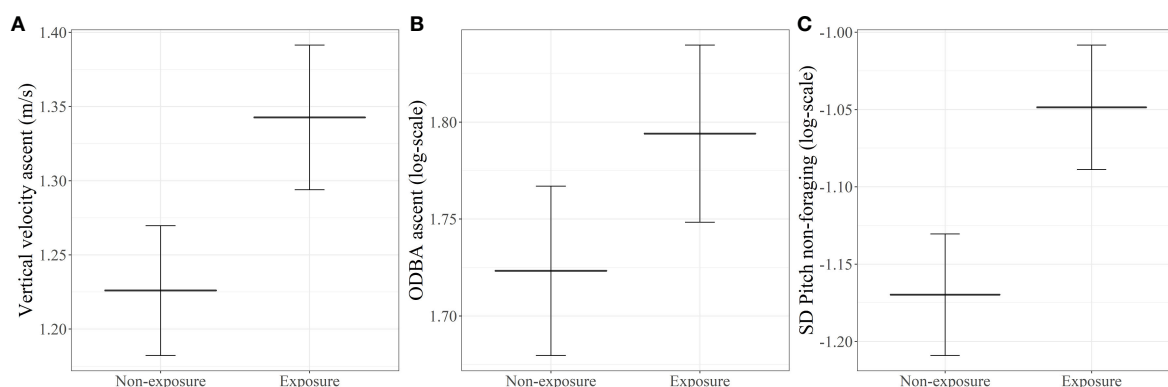


FIGURE 3

Model-predicted effects on the vertical velocity during ascent periods (A), ODBA during ascent periods (B), and on the SD of pitch (on the log scale) during non-foraging periods (C), for non-exposure and exposure periods to whale watching vessels. Error bars correspond to standard errors.

watching vessels, sperm whales perform fastest vertical ascents from foraging dives, expend more energy during those ascents, and have more disturbed non-foraging periods.

Sperm whale underwater behavior during whale watching vessel exposure

We did not detect significant differences in the number of prey capture attempts per minute (buzzes/minute) between non-exposed and exposed dives. In New Zealand, in a study performed with towed-array hydrophones, there were also no changes in the parameters related to prey encounter rates that could be attributed to whale watching vessels (Isojunno et al., 2011). Additionally, changes in other variables associated to foraging effort and dive behavior such as dive duration, search, foraging and bottom phase ratios, and body pitch during dive descents or ascents, were also small and not significant. Hence, there was no evidence for short-term changes in energy intake during exposure to whale watching vessels. Likewise, differences between exposed and non-exposed dives in descent phase and bottom phase ODBA, a proxy for locomotion effort, were not statistically significant.

Sperm whale's vertical velocity during ascent was significantly higher in dives exposed to whale watching vessels than in non-exposed dives. In marine mammals, energy expenditure and oxygen consumption increase rapidly with speed during active swimming (Kooyman, 1989; Hind and Gurney, 1997; Otani et al., 2001). To maximize oxygen available to foraging at depth, diving animals should conserve energy during descent and ascent transits by adopting optimal speeds during active stroking, and glide passively whenever buoyancy assists movement in the right direction (Williams et al., 2000; Sato et al., 2003; Miller et al., 2004b). The predominant swimming style in sperm whales is steady fluking

during descent, and stroke-and-glide during ascent, with prolonged gliding during the terminal part of the ascent (Miller et al., 2004b; Oliveira, 2014). While buoyancy and drag forces influence gliding behavior and optimal swim speed both across dives and individuals (Miller et al., 2004b; Aoki et al., 2017), it is unlikely that these forces changed between exposure and non-exposure conditions in this study. Hence, even though we were unable to calculate fluke rates and duration of gliding, the higher vertical velocity during ascents in exposed dives without any changes in pitch angle, suggests that sperm whales increased the stroke frequency. An increase in active stroking is consistent with the increased ODBA during ascents exposed to whale watching vessels relative to non-exposed ascents, which indicates a higher energetic cost during exposed dives, when compared to non-exposed dives.

In the Azores, whale watching vessels attempt to observe several fluke-ups in the same trip, often transiting at high speed across the sperm whale foraging area to reach surfacing whales before they dive. The behavior by whale watching vessels combined with higher sperm whale vertical velocities while ascending from foraging dives, can expose whales to risk of collisions with vessels, as this species shows difficulties in performing escape maneuvers during approaches from fast vessels (Gannier and Marty, 2015). Studies assessing the risk of vessel collisions with sperm whales will be necessary to understand the magnitude of the problem.

Sperm whale near-surface behavior during whale watching vessel exposure

While exposed to whale watching vessels during non-foraging periods, sperm whales exhibited a significant increase

in the SD of body pitch. Increased variability in pitch did not arise from orientation shifts while whales were vertically resting (Miller et al., 2008), as these were removed prior to the analysis. This higher variability could reflect a greater frequency of shallow evading dives (Lundquist et al., 2008), as was the case of mature males off Northern Norway (Cosentino, 2016). However, in our study the number of shallow dives was not significantly different between exposure and non-exposure non-foraging periods. Another possible explanation for the change in pitch variation would be an increase in social interactions. However, this activity is generally associated with higher variability in body roll movements (Gordon, 1998) and, in the present study, SD body roll did not differ between exposure and non-exposure periods. On the other hand, if presence of whale watching vessels disrupted social interactions, we would expect to see a decrease in SD roll. A third and, more likely explanation, is that the increased pitch variability reflects increased movement during resting periods when sperm whales are supposed to remain with a more less constant pitch (horizontal resting with pitch $\sim 0^\circ$ (0 radians) and vertical resting in drifting position [pitch near $\pm 90^\circ$ (± 1.57 radians); Miller et al. (2008)]. Altogether, these results suggest that presence of whale watching vessels disrupts resting activity in sperm whales.

The most consistent finding across studies examining changes in cetacean activity budgets in response to presence of whale watching vessels was an increase in time spent travelling, and consequently in energy expenditure, and reduction in time allocated to resting, as well as to foraging (Senigaglia et al., 2016). Although we haven't measured activity budgets of sperm whales, increased movements during resting and social periods also suggests increased energetic costs for whales exposed to whale watching vessels. These costs were not compensated by an increase in prey capture attempts, or any other proxy for foraging effort, suggesting an imbalance between energy intake and energy expenditure at least in the short-term. Additionally, sleep is a critical behavior, believed to play a key role in support of the central nervous system of animals (Rattenborg et al., 2017), and sleep disturbance has been shown to result in a range of negative health effects (Shaw et al., 2002; Andersen et al., 2009). If repeated over time, disruption of resting could impact the individual's health and energetic balance, and affect other vital activities such as feeding, nursing or mating (Bejder et al., 2006; Lusseau et al., 2006b; Christiansen and Lusseau, 2014).

Limitations of this study

The power to detect significant effects in our analyses was likely constrained by the small sample of exposure periods, the unbalanced sample between exposure and non-exposure, as well

as the high amounts of unexplained variation in sperm whale behavior.

Although we collected data from a healthy number of DTAG deployments ($n=24$), this study was based on opportunistic observations, which implies that we had no control on the number of exposures and non-exposures. Moreover, premature tag detachments due to breaching events and occasionally imperfect suction cup attachments, contributed to short tagging durations, thereby reducing the likelihood of whale exposures to whale watching vessels. In several deployments the tag slid to the whale's flank, reducing the efficiency of VHF tracking and making it difficult to focal-follow the tagged individuals and visually detect interactions with whale watching vessels. To overcome this limitation and increase sample size, we used the data recorded by DTAG hydrophones to detect noise from whale watching vessels. Although acoustic detection may not have been 100% accurate, and some exposure periods could have been missed, the approach proved to be effective at detecting presence of whale watching vessels when tagged whales descended to their foraging dives (Supplementary Table 1). However, the accuracy of acoustic detections dropped when whales were at or near the surface, during the surface phases and non-foraging periods, and we had to rely only on data from visual observations. As a result, we could not compare exposure and non-exposure during surface phases, and the comparison during non-foraging periods, albeit possible, suffered from low sample size.

High intra- and inter-individual variability in sperm whale behavior also limited our ability to detect significant exposure effects, albeit the inclusion of individual ID as a random term in the models. Part of this variability was likely driven by intrinsic individual differences in behavior, as well as changes in internal state, social context, or environmental conditions over time. However, differences in exposure conditions across observations were probably responsible for an important part of this variability. For example, the number and distance of whale watching vessels are known to influence the severity of behavioral responses in a number of cetaceans (Williams and Ashe, 2007; Stamation et al., 2010; Steckenreuter et al., 2011; Villagra et al., 2021). Here, because of the way observations were conducted and limitations in sample size, we could not account for either factor in the analysis. Converting the full range of exposure conditions into a binary variable (i.e., presence/absence of whale watching vessels) and contrasting the average response of whales, may have obscured real responses and weakened the detectability of significant effects (Williams and Ashe, 2007). Additionally, our ability to detect changes in behavior may have also been affected by potential cumulative effects of disturbance, if previous exposure to whale watching vessels conditioned whale's response during observed exposure periods, or their behavior during periods of non-exposure. However, unless cumulative effects subsist only for hours, this problem is

difficult to circumvent in studies conducted in whale watching areas.

Finally, our analyses involved multiple statistical tests on many behavioral variables, which is known to increase the probability of wrongly rejecting a null hypothesis. To account for this problem, we adjusted the p-values to control the false discovery rate (FDR), i.e., the rate at which null hypotheses are falsely rejected (Benjamini and Hochberg, 1995). Methods that control the FDR are becoming increasingly popular because they enable controlling the proportion of type I errors at or below a specified level and show greater power to detect true positives compared to more traditional approaches (e.g., Bonferroni corrections) (Benjamini and Hochberg, 1995). Nevertheless, more flexible modelling approaches such as generalized additive mixed models or multi-state hidden Markov models should be explored in the future to enable a better understanding of some of our results. Specifically, statistically significant differences prior FDR control in relative durations of bottom and foraging phases between exposed and non-exposed dives warrant further investigation.

Conclusions

Despite the caveats mentioned, this study provides novel insights on the short-term effects of whale watching vessels on sperm whale foraging and non-foraging behavior. Our findings indicate that exposure to whale watching vessels had no detectable effect on the individuals' foraging effort and behavior, including on prey capture attempts. In contrast, sperm whales increased the vertical speed and body acceleration during dive ascents, and showed increased movements during resting, suggesting that sperm whale responses to disturbance from whale watching likely carry energetic costs.

In the Azores, most individually identified sperm whales are transients but several social units are known to remain months in the area and return nearly every year (Boys et al., 2019). Individuals within these social units may be subjected to repeated interactions with whale watching vessels and may be under cumulative effects of vessel disturbance for prolonged periods of time. Moreover, some of these social units also use the waters around Madeira and Canary Islands (Steiner et al., 2015) and may be exposed to whale watching activities there. Therefore, it is essential to understand how sperm whales respond to repeated disturbance from whale watching vessels and assess the potential long-term consequences of these responses.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: The datasets analyzed

for this study can be found in the https://figshare.com/articles/dataset/Exposure_to_whale_watching_vessels_affects_dive_ascents_and_resting_behavior_in_sperm_whales/21355338.

Ethics statement

The animal study was reviewed and approved by Regional Secretariat of Science and Technology, Regional Directorate of Sea Affairs.

