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Ecological and behavioral traits of apex predators in oceanic insular ecosystems: Advances and challenges in research and conservation

Edited by
Filipe Alves, Nuno Queiroz and Patrick Jodice

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Ecological and behavioral traits of apex predators in oceanic insular ecosystems: Advances and challenges in research and conservation

Topic editors
Filipe Alves — Center for Marine and Environmental Sciences (MARE), Portugal
Nuno Queiroz — Centro de Investigacao em Biodiversidade e Recursos Geneticos (CIBIO-InBIO), Portugal
Patrick Jodice — United States Geological Survey (USGS), United States Department of the Interior, United States

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Pedro Morais,
Florida International University,
United States

*CORRESPONDENCE
Filipe Alves
filipe.alves@mare-centre.pt

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Editorial: Ecological and behavioral traits of apex predators in oceanic insular ecosystems: advances and challenges in research and conservation

Filipe Alves[1]*, Nuno Queiroz[2,3] and Patrick G. R. Jodice[4]

[1]Marine and Environmental Sciences Centre (MARE)/Aquatic Research Network (ARNET), Regional Agency for the Development of Research, Technology and Innovation (ARDITI), Madeira, Portugal, [2]CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Universidade do Porto, Vairão, Portugal, [3]BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Vairão, Portugal, [4]U.S. Geological Survey, South Carolina Cooperative Fish and Wildlife Research Unit, Clemson University, Clemson, South Carolina, United States

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Editorial on the Research Topic
Ecological and behavioral traits of apex predators in oceanic insular ecosystems: advances and challenges in research and conservation

Island ecosystems can be highly sensitive to anthropogenic and natural disturbances due in part to their unique ecology and biogeography as well as their high levels of endemism (Russell and Kueffer, 2019). Remote archipelagos surrounded by pelagic environments are often hotspots for biodiversity, providing unique habitats to a wide array of taxa (Chandelier et al., 2023). Within these oceanic hotspots, apex predators fulfil a pivotal ecosystem service by maintaining the structure and function of marine and terrestrial habitats (Figure 1), serving as indicators of ecosystem health, and mitigating the effects of climate change on communities and systems (Pearson et al., 2023). Within marine and island systems, apex predators include animals from several taxonomic groups (e.g., mammals, fishes, reptiles, birds, cephalopods), many of which are threatened by varying levels of human-induced pressures including but not limited to overfishing, pollution, marine traffic, marine litter, and climate change (Queiroz et al., 2019; Sequeira et al., 2019; Alves et al., 2022). Nevertheless, remote insular or oceanic environments tend to be understudied and face numerous logistical challenges compared to, for example, coastal habitats.

This Research Topic aimed to advance our understanding of the ecological and behavioral traits of apex predators that inhabit, permanently or temporarily, marine waters adjacent to remote or small islands. The collection of 13 papers from 76 authors comprises a broad taxonomic representation of apex predators spanning cetaceans (including delphinids, beaked whales, and great whales), seals, sea turtles, sharks, manta

FIGURE 1
A group of apex predators, the short-beaked common dolphin *Delphinus delphis*, feeds on a school of small epipelagic fish in the insular oceanic waters of the Azores. © Nuno Sá.

rays, marlins, and seabirds. Through 11 original research papers and two reviews, it addresses broad temporal (i.e., decadal datasets) and spatial scales – both horizontally, by covering the major ocean basins, and vertically, by targeting species inhabiting the epi-, meso-, and bathy-pelagic zones, as well as the aerial (i.e., seabirds) and terrestrial ecosystems (i.e., seals and penguins).

The contributing papers of this Research Topic fill knowledge gaps on the behavior, ecology, habitat use, population parameters, foraging, breeding, and conservation of apex predators in insular oceanic habitats through state-of-the-art, multidisciplinary and, in some cases, novel techniques. The resulting information contributes to the discussion of four main findings, as discussed below.

Studies of behavioral, population, and spatial ecology of apex predators in oceanic systems are challenging and require long-term data sets

Addressing social and ecological processes or demographic parameters, such as the relationships between individuals in social structures or the mechanisms driving habitat selection and movement, are key components for ecosystem-based management (Badenas et al.; Borja, 2014). These studies often require longitudinal information at the individual and community ecology levels, preferably on a decadal scale (Gusmao et al.; Setyawan et al.). Such data are, however, difficult to obtain for most pelagic predators due to their highly dynamic nature and the constraints (i.e., time, logistics, and costs) associated with surveying oceanic habitats (Guillemin et al.; Palacios and Cantor). Oceanic islands can, however, offer somewhat easier access to the pelagic environment, and the use of citizen science and platforms of opportunity has proven reliable in obtaining long-term scientific data for reduced financial costs, as exemplified in this Research Topic for cetaceans, turtles, and manta rays (Badenas et al.; Courtin et al.; Ferreira et al.; Dellinger et al.; Setyawan et al.).

Multimethodological approaches provide robust results for studying the biological and ecological traits of apex predators in oceanic systems

Enhanced management of anthropogenic threats can benefit wildlife (as well as humans) when addressed with an interdisciplinary approach (Lent, 2015). In this Research Topic, Palacios and Cantor identified priorities for ecological research on cetaceans in the Galápagos region along five topical areas, and suggested a broad suite of methodological approaches. Moreover, Medrano et al. assessed the breeding phenology, population connectivity, and niche differentiation of two allochronic populations of the Cape Verde storm-petrel (*Hydrobates jabejabe*) through four distinct methodologies, while Reinhold et al. presented a novel application of stable isotope and trace element techniques to identify the source colony of little penguins (*Eudyptula minor*) predated by long-nosed fur seals (*Arctocephalus forsteri*).

Oceanic islands are a hotspot for apex predators

Oceanic islands appear to constitute areas with a high density of apex predators (Vandeperre et al., 2014), likely due to the island mass effect, which is linked to nutrient and biological impacts (Caldeira and Reis, 2017; Chandelier et al., 2023). The two review papers included in this Research Topic support that supposition, describing a high diversity of cetaceans in the Galápagos region (Palacios and Cantor) and a high diversity of marine megafauna species (comprising mammals, turtles, and fish) in Macaronesia (McIvor et al.). In addition, Afonso et al. combined acoustic and satellite telemetry to show the preference for coastal nurseries adjacent to oceanic islands by juvenile smooth hammerhead sharks (*Sphyrna zygaena*).

Islands within networks of Marine Protected Areas provide positive conservation impacts when combined with ecosystem-based approaches

Highly or fully marine protected areas (MPAs) can mitigate overfishing, climate change, and other human-induced pressures (Sala et al., 2021). Here, Setyawan et al. demonstrated the positive impact of a suite of long-term conservation efforts on increasing the abundance of reef manta rays (*Mobula alfredi*) in the Raja Ampat network of MPAs, and how informative its results can be if combined with an ecosystem-based approach. Such an approach was also used by Fariñas-Bermejo et al. to investigate potential changes in the ecosystem and the impact on predators associated with prey decline, and by Gusmao et al. to analyse the trait diversity of nesting seabird assemblages.