Author contributions

MAS, CO and RP conceived and designed the study, secured funding and managed the project. RP, CO, MAS, PJW, IC and SPJ collected the data. CO, IC, RP and MAS processed the data. CO and SPJ analyzed the data. CO wrote the first manuscript draft. CO, SPJ and MAS reviewed and wrote the revised manuscript. All authors commented on all previous versions of the manuscript and read and approved the final manuscript.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.914397/full#supplementary-material>

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Year-round foraging across large spatial scales suggest that bowhead whales have the potential to adapt to climate change

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The ecological impact of environmental changes at high latitudes (e.g., increasing temperature, and decreased sea ice cover) on low-trophic species, such as bowhead whales, are poorly understood. Key to understanding the vulnerability of zooplanktivorous predators to climatic shifts in prey is knowing whether they can make behavioural or distributional adjustments to maintain sufficient prey acquisition rates. However, little is known about how foraging behaviour and associated environmental conditions fluctuate over space and time. We collected long-term movement (average satellite transmission days were 397 (\pm 204 SD) in 2012 and 484 (\pm 245 SD) in 2013) and dive behaviour data for 25 bowhead whales (*Balaena mysticetus*) equipped with time-depth telemetry tags, and used hierarchical switching-state-space models to quantify their movements and behaviours (resident and transit). We examined trends in inferred two-dimensional foraging behaviours based on dive shape of Eastern Canada-West Greenland bowhead whales in relation to season and sea ice, as well as animal sex and age *via* size. We found no differences with regards to whale sex and size, but we did find evidence that subsurface foraging occurs year-round, with peak foraging occurring in fall (7.3 hrs d⁻¹ \pm 5.70 SD; October) and reduced feeding during spring (2.7 hrs d⁻¹ \pm 2.55 SD; May). Although sea ice cover is lowest during summer foraging, whales selected areas with 65% (\pm 36.1 SD) sea ice cover. During winter, bowheads occurred in areas with 90% (\pm 15.5 SD) ice cover, providing some open water for breathing. The depth of probable foraging varied across seasons with animals conducting epipelagic foraging dives (< 200 m) during spring and summer, and deeper mesopelagic dives (> 400 m) during fall and winter that approached the sea bottom, following the seasonal vertical migration of lipid-rich zooplankton. Our findings suggest that, compared to related species (e.g., right whales), bowheads forage at relatively low rates and over a large geographic area throughout the year. This suggests

that bowhead whales have the potential to adjust their behaviours (e.g., increased time allocated to feeding) and shift their distributions (e.g., occupy higher latitude foraging grounds) to adapt to climate-change induced environmental conditions. However, the extent to which energetic consumption may vary seasonally is yet to be determined.

KEYWORDS

state-space modelling, satellite-telemetry, time-depth recorder (TDR), Arctic, behavioural flexibility, zooplankton, sea ice, bathymetry

Introduction

Climate change is a leading threat to marine biodiversity worldwide (Worm and Lotze, 2021) because of the critical role environmental conditions (e.g., temperature, sea ice, stratification) play in species distribution and diversity in the oceans (Pacifi et al., 2015; Worm and Lotze, 2021). Based on forecasted global temperature increases, up to one in six species may be lost due to ecosystem shifts (Urban, 2015). The ecological mechanisms driving such extinction include habitat loss or degradation, reduced prey acquisition, lowered reproductive success, and higher rates of mortality (Beissinger, 2000; Strona and Bradshaw, 2018; Román-Palacios and Wiens, 2020). Species may also experience temperatures that exceed their physiological limits leading to metabolic challenges (e.g., fish) (Cahill et al., 2013) or phenological responses that alter lifecycles through changed growth rates, development times and molting rates (e.g., calanoid copepods—zooplankton). This in turn can affect recruitment and interspecific competition for resources (Usov et al., 2021). Subsequent shifts in the distribution and abundance of energetically rich prey species (Cahill et al., 2013) in response to abiotic stressors (temperature) may result in population level impacts for comparatively higher trophic species including marine mammals.

Zooplankton serve an important role in the transfer of organic matter and energy in marine food webs (Armengol et al., 2019) and are sensitive to changes in environmental conditions such as temperature, salinity and sea ice cover (Ershova et al., 2021). Poleward shifts in the distribution of ecologically important zooplankton taxa such as *Calanus* spp. have been documented in the North Atlantic Ocean, along with the borealization (i.e., northern shift in distribution of boreal species; Renaud et al., 2018) of zooplankton in the Davis Strait (Møller and Nielsen, 2020). Given these existing shifts in zooplankton and the critically important role they play in the stability of marine food-webs (Venkataramana et al., 2019), low-trophic, zooplanktivorous predators may be particularly vulnerable to climatic shifts.

Climate change impacts on population dynamics (Jenouvrier et al., 2018) may be particularly pronounced for

balaenid whales, specifically, bowhead (*Balaena mysticetus*) and North Atlantic right whales (*Eubalaena glacialis*). Although both species are genetically related with similar morphologies and diets, their population trajectories and life-history characteristics are markedly different. They may also have physiological adaptations making it easier for bowheads to meet their metabolic needs (e.g., hypometabolic rate; George et al., 2021) under future climatic conditions compared to right whales. Unlike other zooplanktivorous polar predators, such as humpback whales (*Megaptera novaeangliae*), little auk (*Alle alle*), and ringed seal (*Pusa hispida*) (Jakubas et al., 2017; Bengtson Nash et al., 2018; Ross et al., 2022), bowhead whales may be particularly vulnerable to climate-induced shifts in prey, since their long generation times may limit the capacity for adaptive evolution to help compensate for environmental fluctuation (Refsnider and Janzen, 2012; Silber et al., 2017). Consequently, behavioural plasticity and dispersal may be the most important means by which bowhead and right whales can contend with climatic changes. However, the inherent sensitivity of both species to climate-induced shifts in prey and their capacity to adapt is unknown.

Although northward habitat shifts have been observed for right whales (Simard et al., 2019), little is known about the energetic impact of prey alterations (Gavrilchuk et al., 2021) for future populations (Meyer-Gutbrod and Greene, 2018). Unlike more generalist predators such as sei whales (*Balaenoptera borealis*) that can exploit both calanoid copepods and small schooling fish (Burkhardt-Holm and N'Guyen, 2019), balaenids are not morphologically adapted to efficiently capture evasive fish prey. Slow swim speeds conducive to continuous ram-filtration require that bowheads and right whales target smaller, less mobile but densely aggregated prey compared to the *Balaenopteridae* family that use fast lunges and expanding throat grooves to maximize consumption of mobile taxa (Goldbogen et al., 2017). Consequently, the specialized foraging strategy of balaenids may make them particularly sensitive to climatic shifts in prey. Furthermore, research indicates that bowheads will experience a 50% loss in suitable habitat by 2100 (Foote et al., 2013), as lipid-rich Arctic calanoid

copepods (*Calanus glacialis*) become replaced by smaller temperate species (*C. finmarchicus*) that are lower in lipid content (Møller and Nielsen, 2020). However, it is yet to be determined whether bowheads will be able to adjust their energy budget by allocating more time to foraging (behavioural) or shift their distribution (dispersal) as they did during the Late Pleistocene (Foote et al., 2013) when pronounced fluctuations in environmental conditions occurred. Central to understanding the role that behavioural flexibility (i.e., plasticity) (Refsnider and Janzen, 2012; Samarra and Miller, 2015; Beever et al., 2017; Buchholz et al., 2019) may play in mitigating population level impacts of climate change is knowing to what extent bowhead whales (Reeves et al., 1983; Richardson et al., 1995; Fortune et al., 2020c) forage seasonally (Matthews and Ferguson, 2015; Pomerleau et al., 2018).

Behavioural flexibility or plasticity has been identified as a potential mechanism for disparate responses to environmental fluctuations (Buchholz et al., 2019). However, capacity to evaluate the degree to which behavioural flexibility may buffer climatic shifts—particularly in response to changes in the distribution, abundance and species composition of prey—is contingent upon comprehensive knowledge of the movements, habitat-use patterns (Pomerleau et al., 2011; Heide-Jørgensen et al., 2012; Chambault et al., 2018) and behaviours (Nielsen et al., 2015; Citta et al., 2021) of individuals under present conditions. To evaluate the capacity for individuals to alter their behaviour (e.g., activity budgets) in response to prey alterations, requires knowing where and for how long different age-sex groups of whales forage throughout their range. Much of what is known about large whale foraging ecology has come from short-term biologgers that record data for hours to days (Baumgartner and Mate, 2003; Simon et al., 2009; Goldbogen et al., 2015; Baumgartner et al., 2017; van der Hoop et al., 2019). Although informative, these studies provide a spatially and temporally limited understanding of behaviour, leaving little capability to quantify to what degree individual species like bowhead whales may be able to make behavioural adjustments.

To assess the potential for behavioural plasticity and dispersal to help buffer Eastern Canada-West Greenland bowhead whales against forecasted ecosystem changes, we used long-term satellite telemetry, time-depth recorder data (>365 days), and georeferenced bathymetry and sea ice condition data to examine: 1) the proportion of time individuals allocate to probable foraging on a daily and seasonal timescale; 2) what environmental conditions currently support successful foraging (e.g., sea ice conditions); and 3) how vertical foraging behaviour (e.g., depth) changes across seasons for individuals of different sexes and body lengths. Since Eastern Canada-West Greenland bowhead whales make predictable seasonal movements (Heide-Jørgensen et al., 2010; Nielsen et al., 2015; Fortune et al., 2020c) from southern regions in winter and spring to higher latitude areas in summer and fall, we can infer habitat-use patterns based on season. We predicted

that seasonally high foraging effort under present environmental conditions would indicate a reduced capacity to adjust activity budgets in a changing environment, and that low effort may reflect greater potential for compensation *via* behavioural plasticity. We also expected that small spatial extent would indicate poor capacity for dispersal and vice versa—assuming that spatial extent of seasonal foraging areas is an indicator of suitable habitat. Consequently, we utilized longitudinal data to quantify patterns in the time spent foraging to evaluate how climate-change resilient bowhead whales are likely to be. Finally, we compared our findings with what is known for a closely related but apparently nutritionally stressed species—the North Atlantic right whale.

Materials and methods

Telemetry

A total of 25 bowhead whales were equipped with long-term satellite telemetry tags that included time-depth recorders (Wildlife Computers SPLASH MK10). Whales were tagged in Foxe Basin and Cumberland Sound, Nunavut (Figure 1). The SPLASH tags recorded date, time, location, and summary dive behaviour (i.e., depth, duration, and shape of dive). Dive behaviour is continuously logged *via* time-depth recorder and all summary statistics are transmitted during successful satellite transmission. The Platform transmitter terminals (PTTs) were programmed to maximize tag longevity to cover as much of the annual whale migrations as possible. Consequently, the tags were programmed to transmit up to 400 times a day every second hour during the summertime and only 100 times every second day during winter.

A ~20 cm stainless steel anchor was used to attach the tag to the whale's blubber, and a 4 cm biopsy tip simultaneously collected a skin and blubber sample for genetic analysis and to determine sex. A 1:10 bleach/water solution was used to sterilize the anchor and biopsy tip prior to use. The tags were deployed using an 8 m fiberglass hand-held tagging pole and attached in the middle of the back posterior to the blowholes. Placing the tag in this location improved data transmission by maximizing the time the transmitter was above the water. Body length was estimated relative to the known length of the tagging vessel during each tagging event. Age-classes were determined based on estimated median body length of tagged whales ($n=23$) whereby juveniles include individuals 10 m, sub-adults represent animals >10 m and <13 m and adults were ≥ 13 m.

Horizontal movement analysis

We used the Square Root Unscented Kalman Filter (SRUKF) algorithm developed by Service Argos to re-process the raw

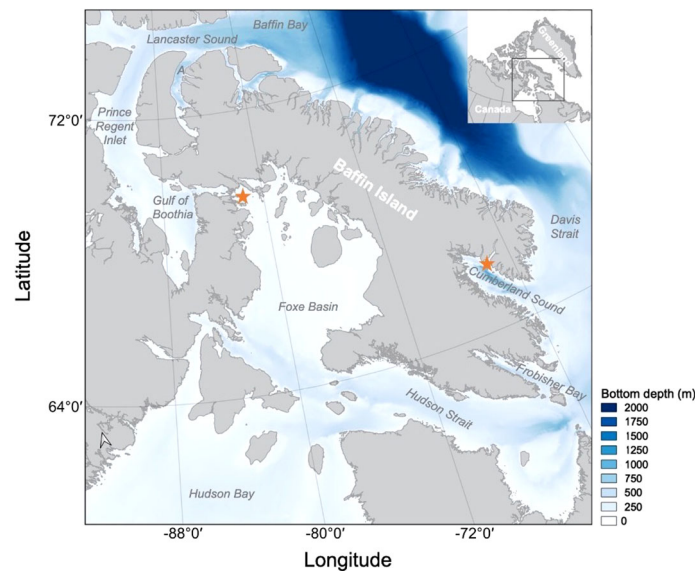


FIGURE 1

Study area for Eastern Canada-West Greenland bowhead whales tagged in Foxe Basin and Cumberland Sound Nunavut with bathymetric data indicating the depth of the sea bottom ranging from 0 m (white) to 2000 m (dark blue). Regions of interest (Hudson Bay, Hudson Strait, Foxe Basin, Gulf of Boothia/Prince Regent Inlet, Admiralty Inlet, Cumberland Sound and Frobisher Bay) are indicated with 'A' representing Admiralty Inlet. Tagging locations off Igloodik (Foxe Basin) and Pangnirtung (Cumberland Sound) are indicated (★). QGIS 3.10 (QGIS Development Team, 2018) and General Bathymetric Chart of the Oceans (GEBCO) global 453 terrain model for ocean and land (GEBCO Compilation Group, 2021) was used to construct this map.

Argos locations. This algorithm consists of a correlated random walk model that uses the individual's previous location and estimated error to predict an animal's future position (Silva et al., 2014). We selected the Kalman Filter over the Least-squares algorithm because it typically results in an increased number of positions and improved accuracy of low-quality Argos locations (e.g., location classes 0, A and B) that are common for large whale tagging studies (Silva et al., 2014; Lowther et al., 2015). The bowhead whale telemetry data are typically biased towards low-quality locations due to diving behaviour (e.g., short surface intervals between dives) and the environment (e.g., seasonally ice covered).

Argos location data for marine animals often contain some poor-quality records. We therefore filtered the data using a speed filter (vmask function in the argosfilter package in R; R Core Team, 2020) to remove SRUKF Argos locations that would have resulted from biologically improbable swimming speeds. We set a speed threshold of 2 m s^{-1} based on previous measurements of balaenid swim speed while foraging and travelling (Mayo and Marx, 1990; Baumgartner and Mate, 2003; Werth, 2004; Simon et al., 2009; Nielsen et al., 2015), and removed locations with swimming speeds greater than this from the data set.

We used a hierarchical switching-state-space model or 'HSSSM' (Jonsen et al., 2005; Jonsen et al., 2013) to estimate the movement of individual whales and determine the probable behavioural state associated with each location (e.g., travelling

and resident behaviours). Jonsen et al. (2013) provided the R package 'bsam' (R Core Team, 2020), which we used to fit a correlated random walk model (CRW). The CRW switched between two CRWs, one that reflected resident or area-restricted movement behaviour and another that reflected transit behaviour (Jonsen et al., 2005). Mean turn angle and swimming speed were used to differentiate the two CRWs and the associated behavioural states (Jonsen et al., 2005). Low swimming speeds and high turning angles reflected 'resident' behaviour, whereas faster and more linear movements reflected 'transit' behaviour. Resident behaviour is expected to be associated with foraging (e.g., Haskell 1997; Hill et al., 2000; Fauchald and Tveraa 2003; Thums et al., 2011; Byrne and Chamberlain, 2012) and other spatially limited behaviours such as reproduction (Würsig et al., 1993; Kraus and Hatch, 2001) and rock-rubbing (Fortune et al., 2017). During winter when sea ice thickness and cover are maximized, resident behaviour may also reflect a degree of spatial restriction such that horizontal movement is limited. In the absence of extensive ice cover, multi-scale biologging and simultaneous prey-field sampling studies have corroborated that resident behaviour is associated with foraging behaviour (Fortune et al., 2020a).

We selected the hierarchical switching-state-space model because it provides regularly spaced location estimates and categorizes behaviour, both needed to determine the seasonal foraging behaviour of bowhead whales in the Eastern Canadian

Arctic. We defined seasons as being summer (June, July, August), fall (September, October, November), winter (December, January, February) and spring (March, April, May), and used mean estimates from the Markov Chain Monte Carlo (MCMC) samples to classify behaviour states (b), which assumed that $b=1$ was transit and $b=2$ was resident mode. We used the same cut off points for b as used by others (Jonsen et al., 2007; Fortune et al., 2020b; Fortune et al., 2020c) such that locations with mean estimates of $b > 1.75$ were assumed to reflect resident and $b < 1.25$ reflected transit behaviour. Values of b that fell between 1.25 and 1.75 were assigned an unclassified behavioural state.

To determine physical environmental conditions associated with tagged whales, HSSSM predicted locations were georeferenced with bathymetry and sea ice datasets. We used satellite derived sea-ice concentration data from the Advanced Microwave Scanning Radiometer 2 (AMSR2) sensor (Institute of Environmental Physics, University of Bremen) (Spreen et al., 2008) to determine monthly sea ice concentration. To obtain an estimate of sea ice conditions encountered by tagged whales, we used one raster image from the beginning of the month for each year (2012–2015) with a 3.125 km spatial resolution. For bathymetry, we used the 2020 gridded bathymetric data set from General Bathymetric Chart of the Oceans (GEBCO) global terrain model for ocean and land. This data set provided elevation information in metres on a 15 arc-second interval grid. Using QGIS (version 3.10; Development Team, 2018), we used the point sampling tool to extract bathymetric and sea ice cover data associated with each HSSSM location. We subsequently removed any corresponding values resulting from HSSSM locations occurring on land as well as erroneous bathymetric readings (< 0 m).

Vertical movement analysis

We analyzed bowhead diving behaviour using summary time-depth-recorder (TDR) dive data telemetered over the duration of the tag attachment period to: 1) refine predictions of foraging behaviour based on horizontal movement; 2) evaluate spatio-temporal trends in 2D foraging behaviour (e.g., square dives); 3) determine how environmental covariates such as sea ice cover and bathymetry impact diving behaviour as well as sex, body length and season; and 4) quantify time spent foraging seasonally throughout their range. The TDR recorded several dive statistics such as dive shape (V, U or square), maximum dive depth and duration. Dives were defined as excursions to depths ≥ 8 m. Consequently, dives that were shallower than 8 m were not included in the analysis. The shape of the dive was classified using Wildlife Computers' three broad categories: V-shaped dives included dives where $\leq 20\%$ of total duration was spent at maximum depth; U-shaped dives occurred when $> 20\%$ and $\leq 50\%$ of total duration was

spent at maximum depth; and square dives included those where $> 50\%$ of the duration was spent at maximum depth.

Dive shape classification may be used to infer behaviour. Previous foraging ecology studies of bowhead whales have concluded that square and U-shaped dives that maximize bottom time reflect foraging dives (Laidre et al., 2007; Heide-Jørgensen et al., 2013). For example, bowhead whales off the coast of Disko Bay during spring, conducted deep U-shaped dives to depths where high abundances of pre-ascension *Calanus finmarchicus* were concentrated (Laidre et al., 2007). Furthermore, bowhead whales appear to temporally adjust the depth of their U-shape dives, suggesting that individuals alter their feeding behaviour based on the vertical distribution of their prey (Heide-Jørgensen et al., 2013; Fortune et al., 2020a). We defined foraging behaviour as square-shaped dives conducted during resident behavior, and estimated the time spent foraging per day for each whale by summing the duration of square-shape dives (including descent, bottom and ascent phase) during resident behaviour. To account for gaps in predicted locations from the satellite-telemetry data, we calculated a daily estimate of foraging time aggregated across months and do not provide a cumulative estimate.

As well as prior data screening previously described, we further excluded locations predicted from the HSSSM that resulted from gaps exceeding four consecutive days in the 'raw' SRUKF data. We subsequently merged the behavioural data with the Argos location data based on matching dates and assumed that animals remained in a specific habitat for the entire day as this matched previous observation of bowhead movement in Cumberland Sound based on focal follows of tagged individuals (Fortune et al., 2020a). We also assumed that if there was a resident associated HSSSM location within a habitat on a particular day, all dives occurring during that same day were similarly conducted inside that habitat. This assumption was based on observed multi-scale bowhead whale tagging and focal follow data that showed individuals resided in a region of interest (e.g., Cumberland Sound) for consecutive weeks to months (Fortune et al., 2020a; Fortune et al., 2020b). Furthermore, observed patterns in HSSSM data demonstrate that transit locations occur when individuals are exiting a region of interest (Fortune et al., 2020a; Fortune et al., 2020b).

Examining patterns in horizontal and vertical movements

Once data were prepared, we first used graphical approaches and simple data summaries to examine spatio-temporal patterns in two-dimensional behaviours. Specifically, we examined the spatial extents of resident, transient, and unknown behavioural states using the HSSSM predicted locations and mapping software (i.e., QGIS 3.10; QGIS Development Team, 2018). To evaluate how much horizontal behaviour might reflect actual

foraging, we examined the proportion of all dives by shape associated with predicted resident locations. Assuming square-shaped dives (≥ 8 m) were foraging dives based on prior research (Fortune et al., 2020a) or behavioural changes within years, we graphed the percent sea ice cover by month (2013 and 2014 only). We used faceted heatmaps to examine monthly and diel patterns in putative foraging dive behaviour, and used ridgeline plots to compare the distributional changes in bathymetric and sea ice cover data across months and behavioural states (i.e., resident, transient and unknown). We also summarized the information on square-shaped dive depths, proximity to the sea bottom, and associated ice conditions using boxplots. Finally, seasonal and regional changes in average time spent feeding per day was elucidated with heatmaps, boxplots and violin plots (showing raw data distribution).

We then used models to specifically look for effects of four fixed-effects factors, namely, the two class variables, season (spring, summer, winter, fall) and sex (male or female), and the two continuous variables, median body length (m) and percent sea ice cover on vertical models, namely foraging dives considered to be the square-shaped dives only (Laidre et al., 2007; Heide-Jørgensen et al., 2013; Fortune et al., 2020b). For this, 23 of the 25 whales were included, since two whales (PTT 114501 and 128149 removed) were missing one or more of these four factors. We scaled dive depths for varying sea water depths by calculating: 1) the distance between the maximum depth of putative foraging dives (square-shaped dives) and sea bottom (i.e., maximum bathymetry), labeled hereafter as 'distance to bottom'; and 2) the ratio of the maximum depth of square-shaped dives relative to maximum bathymetry, henceforth called 'fraction of water column'. We included 'distance to bottom' in our models because it represents the proximity of probable foraging dives to the sea bottom providing an indication of when bowheads are likely feeding on deep prey aggregations (i.e., benthic dives) such as diapausing life-stages of lipid-rich copepods. A small difference indicates whales are near the sea bottom (e.g., 5 m) conducting benthic dives, whereas a large difference (e.g., 100 m) reflects more epipelagic dives in the photic zone. The fraction of the water column was also included as this variable provides a proportional measure of proximity of maximum depth of square-shaped foraging dives associated with resident locations to the sea bottom. Data were filtered such that any instances where the max dive depth was greater than the sea bottom depth were deemed erroneous and were removed from our analysis. Values closer to 0 are near the surface, whereas values closer to 1 indicate the deep dives near the sea floor.

Using distance to bottom as the response variable, the modelling approach was as follows:

1. We used estimated generalized least squares fitted using the function 'gls' of the R package 'nlme' to fit alternative models using combinations of the four factors and interactions between the class variables as

well as between the class and continuous variables (21 models).

2. For these models, we used a natural logarithmic of the distance to bottom variable to meet assumptions of normality and equal variances. We also standardized the two continuous variables, length and sea ice, to zero means and unit standard deviations to remove differing measurement scale effects on estimated fixed-effects parameters.
3. We accounted for the autocorrelation of multiple dive records per animal (repeated measures) using a first-order continuous autocorrelation process (i.e., CAR(1) using Julian date) within each animal given the irregularly spaced measures in time (Pinheiro and Bates, 2000). However, we also investigated possible higher-level correlations using first- to fourth-order autocorrelation (AR) processes, since higher-level CAR processes are difficult to model and, consequently, have not been included in nlme (nor in other R packages). Although some evidence was found for possible higher order autocorrelations using AR processes, the largest was first order, as expected. Given that over-specifying the correlation model can lead to a removal of the signal in the data, and also that higher orders of CAR processes were not available using nlme, CAR(1) was retained for all models.
4. Since interpretation of the magnitude and direction of estimated fixed-effects parameters would be of interest for models without interactions, we used the variance inflation factor (VIF) as a measure of multicollinearity implemented in R using collinearity() and vif() functions. VIFs were all <1.5 in the model with all four factors (no interactions). For models with interactions, variables are related given the nature of interactions and VIFs tend to be inflated. In any case, estimated fixed-effects parameters of models with interactions among variables cannot be separately interpreted, but must be jointly interpreted.
5. The log likelihood and Akaike's Information Criterion (AIC) were used to select among the models, along with likelihood ratio tests for a subset of nested models ($\alpha=0.05$).