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

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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References

Alves, F., Rosso, M., Li, S., and Nowacek, D. P. (2022). A sea of possibilities for marine megafauna. *Science* 375, 391–392. doi: 10.1126/science.abn6022

Borja, A. (2014). Grand challenges in marine ecosystems ecology. *Front. Mar. Sci.* 1. doi: 10.3389/fmars.2014.00001

Caldeira, R. M. A., and Reis, J. C. (2017). The azores confluence zone. *Front. Mar. Sci.* 4. doi: 10.3389/fmars.2017.00037

Chandelier, G., Kiszka, J. J., Dulau-Drouot, V., Jean, C., Poirout, T., Estrade, V., et al. (2023). Isotopic niche partitioning of co-occurring large marine vertebrates around an Indian ocean tropical oceanic island. *Mar. Environ. Res.* 183, 105835. doi: 10.1016/j.marenvres.2022.105835

Lent, R. J. (2015). Conservation benefits of an interdisciplinary approach to marine mammal science. *Front. Mar. Sci.* 2. doi: 10.3389/fmars.2015.00067

Pearson, H. C., Savoca, M. S., Costa, D. P., Lomas, M. W., Molina, R., Pershing, A. J., et al. (2023). Whales in the carbon cycle: can recovery remove carbon dioxide? *TREE* 38, 238–249. doi: 10.1016/j.tree.2022.10.012

Queiroz, N., Humphries, N. E., Couto, A., Vedor, M., da Costa, I., Sequeira, A. M. M., et al. (2019). Global spatial risk assessment of sharks under the footprint of fisheries. *Nature* 572, 461–466. doi: 10.1038/s41586-019-1444-4

Russell, J. C., and Kueffer, C. (2019). Island biodiversity in the anthropocene. *Annu. Rev. Environ. Resour.* 44, 31–60. doi: 10.1146/annurev-environ-101718-033245

Sala, E., Mayorga, J., Bradley, D., Cabral, R. B., Atwood, T. B., Auber, A., et al. (2021). Protecting the global ocean for biodiversity, food and climate. *Nature* 592, 397–402. doi: 10.1038/s41586-021-03371-z

Sequeira, A. M. M., Hays, G. C., Sims, D. W., Eguíluz, V. M., Rodríguez, J. P., Heupel, M. R., et al. (2019). Overhauling ocean spatial planning to improve marine megafauna conservation. *Front. Mar. Sci.* 6. doi: 10.3389/fmars.2019.00639

Vandeperre, F., Aires-da-Silva, A., Fontes, J., Santos, M., Serrão Santos, R., and Afonso, P. (2014). Movements of blue sharks (*Prionace glauca*) across their life history. *PloS One* 9, e103538. doi: 10.1371/journal.pone.0103538

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Behavioural Ecology Traits of Elusive Deep-Diver Whales Unravel a Complex Social Structure Influenced by Female Philopatry and Defence Polygyny

Anja Badenas[1†], Ana Dinis[1,2], Rita Ferreira[1,2,3], Annalisa Sambolino[1,3], Eliette Hamard[2,4], Leonardo G. Berninsone[5], Marc Fernandez[1,6] and Filipe Alves[1,2†]*

[1] MARE - Marine and Environmental Sciences Centre, ARDITI, Madeira, Portugal, [2] Oceanic Observatory of Madeira, Funchal, Portugal, [3] Faculty of Life Sciences, University of Madeira, Funchal, Portugal, [4] Pytheas Institute, Aix-Marseille University, Marseille, France, [5] AquaMarina - Centro de Estudios en Ciencias Marinas, Buenos Aires, Argentina, [6] cE3c - Centre for Ecology, Evolution and Environmental Changes/Azorean Biodiversity Group, University of the Azores, Ponta Delgada, Portugal

Edited by:
Lyne Morissette,
M – Expertise Marine, Canada

Reviewed by:
Mauricio Cantor,
Max Planck Institute of Animal Behaviour, Germany
Randall William Davis,
Texas A&M University at Galveston, United States

***Correspondence:**
Filipe Alves
filipe.alves@mare-centre.pt

† These authors have contributed equally to this work

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Knowledge of the role of individual associations has provided an insightful understanding of the structures of animal societies, especially in highly social mammals such as primates. Yet, this is unbalanced towards marine mammals, particularly to beaked whales, due to their elusive nature. In addition, information on the fundamental drivers of the social structure of these deep-diving animals is still scarce. Here, the hypothesis of female defence polygyny was tested in Blainville's beaked whales (*Mesoplodon densirostris*) and discussed within the context of marine and terrestrial organisms displaying similar patterns, by (i) estimating residency times to obtain information on the movements into and out of the area, (ii) analysing social networks to assess individual association metrics, (iii) measuring the strength of the associations to assess the existence of preferred or avoided relationships among individuals, and (iv) modelling different social structures to address temporal patterns in social relationships. Using a 9-year photographic dataset derived from the pelagic habitat, individual associations were inferred based on likelihood techniques. This approach allowed to infer on the species' social structure in relation to age class, sex, residency status, and spatio-temporal patterns, which can be a good practice to be applied for other taxa. Heterogeneity in capture probability and residency times was observed between age-sex classes, with adult females exhibiting long-term site fidelity. This suggests different habitat roles and spatial structuring within this social organisation. Strong and long dyadic associations occurred between adult females and immatures, contrarily to between males, and the best-fitting models of the temporal patterns suggested long-lasting and temporary associations. The present findings unravel a complex social structure stratified by age-sex class and influenced by female philopatry and defence polygyny, like an unimale group mating system, which varies from other beaked whales but is similar to some birds, pinnipeds, or non-human primates.

Keywords: age/sex-specific, beaked whales, individual temporal associations, island systems, megafauna, movement and residency patterns, pelagic habitat, social network

INTRODUCTION

Movement patterns and habitat composition are known to influence complex animal social structures (He et al., 2019). Animal movements are generally driven by resource availability, mating accessibility, predator avoidance and habitat complexity (e.g., Bailey and Thompson, 2006; Duijns et al., 2019), which in turn modulate social behaviour, group composition and population dynamics at a broader scale (Morales et al., 2010). The resulting social structure plays a pivotal role in the population's ecology since it influences the spread of diseases and genetic flow (Sutherland, 1998). Therefore, social structure is considered a determining factor in conservation management plans (Wilson, 1975).