To examine the possible impacts of the four fixed-effects factors on the fraction of the water column as the response variable, some changes were made to the modelling approach since this variable is a ratio bounded by 0 and 1. First, we considered two alternative probability distributions for this ratio response variable, specifically the binomial distribution with a logit link that has commonly been used for proportions or ratios and the beta distribution also with a logit link. The binomial distribution is not ideal since there are technically no 'successes' and 'trials' used in obtaining the fraction of the water column values. As a result, the beta distribution has

been more recently recommended for proportions and ratios (e.g., Ferrari and Cribari-Neto, 2010; Damgaard and Irvine, 2019). However, the beta distribution requires all values to be in the (0,1) interval, meaning that all values exactly equal to 0 or to 1 must be removed or the response variable must be rescaled to avoid these endpoints. Also, algorithms using the beta distribution that also account for correlated data and/or random effects are generally not available. Conversely, the binomial distribution has been used for some time for successes out of trials as well as for proportions and ratios. As a result, algorithms to account for correlated data and random effects have been developed and well-tested. Overall, a clear choice for the fraction of the water column models would appear to be using a binomial distribution and CAR1 to account for irregularly-spaced time intervals, as with the distance to bottom response variable. Unfortunately, the algorithms for a binomially distributed response variable with correlations in time use pseudo-likelihood to find a solution. As a result, there is no log likelihood and therefore no AIC to compare models; other measures of goodness-of-fit, such as the sum of squared deviances, sum of squared differences between the measured ('y') and ('yhat') estimated proportions, and/or root mean squared difference between y and yhat must be used instead. Furthermore, hypothesis tests of groups of variables are not easily done, including testing nested models. As well, higher levels of correlation are generally not implemented, meaning that only AR1 or CAR1 can be included in the models. Given these challenges and focusing on examining any impacts of the four factors, we used the following modelling approach for the fraction of the water column response variable:

1. First, we used the R package 'glmmPQL' to fit a generalized linear model with a binomial distribution, a logit link, random intercept by animal, and a CAR1 within animal correlated error structure. We did also examine alternative algorithms based on reported reliabilities. specifically the R package 'lme4' using the 'glmer()' function, but that allowed for a random intercept by animal only, a correlation structure that does not represent the repeated measures within animal data used in this study. We initially also fitted all models using the R package 'betareg', since the beta distribution had been recommended, but given the inability to include correlation structures, and the need to rescale the fraction of the water column to remove any 0's or 1's, these were dropped.
2. As with models for distance to bottom, we standardized the two continuous variables and combinations of variables without and with interactions (21 models for fraction of the water column).
3. To compare the models, we used the sum of squared deviances as well as the sum of squared differences between the measured and estimated ('SSE') fraction

of the water column values. The sum of squared deviances were carefully used for model comparison, since the deviances use both the fixed and random effects; consequently, a model with more explanatory variables may not have a smaller (or even the same) sum of squared deviances. The SSE used only the estimated fixed-effects parameters; however, since search algorithms are used to fit these models, again, a model with more fixed-effects variables may not have a lower (or even the same) value.

4. For a selection of models resulting from the comparisons, we also calculated the square root of the mean squared differences. These values indicate the accuracy of fraction of the water column estimates in the same units as fraction of the water column and facilitated model interpretation.

Results

Overview of satellite-telemetry data and HSSSM

The 25 bowhead whales were tagged during summer 2012 and 2013 in two regions of the eastern Canadian Arctic—Foxye Basin and Cumberland Sound. There were 16 whales tagged during July and August 2012 in Foxye Basin (4 females, 3 males and 1 of unknown sex) and Cumberland Sound (3 females and 5 males). In July 2013, 9 juvenile and adult whales (4 non-lactating females, 4 males and 1 of unknown sex) were tagged in Foxye Basin. Females with calves were not approached for tagging. The whales tagged in 2012 transmitted data for 397 ± 204 days on average, while those tagged in 2013 transmitted for 484 ± 245 days (Table 1). The state-space model predicted two daily locations for each animal. The combined data set for all whales contained 16,587 locations throughout the Eastern Canadian Arctic, and the location data were relatively evenly distributed across seasons with 29% (n=4,737) in fall, 25% (n=4,095) winter, 22% (n=3,709) in spring and 24% (n=4,046) in summer. Of all the predicted locations, 73% (n=12,161) were associated with resident behaviour and only 13% (n=2207) were associated with transit behaviour (Figures 1, 2). The greatest proportion of resident locations for all bowhead whales and years combined was during winter (83.2% of n=3,405), followed by fall (69.6%, n=3,297), spring (81.3%, n=3,017) and summer (60.4%, n=2,442). The high number of winter and springtime resident locations corresponds with lower numbers of transit behaviours observed during winter (12%, n=258) and spring (14%, n=301). Conversely, proportionally fewer resident locations were observed during fall (transit; 34%, n=745) and summer (transit:41%, n=903) when transit behaviour was more frequent.

TABLE 1 Summary information for all bowhead whales tagged in Cumberland (CS) and Foxe Basin (FB) with Wildlife Computers SPLASH Tags (MK10) between 2012 and 2013.

PTT	Start	End	Duration (days)	Location	Length (m)	Sex	Age
114494	2012-07-03	2013-05-21	322	FB	12	F	Sub-adult
114495	2012-07-03	2014-06-26	723	FB	11-12	F	Sub-adult
114496	2012-07-03	2013-12-13	528	FB	11	F	Sub-adult
114497	2012-07-06	2013-05-10	308	FB	12	M	Sub-adult
114498	2012-07-06	2013-02-17	226	FB	11	M	Sub-adult
114499	2012-07-06	2013-06-08	337	FB	13-14	F	Adult
114500	2012-07-06	2014-02-21	595	FB	12-13	M	Sub-adult
114501	2012-07-07	2013-01-05	183	FB	–	–	Unk
114502	2012-08-06	2013-07-10	338	CS	10	M	Juvenile
114503	2012-08-06	2014-06-26	689	CS	10	F	Juvenile
114504	2012-08-07	2013-07-19	346	CS	10-11	F	Sub-adult
114505	2012-08-08	2013-06-22	318	CS	11-12	M	Sub-adult
114506	2012-08-08	2012-08-27	19	CS	13-14	F	Adult
114507	2012-08-12	2013-09-19	403	CS	10	M	Juvenile
114508	2012-08-12	2014-08-19	737	CS	9-10	M	Juvenile
114509	2012-08-12	2013-05-26	287	CS	9-10	M	Juvenile
128145	2013-07-03	2014-11-13	498	FB	11-12	F	Sub-adult
128146	2013-07-03	2015-05-22	688	FB	13-14	F	Adult
128148	2013-07-09	2014-06-06	332	FB	13	F	Adult
128149	2013-07-09	2013-07-22	13	FB	12-13	–	Sub-adult
128150	2013-07-09	2015-07-08	729	FB	10	F	Juvenile
128151	2013-07-09	2015-07-01	722	FB	9-10	M	Juvenile
128152	2013-07-09	2015-05-24	684	FB	9-10	M	Juvenile
128153	2013-07-03	2014-07-16	378	FB	12-13	M	Sub-adult
128154	2013-07-03	2014-05-18	319	FB	11-12	M	Sub-adult

Unique animals are identified with the Platform Transmitter Terminal (PTT). The day the animal was tagged is the 'start date' and the day the tag stopped transmitting data is the 'end date'. The region where the animal was tagged is the 'location'. The 'body length' was estimated in metres from observers on board the tagging vessel. The tags transmitted for an average 'Duration' of 428.9 days \pm 218.79 SD.

Diving behaviours

The 25 tagged whales made 206,772 dives, but 22 of recorded dives were removed as outliers because dive durations and depths were biologically improbable with durations exceeding 75 min and depths beyond 700 m. Consequently, 206,750 dives were included in the graphical and initial analyses. We were able to associate 73% ($n=151,279$) of the dives with resident behaviour, 36,379 (18%) with transit and 19,114 (9%) with an unknown behavioral state. Whales spent on average 5.71 hrs (\pm SD: 2.57) diving (all shapes) to depths of ≥ 8 m on a daily basis with an average total of 25.4 ± 11.56 dives per day. Among resident associated dives (Figure 3), 66% ($n=99,780$) were square-shaped, 23% ($n=34,852$) U-shaped, 10% ($n=15,662$) were V-shaped, and 0.65% ($n=985$) were of unknown shape. Of all the square dives that occurred in association with resident behaviour, 17% ($n=16,699$) occurred in winter, 13% ($n=13,311$) in spring, 40% ($n=39,705$) in summer and 30% ($n=30,065$) in fall. However, our analysis did not account for surface foraging behaviour, which likely occurred during late spring/early

summer when zooplankton often concentrate at the surface. During transit behaviour, the whales conducted 36,376 dives where 53% ($n=19,280$) were square-shaped, 32% ($n=11,560$) were U-shaped, 15% ($n=5,335$) were V-shaped and 0.6% ($n=201$) were of unknown shape.

The maximum depth of square dives varied over time (Figure 4 top; Table S1), with the shallowest dives occurring during early summer ($29.63 \text{ m} \pm 21.7 \text{ SD}$; July), progressively deeper and variable dives in fall ($112.67 \text{ m} \pm 111.3$; September), and a maximum in winter ($242.37 \text{ m} \pm 80.3$; December). Minimum dive duration similarly followed seasonal patterns with the shortest dives occurring during early summer ($8.88 \text{ mins} \pm 4.2$; July), becoming longer in fall ($16.07 \text{ mins} \pm 8.7$; September) and greatest in winter ($24.84 \text{ mins} \pm 8.8$; January) (Figure 4; bottom).

Seasonal patterns in bathymetry

Of the 16,587 predicted HSSSM locations, we used 93.6% ($n=15,532$) of them to georeference bathymetric data and

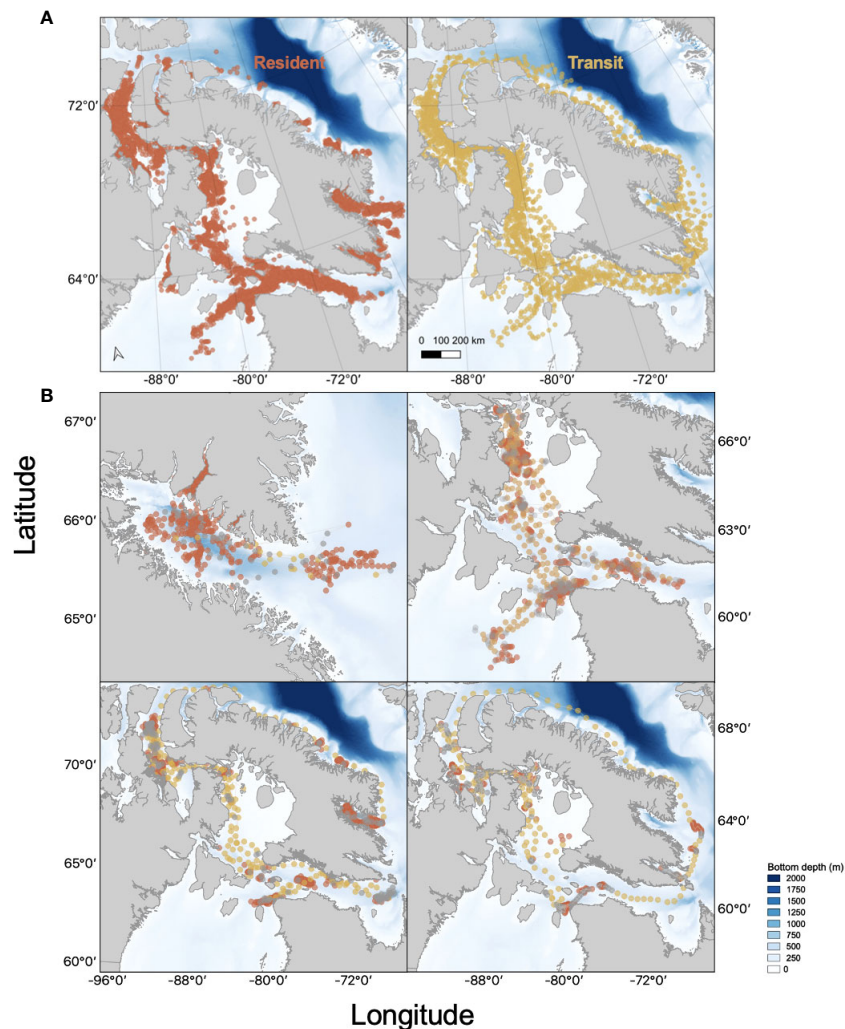


FIGURE 2

(A): Argos Satellite locations for 25 SPLASH tagged bowhead whales in the Eastern Canadian Arctic derived from hierarchical switching state-space models (HSSSM). Resident (●) and transit (●) behavioural states derived from the HSSSM are plotted for each animal. (B): Example of Argos satellite tracks derived from HSSSM predictions for four SPLASH tagged bowhead whales (PTT 114504, 128150, 128152, 128153) resident, transit and unknown (●) behavioural states highlighted behavioural states derived from the HSSSM are shown for each animal.

removed 6.4% ($n=1,065$) that occurred on land. In total, 14,995 bathymetric measurements were associated with predicted whale locations (Figure 5; Table 2). Of these predicted HSSSM locations, there were 124 instances (0.83% of locations; $n=14,995$) where a location associated with resident behaviour occurred on the same day as a transit location for a given whale. Although bathymetry was variable ($223.5 \text{ m} \pm 164.01 \text{ SD}$) when all HSSSM locations were combined, tagged whales occupied consistently shallower areas during resident compared to unknown behaviour during summer (June–August; Table 2) and occasionally resided in shallower waters than while transiting (September bottom depth was 74 m during resident vs. 125 m while transit). A trend towards deeper waters was observed for unknown behaviours during the winter (February) and for all behavioural states during late spring

(March and May) to early summer (June and July). Average depths utilized by bowhead whales were shallowest during fall (e.g., September; $74 \text{ m} \pm 64.87$) and deepest during winter (e.g., January; $315 \text{ m} \pm 96.69$) (Figure 5). However, resident behaviour occurred in areas with greatest variability in bottom depth during spring (e.g., May; $286 \text{ m} \pm 251.21$), when foraging depths were shallow.

Sea ice concentration values were obtained for 90% ($n=14,994$) of all HSSSM predicted locations (Figure S1). This resulted in a total of 10,712 resident, 2,094 transit and 2,188 unknown locations having corresponding sea ice data. While animals engaged in resident movement, the average sea ice concentration across seasons was $69\% \pm 37.60 \text{ SD}$, less ice cover occurred during transit ($61\% \pm 42.16$) and unknown behavioural

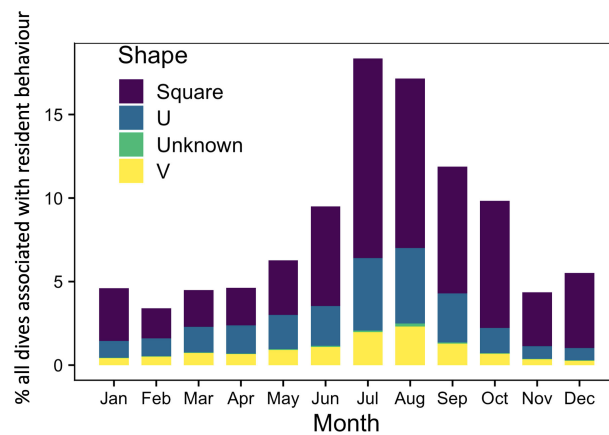


FIGURE 3

Percent of all bowhead whale dives ($n=206,750$) that occurred on the same day as a resident associated Argos location (predicted from the HSSSM) by season and dive shape. Data were pooled across individuals and years.

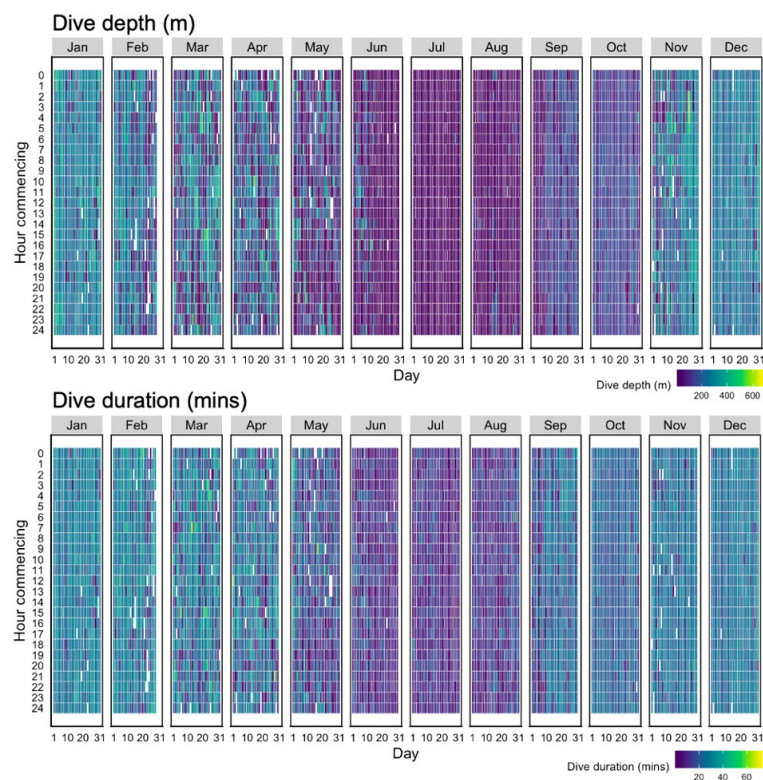


FIGURE 4

Heatmap of the maximum dive depth (m) (top) and minimum dive duration (mins) (bottom) of square-shaped dives ($n=99,780$) associated with resident behaviour for all bowhead whales ($n=25$) by time of day (Hour commencing) and day of the month (Day). Data are pooled across years (2012–2015) and include dives throughout their range (both inside and outside regions of interest).

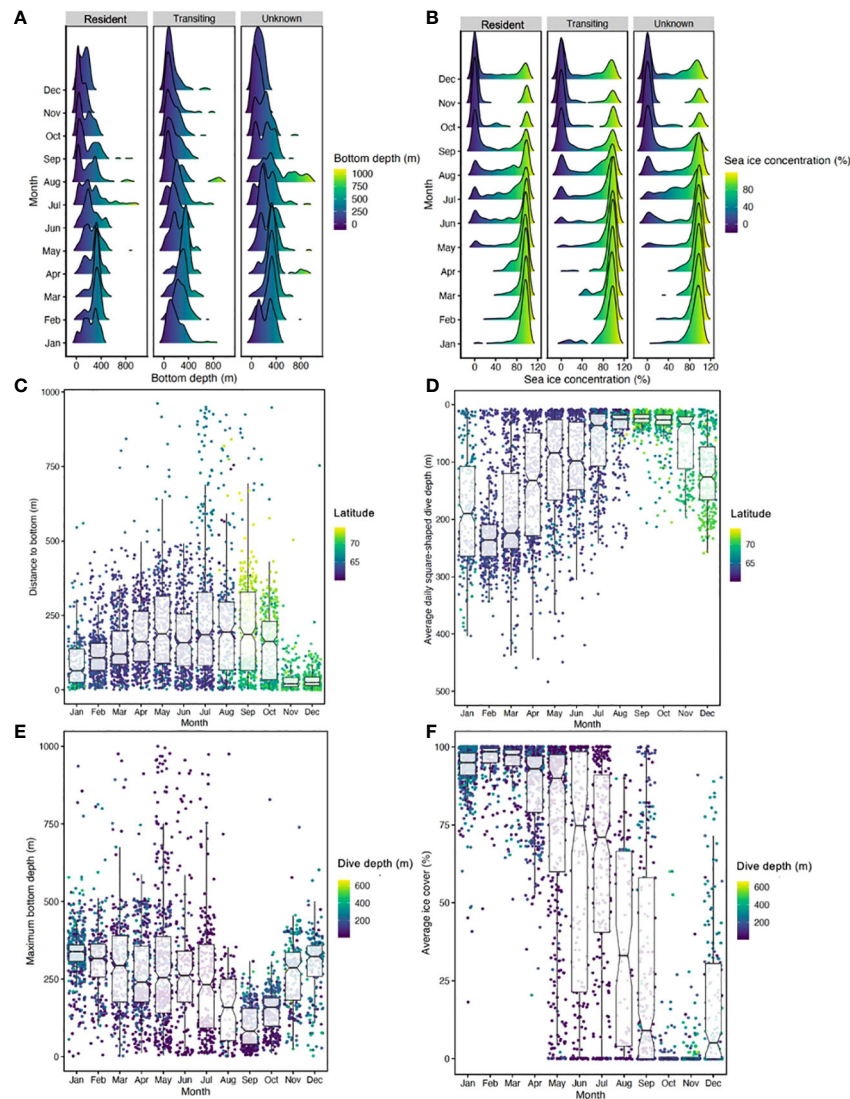


FIGURE 5

(A) Bathymetric (bottom depth) data associated with HSSSM predicted locations for all bowhead whales ($n=25$) by behavioural state and month. Shallow bathymetry is indicated by warm colours and deep bottom depths are denoted by cool colours. Due to location uncertainty, predicted locations occurring on land were removed as bathymetric data could not be determined for these positions. (B) Sea ice concentration associated with HSSSM predicted locations by behavioural state (resident, transit and unknown) and month where warm colours indicate low ice concentration and cool colours denote extensive coverage. (C) Boxplots reflect distance in metres between the average daily maximum depth of square-shaped dives and the mean daily bathymetry associated with resident locations. Scatter points reflect raw data and the colour gradient indicates corresponding latitudinal position. (D) Average daily square-shaped dive depth (putative foraging dive depth) per individual associated with resident locations. Raw data is represented by scatter points and colour coded by latitude whereby warm colours reflect putative foraging dive depth in low latitude regions and cool colors reflect high-latitude behaviours. (E) Maximum bottom depth (bathymetry) by month with the mean depth of square-shaped dives represented by scatter points such that warm colors indicate shallow dive depth and cool colors indicate deep depths. (F) Average percent sea ice cover by month with associated square-shaped dive depths displayed as a scatterplot. Boxplots include notches to indicate potential significant differences (when notches do not overlap) between months.

states ($61\% \pm 41.43$). Maximum percent ice cover occurred in March for resident ($92\% \pm 12.52$) and unknown ($94\% \pm 10.09$) locations—and in February for transit ($94\% \pm 6.71$) locations (Table 3).

We statistically evaluated the impact of season, bathymetry, sea ice, sex and body length on putative foraging behaviour for

23 whales with complete datasets. We first found no interactions among factors (M19, full model versus M20 no interactions) for the distance to bottom response variable. However, we found fairly strong evidence of season and some evidence for percent sea ice cover effects on differences between the maximum depth of probable foraging dives (i.e., square-shaped dives) and

TABLE 2 Bathymetric data (m) associated with HSSSM predicted locations of bowhead whales by behavioural state (resident, transit and unknown) and month.

Month	Resident		Transit		Unknown	
	Mean \pm SD	Min-Max	Mean \pm SD	Min-Max	Mean \pm SD	Min-Max
1	315 \pm 96.69	2-936	278 \pm 114.32	8-587	318 \pm 101.09	14-622
2	279 \pm 116.40	3-922	353 \pm 163.75	54-1108	336 \pm 154.82	7-905
3	259 \pm 148.22	1-1107	229 \pm 128.91	4-530	277 \pm 142.5	6-929
4	238 \pm 143.83	1-1199	198 \pm 105.89	1-423	229 \pm 108.31	30-476
5	286 \pm 251.21	1-1175	261 \pm 231.10	2-1658	269 \pm 192.1	1-1111
6	226 \pm 233.24	1-1720	213 \pm 252.11	2-1466	397 \pm 298.52	2-1433
7	200 \pm 190.69	3-1140	167 \pm 122.96	1-658	226 \pm 136.56	6-663
8	145 \pm 117.68	1-975	153 \pm 114.70	1-668	187 \pm 123.46	2-717
9	74 \pm 64.87	1-342	125 \pm 124.86	2-796	92 \pm 75.33	1-516
10	118 \pm 75.66	1-828	141 \pm 148.58	3-1032	121 \pm 66.09	1-273
11	228 \pm 117.73	1-739	206 \pm 208.39	1-1802	235 \pm 126.10	1-906
12	297 \pm 103.49	1-773	266 \pm 116.93	8-708	294 \pm 113.01	2-787

Data were pooled across individuals and years. Instances where bottom depths (bathymetric data) associated with transit and unknown behaviour states are deeper than those associated with resident behaviour are in bold.

bathymetry (i.e., sea bottom). For example, square-shape dive depth was shallowest in July (27 m \pm 20.238 SD), and was considerably deeper in December (223.8 m \pm 70.312 SD). The difference between the maximum depth of square-dives and the sea bottom was on average 204 m \pm 171.677 in July and 119 m \pm 80.626 SD in December (Table 3, S1; Figure 5). Seasonal patterns in sea ice conditions were also noted such that bowheads occupied areas of low ice cover in fall (49% \pm 3.58 SD; November) and high concentrations in winter (93% \pm 10.311 SD; January) (Table 3; Figure 5). Distance to bottom models treated these two factors as having impacts (Table S2A), with M16 having the lowest AIC (10360.85) suggesting it was the best model. No interactions among factors were found (M19 full model versus M20 no interactions, $p=0.8614$; Table S2B). Other

than season and sea ice cover, we found little evidence of additional impacts of sex or body length on these distances (M16 versus M20, $p=0.4918$; Table S2B). In terms of impact trends, there was a slight curvilinear and upward trend of distance to bottom with sea ice cover (logarithm of distance was used in the model), with summer having the largest differences (i.e., more shallow dives), fall having the smallest differences (i.e., deepest dives), and summer and winter being similar (Table S2C and Figure S2).