To study a population's social structure, data on interactions between known individuals through time are needed (Hinde, 1976; Whitehead, 2008), which can sometimes be challenging to witness. Once associations are established, various tools exist to describe and model social structure (reviewed in Farine and Whitehead, 2015), which has provided a profound understanding of animal associations and their socio-ecological processes in highly social terrestrial mammals (e.g., Schreier and Swedell, 2009; Foerster et al., 2015; Berger et al., 2021). However, little attention had been given to the societies of species whose meaningful relationships are difficult to assess, such as cetaceans (whales and dolphins) (Lusseau et al., 2006; Rendell et al., 2019). Cetaceans associate with conspecifics (and occasionally interspecifically) when survival, access to resources and reproductive success are increased by group formation (Gowans et al., 2007). Nonetheless, the longevity and strength of those associations, and hence social structures, are modulated by the individuals' residency patterns and habitat selection, which differ among and within species. As a result, cetacean's social structures range from highly fluid, so-called fission-fusion societies, where individuals associate in groups that change in composition and size daily (e.g., bottlenose dolphin *Tursiops truncatus*, Connor et al., 2000), to permanent associated matrilineal groups (e.g., killer whales *Orcinus orca*, Baird and Whitehead, 2000).

Nevertheless, most information on cetacean social systems is from common and accessible species (i.e., abundant, inhabiting coastal waters, or easily approachable), thus exists a gap in the knowledge of the societal patterns of lesser studied Families such as beaked whales (Li and Rosso, 2021; Weiss et al., 2021). This is mainly because beaked whales inhabit pelagic and difficult-to-access environments and because of their short surfacing periods and cryptic behaviour (Tyack et al., 2006). Although research on beaked whales has increased in the last two decades (reviewed in Hooker et al., 2019) due to their high vulnerability to anthropogenic noise and specifically to navy sonar (Tyack et al., 2011), studies on these animals' social structures cover only four species (out of at least 24 extant species, Carroll et al., 2021) and are still on their early stages (Baird, 2019; Weiss et al., 2021). In Blainville's beaked whales (*Mesoplodon densirostris*), resident populations of this medium-sized (4–5 m long) deep-diver have only been described in a few remote archipelagos (Hooker et al., 2019) and only one peer-reviewed study, wherever known, has provided insights on its social structure (McSweeney et al., 2007). That study suggested ephemeral relationships and female defence polygyny (characterised when males control females directly by defending them against conspecifics males; Shuster and Wade, 2003), yet it was based on descriptive analyses.

Here, photographic data of Blainville's beaked whales from an oceanic pelagic habitat was used to analyse individual associations and consequently to serve as a model system to infer the social structure in relation to age class, sex, residency status, and spatio-temporal patterns. To better understand the species' socio-behavioural traits and test the hypothesis of female defence polygyny, likelihood techniques were used to (i) estimate residency times, thus providing information on the movements into and out of the area, (ii) analyse the social network to assess individual association metrics, (iii) measure the strength of the associations to assess the existence of preferred or avoided relationships among individuals, and (iv) model different social structures to address temporal patterns in social relationships. Such an integrative approach is expected to contribute to a more comprehensive view of the species' social structure and enlighten the mysterious life habits of elusive and lesser-known animals. Finally, it is expected to advance the theoretical understanding of a specific social strategy related to philopatry, mating, and parental care in free-ranging animals, given that cetaceans provide a powerful outgroup for inferring the evolution of the social structure of other highly related mammals (Pearson, 2011).

MATERIALS AND METHODS

Study Area and Data Collection

Photographic data of Blainville's beaked whales were collected in the southern waters of Madeira Island (Portugal, 32°N 017°W), in a core area covering about 1,000 km^2 up to 15 km off the coast (see Fernandez et al., 2021). The study area is surrounded by warm-temperate Atlantic waters and is characterised by a narrow continental shelf and steep submarine canyons (Geldmacher et al., 2000; Martins et al., 2007). These characteristics offer a privileged access to the pelagic environment where the target species commonly occurs throughout the year (Alves et al., 2018; Fernandez et al., 2021) and where some individuals are likely island-associated (Dinis et al., 2017). The data were collected year-round through whale-watching platforms (see Acknowledgments; procedures detailed in Alves et al., 2018) and in research trips, between 2011 and 2019 (**Table 1** and **Supplementary Table 1**). On each occasion with Blainville's beaked whales, animals were approached and photographed using digital reflex cameras with zoom lenses, independently of age class, sex, and distinctiveness.

Photographic Analysis and Site Fidelity

A previous photographic-identification (hereafter "photo-id") catalogue and dataset of all animals' capture histories from 2011 to 2016 (Dinis et al., 2017) was updated with the newly collected data following standardised procedures (Würsig and Jefferson, 1990). Individuals were identified using unique scarring patterns on the body as well as nicks on dorsal fins (McSweeney et al., 2007; Dinis et al., 2017). The distinctiveness of each whale was rated from 1 (poorly distinctive) to 4

TABLE 1 | Summary of the photographic data used in the analysis, i.e., truncated to distinctive animals and good quality pictures.

Year	No. of photographic occasions	No. of captures	No. of newly identified individuals
2011	13	30	13
2012	6	9	4
2013	7	13	3
2014	9	14	4
2015	20	47	18
2016	17	41	12
2017	29	52	8
2018	23	52	9
2019	30	67	8
Total	154	325	79

(very distinctive) following McSweeney et al. (2007), and the photographs were assigned a quality grade ranging from 1 to 4 (low- to high-quality) based on Alves et al. (2013). Only good quality pictures (grade 3 or 4) and individuals with distinctiveness 2–4 (slightly to very distinctive) were used in the analyses to enhance the reliability of the data. A capture was defined as an individual identification from a photographic occasion (Würsig and Jefferson, 1990).

Three catalogues were compiled: one for females, one for males, and one for immature whales of unknown sex. Sex and age class (immature, subadult male, adult male, or adult female) was determined based on body size and colour, body scarring, association with calves, and the presence or absence of erupted teeth in the lower jaws (Claridge, 2006; McSweeney et al., 2007; Dinis et al., 2017). Photographic comparisons were performed visually (Robbins et al., 2011; Alves et al., 2019), and at least two co-authors confirmed individual matches, sex, and age class.

Additionally, a residency pattern was attributed to each individual. Three residency patterns were established based on the capture histories. Individuals that exhibited multi-year and year-round site fidelity (captured in at least 4 years and three seasons, i.e., January–March, April–June, July–September, October-December) were termed residents; individuals captured only once or a few times within a week and never captured again were termed transients; and individuals that fell between these two categories were considered emigrants/immigrants or regular visitors and were consequently termed visitors (adapted from Alves et al., 2013). Two exceptions were made for whales Md99 and Md119 that were only seen during 3 (consecutive) years but during the four seasons and always with resident whales, and therefore were termed residents.

A discovery curve was plotted using the capture histories, and the recapture rates (RRs) per age class were calculated to assess site fidelity. The discovery curve was created by plotting the cumulative number of identified individuals against the cumulative number of captures. The RRs were calculated by dividing the number of individuals with $\geq$2 captures by the total number of individuals. Recaptures within the same day were excluded.