For the fraction of water column (i.e., maximum depth of square-shaped dives relative to bathymetry), season showed the highest impact relative to the other models with only one factor (i.e., M2 versus M1, M3, and M12; Table S3). Furthermore, the model with just season showed the biggest drop in both sum of

TABLE 3 Sea ice concentration (%) values by season associated with HSSSM predicted locations of bowhead whales by behavioural state averaged across individuals and years.

Month	Resident ice (%)	Transit ice (%)	Unknown ice (%)
1	89.15 \pm 18.045	85.11 \pm 24.688	88.36 \pm 17.03
2	90.04 \pm 15.440	93.64 \pm 6.71	91.85 \pm 14.094
3	91.57 \pm 12.521	91.48 \pm 14.9	93.96 \pm 10.094
4	88.39 \pm 14.145	92.64 \pm 16.616	92.06 \pm 11.374
5	80.08 \pm 29.482	85.53 \pm 23.253	83.94 \pm 27.758
6	67.6 \pm 37.009	83.19 \pm 31.042	74.68 \pm 36.838
7	66.85 \pm 33.363	71.99 \pm 34.538	64.82 \pm 31.631
8	61.42 \pm 36.558	61.32 \pm 38.634	64.68 \pm 39.085
9	43.92 \pm 42.058	41.43 \pm 43.02	36.93 \pm 41.287
10	26.58 \pm 39.672	30.22 \pm 42.814	23.97 \pm 39.283
11	25.27 \pm 41.642	23.45 \pm 39.032	20.82 \pm 39.112
12	40.79 \pm 39.445	43.19 \pm 41.396	43.34 \pm 40.324

Data are expressed as mean values with standard deviations.

squared deviances and SSE relative to the null model (i.e., SSE of 358.93 and 263.86 for M0 (null) versus M2 (season), respectively, [Table S3](#)). Adding in other factors and interactions among factors resulted in only very modest drops [e.g., SSE of 263.86 and 261.33 for M2 (season) versus M19 (full model)]. This evidence indicates that season was the most important factor related to changes in the relative feeding dive depths. For example, fraction of the water column was $0.76\% \pm 0.209$ SD in October showing close agreement to the maximum depth of putative foraging dives and the depth of the sea floor ([Table 5](#) and [Figure 5](#)). However, during early summer, fraction of the water column was $0.22\% \pm 0.224$ SD in July indicating a mismatch between diving behaviour and bathymetry ([Table 5](#)). Unlike distance to bottom, which represents the distance in metres between the maximum depth of square-shaped dives and the associated depth of the sea bottom, fraction of the water column is a scaled measure indicating relative agreement between bowhead dive behaviour and bathymetry.

Foraging time

Combining all square-shaped dives ($n=6,029$) that occurred in the six core-use regions we found evidence of putative foraging behaviour across seasons ([Table 5](#)). Estimated time spent foraging was lowest during spring (2.68 hrs ± 2.547 SD; May) when dive depth was shallow (52.67 m ± 81.972 SD) and greatest in fall (7.34 hrs ± 5.697 SD; October) when foraging depth was comparatively deeper (141.59 m ± 112.103 SD) ([Figure 6](#)). Year-round foraging behaviour (i.e., consistent occurrence of square-shaped dives) was observed in three regions—Cumberland Sound, Hudson Bay and Hudson Strait. Within season, daily foraging time was elevated in Gulf of Boothia/Prince Regent Inlet and Central East Baffin Coast compared to Cumberland Sound, Hudson Bay and Hudson Strait. Accounting for estimated median body length to infer age-class of tagged whales, we found that juveniles conducted a total of 2,410 dives, while sub-adults made 2,587 dives and adults dove 875 times across all seasons and years.

Discussion

Summary of findings and limitations

Our analysis of multi-dimensional behaviour revealed that bowheads engage in putative foraging year-round that varies seasonally in depth, intensity (i.e., hours per day), and with sea ice cover ([Figures 5, 6](#)). Although evidence of peak foraging occurred during fall when a daily average of 7.3 hrs ([Table 5](#)) were allocated to putative foraging dives in October, feeding continued throughout the winter (e.g., 5.7 hrs in December; [Table 5](#)). Probable foraging dives to the sea bottom ([Figure 5D](#))

varied across seasons and sea ice conditions for distance to bottom (absolute measure of distance between probable foraging dive depth and depth of sea bottom) and across season only for fraction of the water column (relative measure of agreement between feeding depth and bathymetry). Accounting for the absolute distance to bottom (m) provides insight into whether whales were likely targeting diapausing *Calanus* spp. found near the seafloor ([Kvile et al., 2019](#); [Banas et al., 2021](#)), whereas relative (fraction of water column) differences provided behavioural information about the general characteristics of the putative foraging dive. The strong support for seasonal impacts on foraging behaviour and proximity to the seafloor, along with the seasonal vertical ontogenetic migration of copepods in the Calanidae family ([Madsen et al., 2001](#); [Baumgartner and Tarrant, 2017](#)), indicate that bowheads were mostly likely exploiting high-energy, diapausing life-stages during fall and winter and surface aggregations of feeding copepods during spring and summer ([Madsen et al., 2001](#); [Fortune et al., 2020b](#)). This finding is consistent with the Bering-Chukchi-Beaufort bowhead population that exploit prey aggregations near the sea bottom during fall ([Olness et al., 2020](#)). To a lesser extent, shallow epipelagic dives during early summer may have also reflected consumption of mysids, euphausiids and chaetognaths ([Pomerleau et al., 2012](#)).

Sea ice conditions varied seasonally along with feeding behaviour as whales selected areas where sea ice persisted during summer (61% cover in August; [Table 4](#)) and where some open water remained during winter (93% in January; [Table 4](#)). However, sea ice impacts were only detected for the model that accounted for the absolute differences (distances to sea bottom; [Table S2](#)) between putative foraging dive depth and the seafloor. No evidence of sea ice effects was observed for models that included relative differences (i.e., fraction of water column; [Table S3](#)). Selection for greater sea ice cover during the open-water summer season, may provide refuge ([Ferguson et al., 2010](#)) from mammal-eating killer whales that are known to predate on bowheads ([Reinhart et al., 2013](#); [Young et al., 2019](#); [Matthews et al., 2020](#)). The apparent preference for sea ice cover during early summer may also reflect initiation of the phytoplankton bloom and consumption of recently ascended late-life stages and early life-stages of copepods ([Baumgartner and Tarrant, 2017](#); [Sampei et al., 2021](#)). Occupying areas with open water in winter likely provide bowhead whales with breathing access and reduce risk of entrapment for younger animals ([Mitchell and Reeves, 1982](#); [Ferguson et al., 2010](#)). These findings are consistent with year-round foraging with autumn hyperphagia, suggesting that bowheads forage at depth widely throughout their range, but at low rates (hours per day) across the eastern Canadian Arctic.

Although previous studies in Cumberland Sound corroborated that square-shaped dives are a reliable indicator of feeding activity ([Fortune et al., 2020a](#)), similar co-located tagging and prey field sampling studies have not been conducted

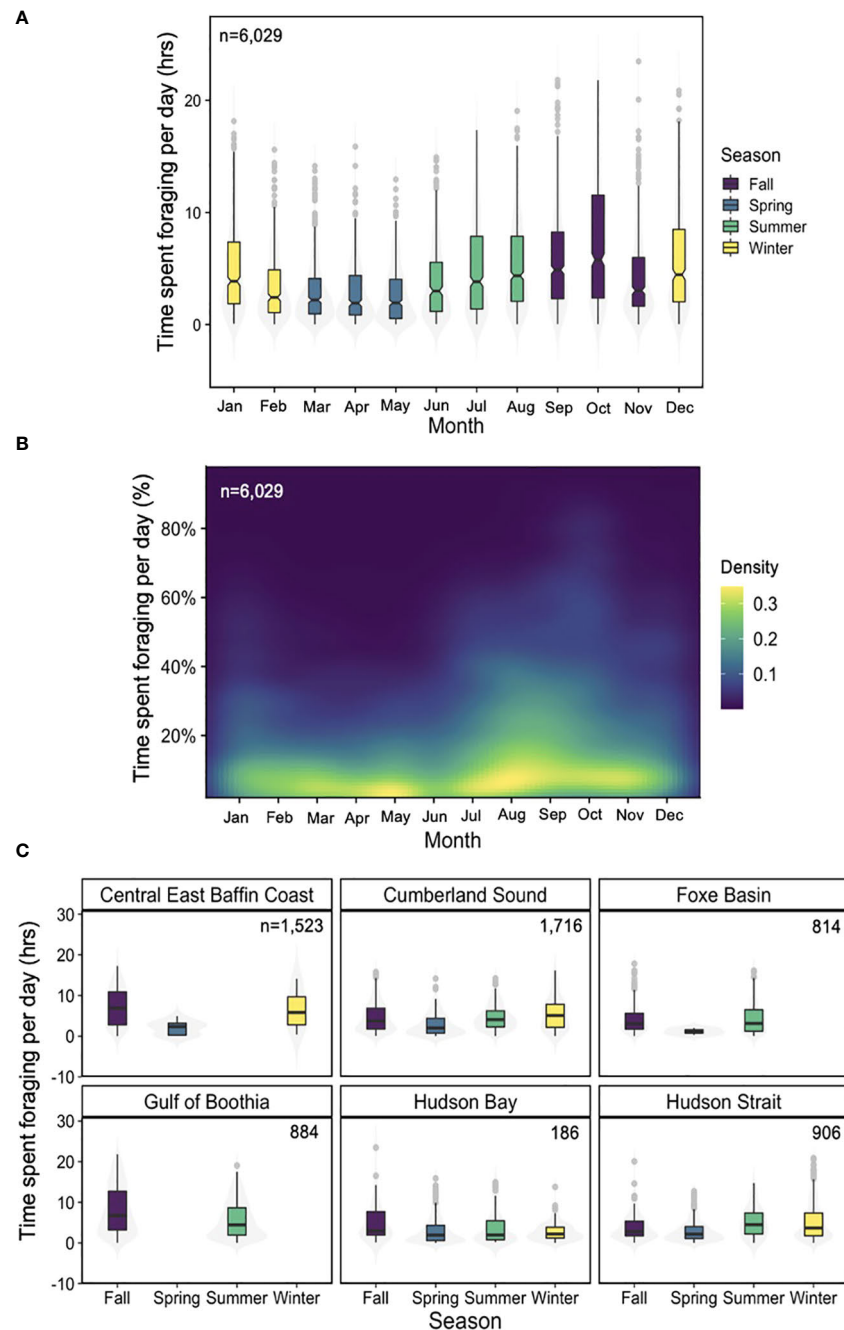


FIGURE 6

(A) Total time spent conducting putative foraging dives (square-shaped) daily by month with data pooled across individuals ($n=25$) and years ($n=4$). Data are colour coded based on season whereby purple = fall, blue = spring, green = summer and yellow = winter. (B) heatmap of the proportion of time (24hrs) spent foraging per day based on the total daily proportion of time spent conducting square-shaped dives. Data pooled across individuals and years. Cool colors (purple) indicate low density of data points and warm colors (yellow) represent comparatively high densities of data. (C) Total time spent conducting putative foraging dives by region and season with data pooled across individuals and years. Boxplots include notches to indicate potential significant differences (when notches do not overlap) between months (A) and seasons (B) and violin plots (grey shaded area) shows the data distribution.

TABLE 4 Summary information on bowhead whale putative foraging behaviour with georeferenced environmental covariates.

Month	Dive depth (m)	Bathymetry (m)	DTB (m)	FWC	Sea ice (%)	Sample (n)	Year (n)
1	198.46 ± 92.135	326.34 ± 72.638	146.34 ± 101.888	0.578 ± 0.255	93.03 ± 10.311	430	3
2	145.03 ± 93.88	289.02 ± 92.898	174.12 ± 108.056	0.461 ± 0.2661	93.02 ± 8.628	281	3
3	113.09 ± 88.519	277.02 ± 128.386	209.14 ± 154.682	0.391 ± 0.2867	90.22 ± 9.927	299	3
4	105.8 ± 74.111	242.16 ± 109.744	179.64 ± 132.325	0.407 ± 0.2747	87.75 ± 9.156	293	3
5	70.72 ± 66.104	264.29 ± 185.373	237.31 ± 212.969	0.304 ± 0.2606	83.55 ± 15.608	306	3
6	45.38 ± 49.662	236.96 ± 174.22	224.32 ± 197.192	0.273 ± 0.2684	79.62 ± 20.118	235	3
7	26.98 ± 20.238	207.69 ± 158.523	204.31 ± 171.677	0.217 ± 0.2242	76.18 ± 19.554	270	4
8	31.74 ± 29.396	183.36 ± 104.819	172.25 ± 125.409	0.257 ± 0.2614	86.08 ± 19.285	236	3
9	78.59 ± 59.518	96.34 ± 62.245	37.42 ± 44.353	0.675 ± 0.2423	60.99 ± 18.79	141	3
10	125.04 ± 62.429	145.73 ± 60.29	34.78 ± 50.907	0.756 ± 0.2092	51.96 ± 8.121	272	3
11	188.19 ± 97.282	252.51 ± 91.657	90.98 ± 86.122	0.678 ± 0.2703	49.07 ± 3.587	191	3
12	223.8 ± 70.312	323.73 ± 63.884	118.8 ± 80.626	0.661 ± 0.2116	78.56 ± 22.154	352	3

Data were first computed as daily means for each individual (n=25) and were subsequently averaged across individuals and sampling years (2012–2015) on a monthly basis. To determine the depth of probable prey ingestion, Dive depth reflects mean daily square-shaped dive depth (metres). To examine the proximity of probable foraging dive depth to the sea bottom and corresponding sea ice conditions, Bathymetry indicates the depth of the seafloor (metres) and Sea ice reflects the percent sea ice concentration associated with area-restricted search locations as predicted by HSSSM. DTB reflects the distance to bottom variable and denotes the distance in metres between the sea bottom and the maximum depth of square-shaped dives and FWC represents the fraction of the water column and indicates the percent difference between the maximum depth of square-shaped dives and the bottom depth (Dive depth/Bathymetry). FWC values close to one reflect dive depths that closely approached the sea bottom and values close to zero indicate comparatively shallow dives that did not approach the sea floor. Sample indicates the number of mean daily dive records and corresponding bathymetry and sea ice condition data and Year represents the number of years of data.

elsewhere in their range. Furthermore, since the quality and quantity of zooplankton prey are known to vary spatially and temporally, it is unlikely that feeding conditions will remain constant year-round. Consequently, net energy gain is expected to vary seasonally and regionally despite consistent foraging effort. To address these limitations, *in-situ* physical and biological oceanographic sampling need to be expanded near bowheads. Given the lack of spatio-temporal data about bowhead whale feeding conditions, we made inferences about prey quality based on the depth of putative foraging dives and the proximity to the sea bottom. However, with limited location information (two predicted HSSSM per day) our estimates of bathymetry are coarse. To obtain a long timeseries of movement data, the daily resolution of locations was sacrificed. In the future, medium duration tags with fast acquisition GPS and inertial sensors (e.g., accelerometers) may be used to increase the number of daily locations while improving location accuracy and permitting the quantification of prey ingestion time. Another consideration is that by considering probable foraging behaviour on days when whales displayed horizontal movement that was consistent with resident behaviour only, we excluded the possibility for intermittent foraging during transit. We also may have overestimated daily foraging time during winter when sea ice conditions preclude movement between regions and resident behaviour is expected to dominate. However, the overall impact of excluding sporadic feeding while migrating between areas is low given the relative sparseness of transient locations and because daily foraging time was calculated based on dive behaviour consistent with foraging (validated through field observations; Fortune et al., 2020a). Another consideration is that the 8 m depth threshold for summary dive data

determined by Wildlife Computers, precluded the inclusion of surface or near surface feeding between 0 and 8 m. Consequently, it is possible that putative foraging time is underestimated during spring when copepods are expected to aggregate near the surface (Madsen et al., 2001). That said, summertime sampling near feeding whales in Cumberland Sound demonstrated that the mixed-layer depth was at 17 m on average and that the shallowest prey layer occurred between 30 and 40 m (Fortune et al., 2020a). Consequently, we don't anticipate that the exclusion of shallow dives less than 8 m in depth resulted in underestimated feeding estimates during other times of year (summer, fall and winter). Furthermore, when including the time spent at the surface with the time spent diving (all shapes) to depths ≥ 8 m when displaying resident behaviour for a randomly selected whale (PTT 11495), we found that this accounted for a total of 20.49 hrs leaving only 3.5 hrs for dives shallower than 8 m on August 1, 2012. This suggests that our dive dataset is comprehensive, providing a complete picture of summary dive behaviour.

Climatic impacts on foraging conditions

There are numerous ways in which future oceanographic shifts can impact the foraging conditions of low-trophic, high-latitude species, such as bowhead whales. Most important, is the thinning and earlier breakup of sea ice (Notz and Stroeve, 2016; Stroeve et al., 2017), which has created new opportunities for phytoplankton blooms to occur below the sea ice. For example, in the Chukchi Sea increased light penetration through the no-longer snow-covered sea ice, is sufficient to support

TABLE 5 Summary information about the Depth (m) of probable foraging of bowhead whales based on the maximum depth and minimum duration [Time foraging (hrs)] of square-shaped dives (Sample n=6,029) by A: month with data pooled across individuals and years and B: region and season. Data are expressed as mean \pm SD.

A

Month	Depth (m)	Time foraging (hrs)	Sample (n)
1	183.37 \pm 120.753	5.06 \pm 4.111	499
2	143.48 \pm 128.265	3.46 \pm 3.148	364
3	108.42 \pm 127.764	3.05 \pm 2.9	386
4	100.18 \pm 112.42	2.98 \pm 2.863	336
5	52.67 \pm 81.972	2.68 \pm 2.547	473
6	37.90 \pm 52.152	3.85 \pm 3.387	326
7	29.00 \pm 25.25	5.12 \pm 4.322	596
8	69.46 \pm 96.536	5.23 \pm 3.84	732
9	111.29 \pm 115.669	5.98 \pm 4.538	686
10	141.59 \pm 112.103	7.34 \pm 5.697	687
11	201.46 \pm 147.224	4.34 \pm 3.824	476
12	210.61 \pm 102.971	5.71 \pm 4.529	468

B

Region	Season	Foraging time (hrs)	Depth (m)	Sample (n)
Central East Baffin Coast	Fall	7.23 \pm 4.516	294.54 \pm 177.349	166
Central East Baffin Coast	Spring	2.04 \pm 1.662	40.82 \pm 35.329	11
Central East Baffin Coast	Winter	6.82 \pm 4.925	194.33 \pm 145.396	9
Cumberland Sound	Fall	4.61 \pm 3.469	219.55 \pm 119.537	369
Cumberland Sound	Spring	2.83 \pm 2.705	96.01 \pm 102.185	175
Cumberland Sound	Summer	4.59 \pm 2.938	127.27 \pm 124.879	264
Cumberland Sound	Winter	5.59 \pm 4.04	237.15 \pm 112.355	98
Foxe Basin	Fall	3.97 \pm 3.186	88.46 \pm 108.864	449
Foxe Basin	Spring	1.15 \pm 0.852	26.67 \pm 13.65	3
Foxe Basin	Summer	4.16 \pm 3.644	33.27 \pm 34.885	432
Gulf of Boothia	Fall	8.07 \pm 5.827	102.76 \pm 78.015	743
Gulf of Boothia	Summer	5.57 \pm 4.356	30.89 \pm 37.952	780
Hudson Bay	Fall	5.05 \pm 5.026	176.49 \pm 109.139	38
Hudson Bay	Spring	2.91 \pm 2.952	84.47 \pm 107.958	552
Hudson Bay	Summer	3.8 \pm 4.056	52.46 \pm 90.61	91
Hudson Bay	Winter	2.76 \pm 2.188	144.95 \pm 129.889	133
Hudson Strait	Fall	3.9 \pm 3.466	200.33 \pm 101.396	84
Hudson Strait	Spring	2.91 \pm 2.555	80.32 \pm 116.602	454
Hudson Strait	Summer	5.03 \pm 3.594	41.87 \pm 46.83	87
Hudson Strait	Winter	5.02 \pm 4.236	181.51 \pm 117.334	1091

phytoplankton growth in the Arctic Ocean (Arrigo et al., 2012; Horvat et al., 2017). Given current trends of decreasing sea ice thickness across the Arctic, sub-ice phytoplankton are likely to continue increasing in occurrence and extent (Horvat et al., 2017). This will likely shift the timing and magnitude of net primary productivity (e.g., diatoms) needed to support the secondary production of herbivorous calanoid copepods (Swailethorp et al., 2011; Darnis and Fortier, 2014). Such shifts in environmental conditions are likely to impact the development, energy needs and recruitment of three dominant

bowhead whale prey species—*Calanus hyperboreus*, *C. glacialis* (Arctic origin) and *C. finmarchicus* (temperate) (Scott et al., 2000; Niehoff et al., 2002; Falk-Petersen et al., 2009).

Faced with climatic shifts, smaller bodied, low-energy temperate species (*C. finmarchicus*) (Falk-Petersen et al., 2009) may have a competitive advantage over slower growing, larger and higher energy Arctic species (*C. hyperboreus* and *C. glacialis*). For example, earlier phytoplankton blooms and warmer water temperatures increase copepod growth rates and metabolic demand, potentially allowing *C. finmarchicus* to reach

reproductive spawning stages of development faster than multi-year Arctic species as has been observed in subarctic waters (Weydmann et al., 2018). Consequently, temperate species may outcompete Arctic taxa because they are more capable of exploiting longer periods of food availability to support spawning (Swailethorp et al., 2011). Such shifts in community composition have begun to be documented in bowhead whale foraging areas (Disko Bay, Greenland) where *C. finmarchicus* and *C. hyperboreus* once represented equal proportions of copepod biomass (1990s), but where *C. finmarchicus* now dominates (Møller and Nielsen, 2020). Since late-stage copepodites of Arctic origin such as *C. hyperboreus* (1.03–1.81 mg lipid for overwintering stage five and adult female individuals) contain over 25 times as much stored lipid as similarly aged temperate species (*C. finmarchicus* contain 0.04–0.08 mg of lipid per individual stage five and adult female), the numerical abundance of lower energy prey must be sufficiently high to offset the energetic loss of lipid-rich Arctic species (Falk-Petersen et al., 2009).

Prey consumption differences

Understanding how prey field characteristics differ based on species composition is important for elucidating the energetic impacts of climate change to balaenids. In Cumberland Sound during summertime (August), bowheads dove to deeper depths (215 m \pm 28.7 SD) and exploited lower densities of prey (285 orgs m⁻³ \pm 175.4 SD) that consisted of a lower proportion of temperate species (7.4% *C. finmarchicus*) and higher proportions of Arctic taxa (26.1% *C. glacialis* and 18.2% *C. hyperboreus*; Fortune et al., 2020b). However, in previously occupied summertime feeding habitats in the lower Bay of Fundy and Scotian Shelf, right whales targeted dense near-bottom layers consisting almost exclusively of diapausing (stage five) life-stages of *C. finmarchicus* (Baumgartner and Mate, 2003; Davies et al., 2013; Baumgartner et al., 2017). On average, whales dove to 121 m (\pm 24.2 SD) encountering prey abundances of 7,481 (\pm 4, 581 SD) orgs per m⁻³ (Baumgartner and Mate, 2003). The higher abundances of prey encountered by right whales may help compensate for the comparatively lower energy value of available copepods, but it may also be necessary to offset their lower filtration rate. Right whales have a smaller mouth gape than bowhead whales and would need to feed on either higher abundances of prey or for longer times to obtain energy ingestion rates similar to bowheads (van der Hoop et al., 2019).

Seasonality in foraging behaviour and fasting

In the absence of foraging ecology studies with similarly high spatio-temporal resolution to our bowhead study, there remains

much guesswork about the seasonal feeding activity of North Atlantic right whales. Currently, only a segment of the North Atlantic population resides on calving grounds where they are presumed to fast (Dombroski et al., 2021). Consequently, a portion of the right whale population is unaccounted for during winter months (Hayes et al., 2018; Charif et al., 2020). Although the time spent foraging per day is unknown for right whales on a monthly basis, movement of individuals between known foraging grounds (e.g., Cape Cod Bay, Massachusetts, USA) and presumed areas of fasting (southeastern US) occurs frequently based on photo-identified individuals. This suggests that even non-reproductive animals likely spend at least a portion of the winter fasting (Brown and Marx, 2000). However, high-resolution archival tags are designed to provide detailed dive data over a short period of time (\leq 24 hrs) and therefore yield an incomplete picture of daily feeding activities that preclude assessing seasonal shifts in foraging effort. Consequently, estimates of annual and even daily foraging effort must be extrapolated beyond the available data (e.g., Savoca et al., 2021). This contrasts with what long-term satellite telemetry and time-depth recorder data have revealed for both the eastern (Laidre and Heide-Jørgensen, 2012; Nielsen et al., 2015; Chambault et al., 2018; Fortune et al., 2020c) and western (Citta et al., 2015; Olness et al., 2020; Citta et al., 2021) bowhead whale populations.