Movement Analysis

The amount of time animals spent within the study area was examined using Lagged Identification Rates (LIR). The LIR is the probability that an individual observed in the area at a given time will still be present τ time-lags later (Whitehead, 2001). Given the difference between the capture histories of the age classes and the fact that immatures were almost always seen with an adult female, two different LIR were performed: one for all males and one for females and immatures. All individuals captured between 2015 and 2019 (years with the higher number of captures, **Table 1**), independently of the number of captures, were included in the analysis. Four models were fitted to each dataset using maximum likelihood, binomial loss, and bootstrapped standard error (SE), following Whitehead (2009). The model with the lowest Quasi Akaike Information Criteria (QAIC) was selected as the best-fitting model (Whitehead, 2008, 2009). The sampling period was defined as day, and associations were defined as individuals grouped within an occasion. LIR was conducted using SOCPROG version 2.9 (Whitehead, 2009).

Social Analyses

Network Analyses

A social network diagram was created using NetDraw 2.158 (Borgatti, 2002) to illustrate the species social structure (Kappeler, 2019). All occasions between 2011 and 2019 were considered, excluding only those resulting in single captures as they did not provide any linking information (and such cases likely represented incomplete sampling effort in photographing the entire group instead of solitary animals, given these were never recorded during the research trips). Residency pattern and age-sex class were included as individual attributes. Nodes correspond to individuals, while lines between nodes represent the strength of association among dyads, with thicker lines indicating stronger associations.

Two network metrics (strength and clustering coefficient) were obtained using SOCPROG's network statistics (Whitehead, 2009). The strength is the sum of the weights of all links of a given node, and can be used as a measure of individual social centrality (Barrat et al., 2004). The clustering coefficient measures whether the associates of an individual are themselves associated (Barrat et al., 2004; Lusseau, 2007). Significant differences in the network measures among attributes of age/sex and residency patterns were tested with a double permutation test (Farine and Carter, 2022) using the *aspine* R package (Farine, 2013).

Preferred Associations

To reduce the chance of including spurious associations, only whales with $\geq$3 captures from occasions with medium- (where at least half of the group was photographed) and high-coverage (where essentially all individuals were photographed) between 2011 and 2019 were included in this analysis. Because of the opportunistic nature of data, the photographic coverage of individuals during sightings was unknown. To overcome this issue, 50 high-quality photographs, including at least three whales in the frame, were selected to calculate the percentage of marked individuals in a group and infer photographic coverage. The rate of distinctive individuals was obtained by dividing the number of marked individuals by the total individuals captured in the frame for each photograph and calculating an overall mean for all pictures. This resulted in 71% (±19%) of the individuals in a group being marked. Based on this and on the Blainville's beaked whales mean group size of 3.7 (*SD* = 1.7) individuals in the study area (Alves et al., 2018; which is similar to other regions, see Ritter and Brederlau, 1999; Claridge, 2006; McSweeney et al., 2007), sightings with ≥2 captures were considered to be of medium- and high-coverage, and were therefore used in the subsequent analyses.

The half-weight association index (HWI) (Cairns and Schwager, 1987) was used to represent the strength of the association between beaked whale dyads (following Whitehead, 2008; Hoppitt and Farine, 2018), where "0" indicated that individuals were never captured together and "1" that individuals were always together. The mean and the maximum of associations were also calculated.

Permutation tests were used to assess whether preferred or avoided relationships among individuals and among age classes existed (Bejder et al., 1998; Whitehead, 1999). The null hypothesis was that individuals were associated with the same probability with other individuals. Observed coefficients of variation (CV) of the pairwise association indices significantly higher than those from permuted datasets were taken as evidence that individuals had preferred companions (Whitehead, 1999; Whitehead et al., 2005). The number of permutations generated was increased until the *p*-values stabilised (Bejder et al., 1998; Whitehead, 1999), at 1,000 trial flips per permutation. Based on the LIR results, three different sampling periods were used to assess associations between individuals and among age classes (adapted from Gero et al., 2015): (1) "hour," hourly sampling period to test for short-term associations, (2) "month," a monthly sampling period to test for medium-term associations, and (3) "year," yearly sampling period to test for long-term associations. This procedure removes any existing autocorrelation between groups that have been sighted together for short periods (hours or days) (personal communication, H. Whitehead, 2020). The association was defined as individuals grouped within an occasion for all three sampling periods, and associations were permuted between sampling periods.

Temporal Patterns

Standardised lagged association rates (SLAR) were used to address temporal patterns in social relationships (Whitehead, 1995). SLAR assessed the probability that two associated individuals at a given time would still be associated at a certain time-lag in the future. To aid in the interpretation of SLAR, the null association rate was also considered (Whitehead, 2009). The moving average was chosen to adjust best between precision and smoothing, and SE was estimated using the temporal jackknife method on each sampling period (Whitehead, 2009). Four exponential models that represented simulated social structures were fitted to the SLAR: the first model had no decay and suggests permanent associations; the second model had a decay down to zero and suggests that associations decrease until complete disassociation; the third model had a decay that levelled off and suggests long-lasting and temporary associations; and the fourth model had two decays and suggests two levels of disassociation, one at shorter and one at longer time lags (Whitehead, 2008). The best fitting model was chosen through the lowest QAIC (Whitehead, 2008, 2009). Since the patterning of all associations is important, data from 2011 to 2019 including all individuals, independently of the number of times captured, during medium- and high-coverage events were used for two SLARs: one for all individuals and other for adult female associations. The sampling period was defined as day, and associations were defined as individuals grouped within an occasion. Preferred association and temporal pattern analyses were performed using SOCPROG 2.9 (Whitehead, 2009).

RESULTS

A total of 325 captures based on good quality pictures were obtained from 154 photographic occasions, allowing the identification of 79 distinctive animals (**Table 1**). There was a mean of 2.1 captures (*SD* = 1.1, range 1–5) per occasion, and of the total catalogued whales, 29 were adult females, 19 were adult males, 12 were subadult males, and 19 were immature (**Table 2**).

Sixty-six percent of the animals (*n* = 52) were captured on multiple occasions (mean = 4 captures, range 2–31). Fifty-seven percent of the animals (*n* = 45) were captured intra-annually and the remaining were captured inter-annually [of which 53% (*n* = 18) were adult females, 21% (*n* = 7) adult males, 9% (*n* = 3) subadult males, and 18% (*n* = 6) immatures]. Inter-annual recaptures ranged from 2 to 8 years, but only adult females were recaptured in > 5 years (**Supplementary Table 1** and **Supplementary Figure 1**).

Residents comprised 14% of the animals (*n* = 11), visitors 39% (*n* = 31), and transients 47% (*n* = 37). Adult females were the dominant age-sex class of residents (64%, 7/11) and visitors (48%, 15/31), whereas adult and subadult males and immatures were mainly transients (**Table 2**).

The overall RR was 0.66. Adult females presented the highest value (*RR* = 0.86), followed by immature individuals (*RR* = 0.63) and adult males (*RR* = 0.58), while subadult males had the lowest (*RR* = 0.42). The discovery curve showed a slight decrease between 200 and 300 cumulative captures, and thereafter the curve begins to stabilise (**Figure 1**).

TABLE 2 | Frequency table of age-sex class per residency patterns of Blainville's beaked whales in Madeira.