We found evidence of year-round foraging in three regions across the eastern Canadian Arctic—Cumberland Sound, Central East Baffin Coast and Hudson Strait. For example, whales spent an average of 5 hrs (\pm 4.2 SD) conducting putative foraging dives during winter in Hudson Strait (Table 4). Since different age-sex groups of bowhead whales occupy Hudson Strait during winter (Heide-Jørgensen et al., 2010; Higdon and Ferguson, 2010; Fortune et al., 2020c), it appears all demographic groups likely consume prey during winter, unlike North Atlantic right whales (Dombroski et al., 2021). Although juvenile males appear to allocate more time to feeding across seasons compared to females, this may be an artifact of an unbalanced sample size given that foraging effort for sub-adult males and females (equal sample sizes) shows close agreement, providing support of year-round foraging effort despite demography. Furthermore, wintertime feeding has been corroborated for the eastern population by longitudinal analysis of stable isotopes and mercury analysis from bowhead baleen (Matthews and Ferguson, 2015; Pomerleau et al., 2018). Behavioural evidence of year-round foraging has been detected for the western population in the Gulf of Anadyr in the Bering Sea, where whales conduct probable foraging dives to the seafloor where diapausing life-stages of copepods are anticipated to aggregate (Citta et al., 2015). Year-round feeding was also inferred for the EC-WG population based on dive frequency data analysis from satellite-telemetry tags with time-depth recorders (Nielsen et al., 2015).

Seasonal differences in prey availability

Ultimately, the divergent life-history characteristics of bowhead and right whale prey may drive observed differences in foraging ecology. *Calanus hyperboreus* has a multi-year life cycle with a life span ranging from 3–4 years, allowing organisms to accumulate stored energy in the form of lipids. They also overwinter several years in a row before molting into an adult and spawning. In addition, adult females are likely multiannual-iteroparous and thus able to spawn in consecutive years (Hirche, 1997, 2013). Consequently, the suspected availability of high-quality prey throughout the year may be sufficient to support the energetic needs of bowhead whales despite their comparatively low daily feeding rates (hours per day). This is supported by our observations of deep putative foraging dives near the sea bottom during winter. Conversely, *Calanus finmarchicus* typically has a one-year (or less) life-cycle (Conversi et al., 2001; Swalethorp et al., 2011) and is comprised of nauplii and early copepodite stages after winter spawning that are small, low in lipids, and potentially poorly filtered by right whale baleen (assuming dead-end filtration; Mayo et al., 2001). In the absence of late-stage *C. finmarchicus* (Baumgartner et al., 2007; Baumgartner et al., 2017), right whales consume a diverse diet of lower energy taxa such as *Centropages* spp. and *Pseudocalanus* spp. in mid-winter to early spring (DeLorenzo Costa et al., 2006a, 2006b; Parks et al., 2011). In the absence of an energetically rich, year-round food resource, right whales may require seasonally higher feeding rates to allow for the accumulation of stored energy (blubber) to survive the period when *C. finmarchicus* is unavailable to them and to support the high costs of reproduction (Miller et al., 2011; Moore et al., 2021).

Differences in whale feeding activity

Should the density of temperate prey (*C. finmarchicus*) be insufficient to compensate for the loss of energy-rich Arctic taxa, balaenid whales may adjust their activity budgets to allocate more time to feeding. Such a behavioural shift presumes that animals would not be feeding at maximum rates under present environmental conditions. Based on short-term, fine-scale biologging studies, right whales forage for 40% (1.85 hrs \pm 1.255 SD; Baumgartner and Mate, 2003) and > 42% (7.16 hrs \pm 4.275 SD; van der Hoop et al., 2019) of the total time they were studied during the summer in the Bay of Fundy, Nova Scotia, Canada. However, long-term tagging (>24 hrs) and co-located prey sampling in the Bay of Fundy and Scotian Shelf found that right whales spent on average 15.07 hrs per day (12–22 hrs per day) feeding during summer (Goodyear, 1996). Foraging behavior was determined based on the presence of long and deep dives (134 m on average) to depths that coincided with maximum calanoid copepod biomass—96% of which were *C. finmarchicus* (Goodyear, 1996). Conversely, during the

same time of year (August), we found that bowheads allocated considerably less time on average to feeding with only 5.23 hrs (\pm 3.84 SD) spent making probable foraging dives. Although bowheads spent apparently less time each day feeding sub-surface than right whales, there was considerable variation in foraging time (i.e., some individuals fed for as little as 1.44 hrs and others as much as 10.52 hrs per day on average in August; Table 5). Such variability suggests bowheads alternated between days of high and low foraging effort. The full extent of right whale foraging and the potential for similar shifts in time-budgets between days remains poorly understood, leaving an incomplete understanding of species-specific foraging strategies under present environmental conditions.

There are several possible explanations for why bowheads and right whales show dissimilar foraging behaviour. Evidence of bowhead year-round feeding indicates a degree of behavioural flexibility, whereby individuals respond to seasonal variation in prey availability. This suggests that bowheads may have a comparative advantage over right whales when it comes to climate change since at least a portion of the declining right whale population fasts during winter (Dombroski et al., 2021). Similar observations have been made in other mammalian species—including Endangered African penguins (*Spheniscus demersus*) that employ a flexible foraging acquisition strategy based on shifts in prey abundance (Campbell et al., 2019). Furthermore, increased foraging effort in endangered Galapagos sea lions (*Zalophus wollebaeki*) is believed to reflect limited availability of resources throughout the year compared to the increasing California sea lion (*Zalophus californianus*) (Villegas-Amtmann et al., 2011). Consequently, the comparatively higher foraging effort of right whales during summer may reflect poor feeding opportunities during other times of year. However, low and variable foraging effort that shifts across latitudinal gradients as whales migrate north to high-latitude foraging grounds during the open-water season, and return south in fall as sea ice reforms (Ferguson et al., 2010; Fortune et al., 2020c), along with evidence of reduced abundances and energetic density of prey, suggests that bowheads may encounter sub-optimal feeding conditions. Bowheads may then need to allocate time to foraging activities throughout the year to offset lower daily energetic gains. Reconciling these observed differences in feeding activity require seasonal observations of right whale dive behaviour on daily time scales as it is unknown how much time individuals allocate to feeding activities during other times of year.

Sensitivity to climate change

Biogeographical shifts through dispersal may be an important mechanism to mitigate adverse impacts from declines in foraging conditions caused by borealization. This may be particularly crucial for polar species as marine

ecosystems are experiencing pronounced shifts in response to climate change (Moore and Huntington, 2008; Tulloch et al., 2019; Huntington et al., 2020). For example, 16.9 km per decade shifts to high-latitude regions have been observed across many terrestrial species (Chen et al., 2011). Consequently, the timing of bowhead whale migration, along with their distribution and residency patterns, particularly during open water season, are likely to change overtime (Chambault et al., 2022).

Understanding where and to what extent suitable foraging habitat occurs throughout their range under present environmental conditions can provide insight into the sensitivity of a species to climatic shifts, whereby small geographic ranges result in higher extinction probability (Purvis et al., 2000). For example, Pacific bluefin tuna (*Thunnus orientalis*) employ flexible migration patterns that help compensate for energetic costs incurred from both climate change and variability in thermal oceanographic conditions (Carroll et al., 2021). Our analysis revealed that bowheads forage widely throughout the eastern Canadian Arctic, supporting earlier reports of probable foraging in nine regions across the eastern Arctic (Disko Bay, Clyde Inlet, Isabella Bay, Broughton Island, Cumberland Sound, Frobisher Bay and northern Foxe Basin) (Nielsen et al., 2015; Fortune et al., 2020c). Utilizing dive behaviour data to infer putative foraging dives (square-shaped) for times when horizontal behaviour was consistent with resident behaviour or area-restricted movement allowed us to quantify foraging time over long timescales (>365 days), revealing that whales foraged extensively below 8 m throughout their range and across seasons. This suggests that there is considerable suitable habitat that supports bowhead foraging under present environmental conditions.

The potential for biogeographical shifts in bowhead distribution and habitat-use during the open water season (e.g., Gulf of Boothia/Prince Regent Inlet and Admiralty Inlet) may help buffer reductions in prey quality that are more likely to occur in the southern portion of their range first. However, to what extent the carrying capacity of high-latitude ecosystems will be able to support a greater population of whales is unknown. Furthermore, population models suggest that the EC-WG bowhead whale population rebounded following commercial exploitation by whaling in the early 1900s more slowly than would be predicted based on demographic expectations (Ferguson et al., 2021). Delayed recovery may indicate that the marine ecosystem was degraded from over exploitation and the population will be unable to recover to pre-exploitation stock sizes or pristine carrying capacity (Savoca et al., 2021). This would suggest that in addition to future shifts in foraging conditions, population growth may be limited despite their apparently flexible foraging behaviour. Assessment of habitat suitability in the high-latitude ecosystems requires: 1) long-term monitoring of the two-dimensional (horizontal and vertical) distribution, abundance, and composition of prey relative to physical conditions across

seasons; 2) knowledge of the demographic composition (age, sex and reproductive status) and abundance of whales currently occupying the area; and 3) detailed diet analysis from *in-situ* prey sampling near feeding whales equipped with biologgers, DNA metabarcoding of scats and stomach content analysis from harvested animals.

Conclusions

Our study provides important insight into the spatio-temporal foraging strategy of bowhead whales in the eastern Canadian Arctic relative to bathymetry and sea ice conditions. With strong evidence of year-round feeding and comparatively low foraging effort across seasons and regions, we suggest that bowheads may be less sensitive to climate-induced shifts in prey compared to North Atlantic right whales, and that there is capacity for both behavioural adjustment (e.g., increased time-spent foraging) and dispersal (northward shift in distribution) to help offset shifts in prey quality and quantity overtime. However, a lack of detailed information about the characteristics of prey consumed by bowheads across regions and seasons precludes us from quantifying spatio-temporal variability in prey consumption. Since calanoid copepods have a life-history that varies seasonally (Falk-Petersen et al., 2009; Jung-Madsen et al., 2013; Weydmann et al., 2018) with lipid content increasing from eggs (spring) to diapausing and adult life-stages (fall), feeding conditions are not expected to be static over time. Consequently, understanding to what degree low-trophic species are likely to incur energetic costs and their ability to counterbalance such deficits through behavioural changes or dispersal requires the simultaneous collection of foraging behaviour data using inertial sensing biologgers (equipped with three-dimensional accelerometers, magnetometers and gyroscopes) and associated physical and biological oceanographic conditions.

Another confounding issue with which bowheads will have to contend as sea ice extent and thickness continues to decline over time is increased pressure from mammal-eating killer whales (Reinhart et al., 2013; Young et al., 2019; Matthews et al., 2020). Given the importance of sea ice during summer foraging, and the potential physical protection this provides from killer whale predation, decreased availability of sea ice in the future may adversely impact foraging effort as whales may need to travel greater distances to access sea ice while foregoing feeding opportunities. However, the degree to which future populations will exhibit reduced feeding opportunities due to predator avoidance or decreased juvenile survival are unknown. With continued sea ice loss and the opening of the Northwest Passage (Heide-Jorgensen et al., 2012; Kochanowicz et al., 2021), new opportunities have emerged for industrial activities through commercial fisheries, shipping, and oil and gas exploration in the Arctic. Although such expansion in human activity presents new economic opportunities, endemic species such as bowhead

whales are likely to face new challenges through acoustic disturbance (vessel noise, sonar and seismic operations) (Robertson et al., 2013; Gulas et al., 2017; Halliday et al., 2020) as well as elevated risk of fishing-gear entanglement and vessel strikes (Citta et al., 2014; McWhinnie et al., 2018).

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Ethics statement

This study was reviewed and approved by the Fisheries and Oceans Canada Freshwater Institute Animal Care Committee (AUP# FWI-ACC-2013 and 2013) and under Fisheries and Oceans Canada License to Fish for Scientific Purposes #S-12/13-1024-NU and S-13/14-1009-NU.

Author contributions

Conceptualization: SMEF, SHF. Methodology: SMEF, VL, SHF, VL. Investigation: SMEF, VL. Visualization: SMEF. Funding acquisition: SHF, SMEF. Project administration: SMEF. Supervision: SMEF, SHF, VL, MB, AT. Writing – original draft: SMEF, SHF, VL, MB, AT. Writing – review and editing: SMEF, SHF, VL, MB, AT. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.853525/full#supplementary-material>

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