	Adult females	Adult males	Subadult males	Immature	Total
Residents	7	2	0	2	11
Visitors	15	6	3	7	31
Transients	7	11	9	10	37
Total	29	19	12	19	79

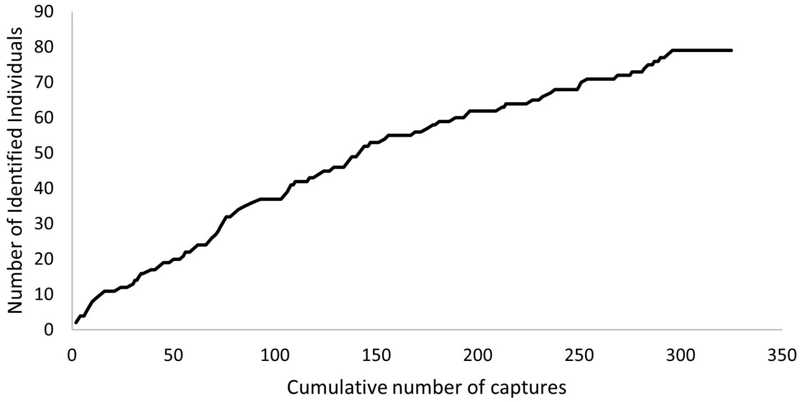

FIGURE 1 | Discovery curve for distinctive whales based on good quality images.

Movement Analysis

The best-fitting LIR model for the adult females and immatures, and for the adult and subadult males, was the "Emigration + Reimmigration + Mortality" (**Table 3**). The model indicates that 11 adult females and immatures (*SE* = 2) spent an average of 214 days (*SE* = 99) in the area before leaving to return after 158 days (*SE* = 448) with a mortality rate of < 0.001 (**Figure 2A**). It also estimated that 1 male (*SE* = 0.94) spends an average of 1 day (*SE* = 21) before leaving to return to the study area 14 days later (*SE* = 44) with a mortality rate of <0.001 (**Figure 2B**).

Social Analyses

Network Analyses

The social network analyses comprised 70 individuals from 97 photographic occasions with a total of 267 captures, of which 28 were adult females, 18 adult males, 9 subadult males, and 15 immature individuals. The network diagram shows that most individuals (92%; *n* = 64) are linked by association in the main social core, while the remaining six individuals (8%) form satellite dyads (**Figure 3**). The main cluster includes all the resident individuals, 29 visitors (93%) and 24 transients (86%). In contrast, the remaining three satellite clusters only include transients and visitors (two visitor-transient dyads and one transient-transient dyad).

Network measures varied greatly between residency patterns but were similar between age classes and sexes (**Figure 4** and **Supplementary Table 2**). The double permutation test showed no significant differences in the strength and clustering coefficient when testing the influence of age-sex classes and residency patterns.

Preferred Associations

The mean association indices were low (HWI = 0.04 ± 0.02), but the maximums were high (**Supplementary Figure 2**). The highest maximum association indices were found between immature whales and adult females (0.51 ± 0.13), followed by adult males with adult females (0.34 ± 0.12), and within adult females (0.25 ± 0.13). The lowest mean and maximum association indices were found for all combinations of subadult males and adult males' dyads (HWI = 0 for subadult-subadult and male-male dyads, HWI = 0.01 ± 0.01 for subadult male—adult male dyads). The sum of association indices indicated that the associates per individual ranged from 1.3 to 4 whales (mean = 2.48 ± 0.59, **Supplementary Figure 3**).

Permutation tests within and between adult males, subadult males, and immature whales, could not be permuted, for which the null hypothesis that individuals associate randomly could not be rejected. However, preferred associations within adult females and between adult females and the other age-sex classes varied for short-, medium-, and long-term sampling periods (**Table 4**). The observed CV was significantly higher than the random CV for the dataset, including all the individuals for short-, medium-, and long-term periods. Adult females had short- and medium-term preferred associations within their category and between all age-sex classes ($p < 0.05$) except for subadult males with whom they associated randomly. The significant monthly associations between adult females and adult males revealed that Md119 (adult resident male) had strong associations with Md55 and Md99 (adult resident females, HWI = 0.45 and 0.48 respectively, $p < 0.05$). Long-term preferred associations occurred within adult females, and between adult females and immatures ($p < 0.05$), and long-term random associations occurred between adult females and all males independently of age class.

Temporal Patterns

The third model was the best-fitting model for all individuals and for adult females (**Table 5**). For all individuals, SLAR was highest for short time lags and started decreasing fast after 100 days, reaching the null association rate in about 1 year (**Figure 5A**). Adult females showed a similar pattern, except that SLAR constantly declined from the short time lags and that the null association rate was reached later (**Figure 5B**).

DISCUSSION

This study provides an analysis of the social structure of Blainville's beaked whales in insular oceanic ecosystems, which

TABLE 3 | Models fitted to Lagged Identification Rates (LIR) for adult females and immatures, and for adult and subadult males of Blainville's beaked whales captured between 2015 and 2019.

Age-sex class	Model	Formula	QAIC
Adult female + immature (*n* = 48)	Closed	1/22.10	4899.37
	Emigration/mortality	$(1/14.97)\ e^{(-\tau\ /1424.11)}$	4848.00
	Emigration + reimmigration	$(1/12.40)\times[(1/800.99) + (1/503.82)\ e^{(-(1/800.99\ +\ 1/503.82)\ \times\ \tau\ )}]/(1/800.99 + 1/503.82)$	4843.14
	Emigration + reimmigration + mortality	$\mathbf{(e^{(-0.0004\ \times\ \tau)}/10.89)\ \times\ [(1/158.43) + (1/214.44)\ e^{(-(1/158.43\ +\ 1/214.44)\ \times\ \tau)}]/(1/158.43 + 1/214.44)}$	**4842.27**
Adult + subadult males (*n* = 31)	Closed	1/17.43	813.78
	Emigration/mortality	$(1/9.80)\ e^{(-\tau\ /862.12)}$	794.42
	Emigration + reimmigration	$(1/2.91)\ \times\ [(1/58.92) + (1/10.61)\ e^{(-(1/58.92\ +\ 1/10.61)\ \times\ \tau\ )}]/(1/58.92 + 1/10.61)$	802.39
	Emigration + reimmigration + mortality	$\mathbf{(e^{(-0.001\ \times\ \tau)}/0.94)\ \times\ [(1/14.36) + (1/1.38)\ e^{(-(1/14.36\ +\ 1/1.38)\ \times\ \tau)}]/(1/14.36 + 1/1.38)}$	**791.08**

τ is time lag in days. The lowest QAIC (in bold) indicates the best-fitting model. Estimated residency parameters and standard errors (SE) for the best-fitting model for adult females and immatures are: population size in the study area at a given time = 10.89 (2.29); residence time in the study area = 214.44 (99.68) days; residence time out of the study area = 158.43 (448.63) days; and mortality = 0.0004 (0.0004). Estimated parameters for the best-fitting model for adult and subadult males are: population size in the study area at a given time = 0.94 (2.13); residence time in the study area = 1.38 (21.16) days; residence time out of the study area = 14.36 (44.48) days; and mortality = 0.001 (0.0006).

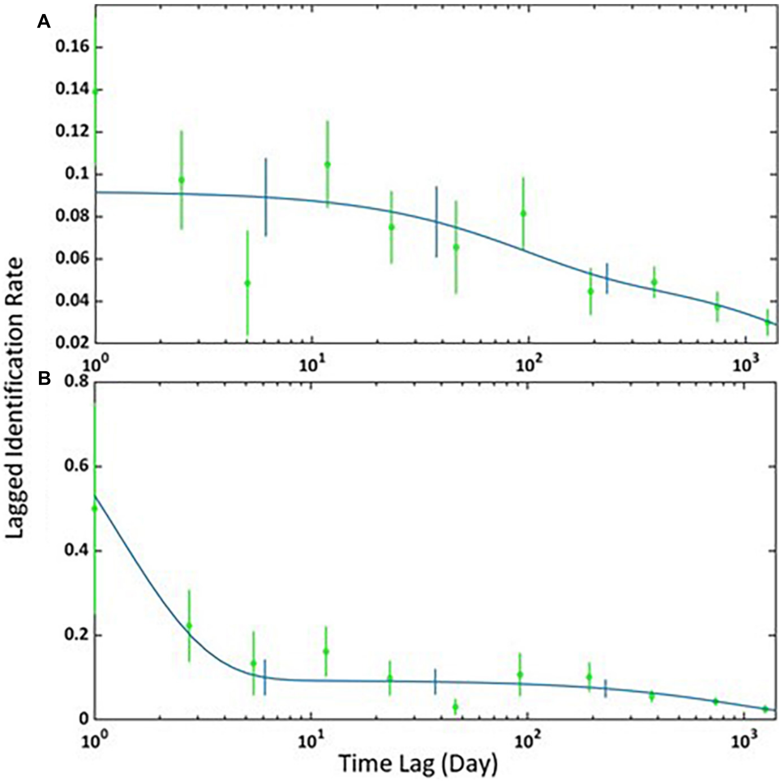

FIGURE 2 | Lagged Identification Rates (LIR) for **(A)** adult females and immatures and **(B)** adult and subadult males in Madeira between 2015 and 2019. The graph shows the probability that an individual Blainville's beaked whale captured at an initial time "0" will be captured again at x time later in the study area. Blue lines represent the best-fitting model according to **Table 3**, green circles represent the data, and vertical bars indicate SE calculated using a bootstrap method on each sampling period.

are characterised by specific topographic and oceanographic variables that are known to influence predators' habits, such as cetaceans (Abecassis et al., 2015; Fernandez et al., 2021). The analysis of a longitudinal dataset on individual associations in relationship to age class, sex, residency status, and spatio-temporal patterns showed a social structure modulated by adult females. This agrees with analyses of mammalians' social complexity where a female-based sociality prevails

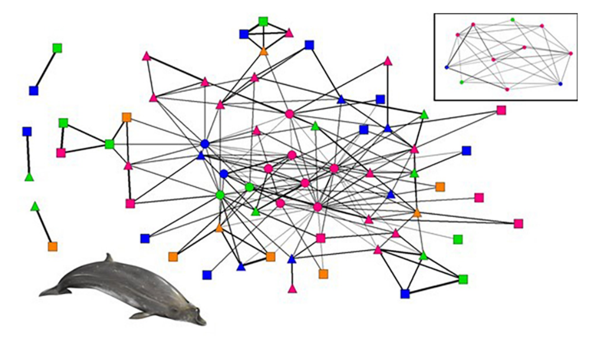

FIGURE 3 | Network diagram of Blainville's beaked whales. Nodes represent individuals and are coloured and shaped for age-sex class and residency attributes: pink- adult female, blue- adult male, orange- subadult male, green- immature; circle- resident, triangle- visitor, and square- transient. The thickness of the lines between nodes represents the strength of association among dyads, where thicker lines correspond to stronger associations. The embedded network at the top right is the network of the resident whales only. Illustration© ARDITI/E. Berninsone.

(Lukas and Clutton-Brock, 2018), in which cetaceans, and especially toothed whales, are no exception (Rendell et al., 2019). The present findings support the hypothesis of female defence polygyny suggested by McSweeney et al. (2007) for a population in Hawaii', as well as reported in the Bahamas and Canary Islands (Claridge, 2006; Suárez, 2018). In addition, the present findings support information on female philopatry based on higher residency levels by adult females and provide a discussion on this social strategy.

The findings obtained in this study are inferred from a good agreement of the combination of movement and social analyses, from which five broad main results have emerged. First, there was heterogeneity in capture probability, given that 60% of the animals were captured on multiple occasions and most of the inter-annual recaptures (and the longer ones; >5 years) were from adult females. Island-associated animals (i.e., residents and visitors) were also mainly adult females, which presented the highest RR (0.86). The asymptotic discovery curve, observed from approximately > 300 cumulative captures, reveals that the studied island-associated population seems relatively small (likely < 50 animals). This also shows that recruits are less common throughout the years and some adult females exhibit high site fidelity, supporting Dinis et al. (2017).

Second, the best-fitting models from the LIR analysis included emigration and reimmigration with (residual rates of) mortality, which suggests temporary migration into and out of the area and transiency, with mortality within expected values given the duration of the study and the long-living nature of this mammal species. Additionally, it shows heterogeneity in residency times between age-sex classes. A higher number of adult females and immatures spent more time in the area than adult and subadult males, but also left for more extended periods. This reinforces the more constant presence of adult females and immatures in Madeira. The differentiated habitat use by Blainville's beaked whales of different age classes, sexes and residency patterns has also been described in the Hawaii', Bahamas and Canaries from photo-id analysis (Claridge, 2006; McSweeney et al., 2007; Suárez, 2018). Moreover, the heterogeneity in residency times between age-sex classes suggests different habitat roles, supporting spatial structuring within the species social organisation, with an indication of female philopatry.

Third, the social network analyses shows that the main cluster includes all the resident individuals and 93% of the visitors, supporting an island-associated population in the study area. This agrees with the previous points and with Dinis et al. (2017). Central individuals can be information carriers in dolphin societies (Lusseau and Newman, 2004), yet there was no

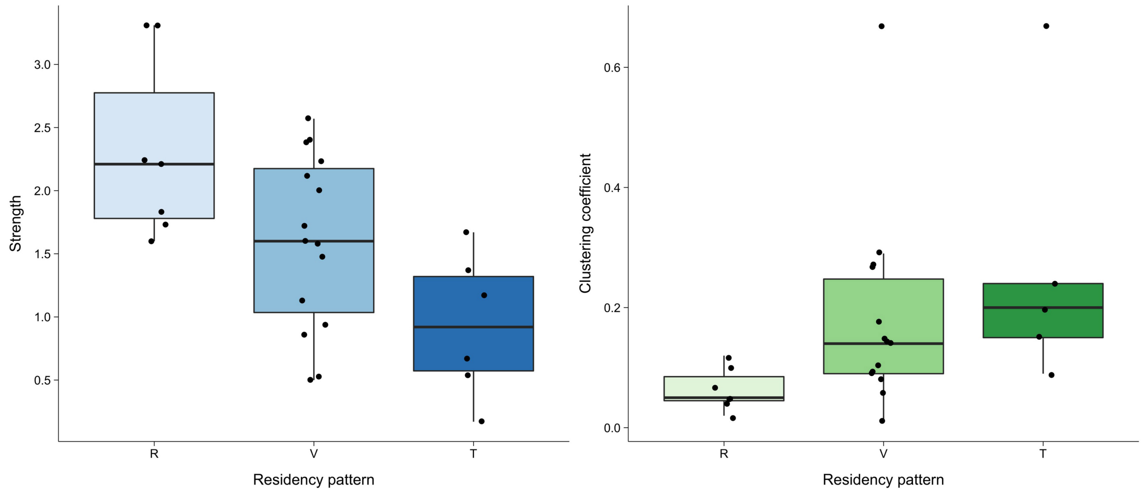

FIGURE 4 | Boxplot for strength and clustering coefficient for each residency pattern (R–resident, V–visitor, T–transient) in adult females (the most representative group). The horizontal line in the box represents the median, the bottom and top of the boxes represent the first and third quartiles and whiskers show values within 1.5 times of the interquartile range from the boxes. Raw data are plotted as single points. A double permutation test showed no significant differences on the influence of residency patterns in the social network structure.

TABLE 4 | Permutation tests for preferred associations within and between age classes and sexes for individuals captured on ≥ 3 occasions for short-, medium-, and long-term between 2011 and 2019.

	CV of observed HWI mean	CV of random HWI mean	*p*-value
Short-term (sampling period hours)			
All individuals (*n* = 36)	2.31	2.00	0.001
Adult female—Adult female (*n* = 19)	2.17	1.99	0.02
Adult female—Adult male (*n* = 26)	1.74	1.61	0.02
Adult female—Subadult male (*n* = 21)	2.34	2.29	0.25
Adult female—Immature (*n* = 26)	2.40	2.04	0.002
Medium-term (sampling period months)			
All individuals	2.26	2.09	0.001
Adult female—Adult female	2.30	2.03	0.003
Adult female—Adult male	1.75	1.63	0.03
Adult female—Subadult male	could not be permuted		
Adult female—Immature	2.25	1.97	0.00
Long-term (sampling period years)			
All individuals	2.26	2.09	0.001
Adult female—Adult female	2.30	2.10	0.01
Adult female—Adult male	1.75	1.68	0.16
Adult female—Subadult male	2.34	2.24	0.13
Adult female—Immature	2.26	2.05	0.01

HWI, half-weight association index; CV, coefficients of variation.

TABLE 5 | Models fitted to the standardised lagged association rate (SLAR) for all individuals and for adult females.

Age-sex class	Model formula	QAIC
All individuals	0.059668	677.34
	$0.164610\, e^{(-0.001975 \times \tau)}$	596.11
	$\mathbf{0.016073 + 0.231560\, e^{(-0.006573 \times \tau)}}$	**568.79**
	$0.229680\, e^{(-0.007026 \times \tau)} + 0.020314\, e^{(-0.000152 \times \tau)}$	570.68
Adult females	0.109860	225.70
	$0.332700\, e^{(-0.001908 \times \tau)}$	190.56
	$\mathbf{0.036611 + 0.457340\, e^{(-0.006697 \times \tau)}}$	**182.97**
	$1.595400\, e^{(-1.4119 \times \tau)} + 0.300120\, e^{(-0.001770 \times \tau)}$	192.40

The lowest QAIC (in bold) indicates the best-fitting model. The first model (with one parameter) suggests permanent associations, the second model (with two parameters) suggests that associations decrease until complete disassociation, the third model (with three parameters) suggests long-lasting and temporary associations, and the fourth model (with four parameters) suggests two levels of disassociation (detailed in section "Material and Methods"). τ *is time lag in days.*

significant influence of the age-sex classes and residency patterns in the network measures. This could be related to the sampling area that likely represents a portion of the home range of these animals, especially of the transients, making it difficult to confirm the role that different residency patterns might play in the social network analyses of Blainville's beaked whales.

Fourth, the tests for preferred associations show strong dyadic associations between adult females and immatures, contrarily to between males, as expected for a long-lived mammal species (Lukas and Clutton-Brock, 2018). This is based on the highest maximum association indices between adult females and immatures and the lowest mean and maximum association indices among all combinations of subadult males and adult males' dyads. The sum of association indices indicated that the typical number of associates per individual ranged from 1.3 to 4, indicating small group sizes similar to other areas (reviewed in Baird, 2019). Adult females exhibited short- and medium-term preferred associations between all age-sex classes, except for subadult males with whom they associated randomly. The significant monthly associations between adult females and adult males were likely influenced by pairs of dyads composed by a particular adult resident male (Md119) with two adult resident females (Md55 and Md99; based on their capture histories, **Supplementary Table 1**). In the long-term, preferred associations occurred only within adult females, and between adult females and immatures, supporting the hypothesis of female defence polygyny in this species.

Fifth, the best-fitting models from the analysis of the temporal pattern included a decay that levelled off and suggested long-lasting and temporary associations. The fast decrease of SLAR after 100 days for all individuals, indicated that many associations between individuals did not last longer than 3 months. The null association rate was reached in about 1 year, meaning that individuals associated randomly more often than expected for about a year. The peaks formed at 400 and ≈1,500 days are, most probably, a sampling by-product. For adult females, the null association rate was reached later (approximately 3.5 years). Therefore, adult females associated more often than expected if they associated randomly for periods of at least 3.5 years, although the SLAR stays above the null association rate for more extended periods. Such period could be related to time invested in nursing and/or alloparental care, which is a socioecological strategy commonly displayed by mammals (Greenwood, 1980; Berger et al., 2021), and particularly by deep-diving cetaceans like pilot (*Globicephala* spp.) or sperm whales (*Physeter macrocephalus*) (Whitehead, 1996; Augusto et al., 2017). While the obtained SLAR slope for adult females declines faster, their association rates are higher than those from all individuals, indicating that other age-sex classes, such as adult males, subadult males, and immatures, have more ephemeral associations between individuals and hence decreased the values of the association rates. The jackknife precision estimates indicate that associations between adult females last longer than all age classes combined.

As an overview, there were intra- and inter-annual preferred associations between females, but preferred associations with males occurred only intra-annually. In addition, adult females and immatures stayed extended periods in the area when compared to adult and subadult males. It is suggested that Blainville's beaked whales exhibit a general pattern of one adult male leading a small group of females during a short- to mid-period of time (hours to months) and that females are the ones "controlling" the area (i.e., higher site fidelity) and displaying longer-term associations; thus having a social structure driven by female philopatry and defence polygyny. This agrees with the

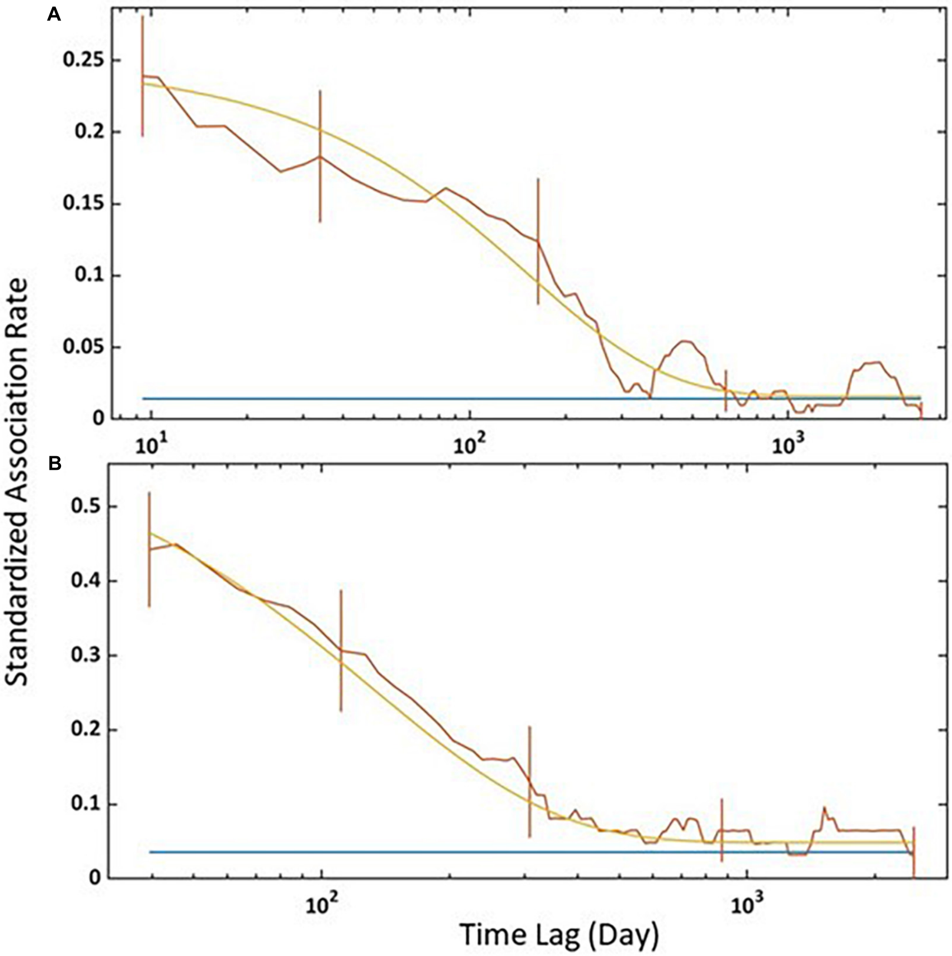

FIGURE 5 | Standardised lagged association rate (SLAR) for **(A)** all individuals and **(B)** adult females captured between 2011 and 2019. Vertical bars indicate SE calculated using the temporal jackknife method. The brown line is the observed data, the yellow line is the best-fitting model according to **Table 5**, and the blue line is the standardised null association rate (i.e., if individuals associated randomly).

unimale group mating system described in Clutton-Brock (1989) where the cost-effectiveness of territoriality declines and males are more likely to defend groups of females or to search receptive females, as observed in several terrestrial mammals (Clutton-Brock, 1989) and similar to sperm whales (Rendell et al., 2019). It can therefore be inferred that Blainville's beaked whales have a social structure stratified by age-sex class, and that they can combine a mix of the sociality found in smaller delphinids where ephemeral relationships usually take place (Gowans et al., 2007) and in mid- to large-sized toothed whales where "matrifocal" or matrilineal systems occur (Rendell et al., 2019). Different or mixed social structures are not uncommon among mammals, such as, for example, the stratified community and the multi-male mating system of Risso's dolphins (*Grampus griseus*) (Hartman et al., 2008, 2015), which differs from the fission-fusion and matrilineal society models.

The findings presented here shed light on a single species of the second-most speciose family (Ziphiidae) of cetaceans. Studies on the social structure of beaked whales exist only for four species (17% of all known beaked whale's species; Carroll et al., 2021), derived from restricted areas (reviewed in Weiss et al., 2021). While for Cuvier's beaked whales (*Ziphius cavirostris*), sperm competition seems to play a role in the mating system (Baird, 2019), in northern bottlenose whales (*Hyperoodon ampullatus*), there are strong associations between males (Gowans et al., 2001), whereas, in Baird's beaked whales (*Berardius bairdii*), there are stable associations among more scarred (old and/or male) individuals (Fedutin et al., 2015). Thus, beaked whales' social structures should not be generalised, given that association patterns, mating structures and societies vary between species (Hooker et al., 2019).

This study also increases our knowledge of the social strategy related to female philopatry and female defence polygyny. Here, both are present, but one does not necessarily imply the other. One and/or the other has been described for birds, pinnipeds, deers, or non-human primates (Greenwood, 1980; Le Boeuf, 1991; Koening et al., 2013; Bose et al., 2017), thus suggesting interspecific flexibility of mating systems and social structure, which could arise from several factors such as more cooperative male resource defence (Koening et al., 2013). The formation of stable associations can be correlated with biological and ecological factors (Morales et al., 2010), with long-term bonds being recorded within age-sex classes and with female-biased kinship organisation being found among larger species (Weiss et al., 2021). Such stable relationships provide certain advantages over sporadic bonds, like allomaternal care in deep-diving species (Rendell et al., 2019) or increased male mating success and herding of females during breeding seasons (Clutton-Brock, 1989; Connor et al., 1992), which could partially explain the described social system of the Blainville's beaked whales.

Potential biases in the present study, especially those related to heterogeneity in capturability and residency, could be related to using data from platforms of opportunity. Nevertheless, likelihood techniques were used to estimate parameters of movement models (Whitehead, 2001), which allowed dealing with the effort associated with collecting the individual identifications that had been neither randomly nor systematically distributed in space-time. In addition, the fact that the data were collected year-round over a relatively long period, and that it was restricted to good quality pictures and distinctive individuals, helped minimising biases. Moreover, the HWI was selected to represent the strength of the behavioural relationships between dyads since it is potentially less biased and recommended to be used when not all individuals have been identified in a sampling period (Whitehead, 2008), as in this case. Although other indices such as the Simple Ratio (Ginsberg and Young, 1992) could also be a good candidate (following Hoppitt and Farine, 2018), the inferences drawn from that index (not shown) were similar to the HWI and therefore the latter was preferred based on Whitehead (2008), even being aware that it does not fully correct biases. Another issue is that, when there is a difference in QAIC by less than two, the second best-fitting model should not be disregarded since it still offers substantial support (Burnham and Anderson, 2002). In this study, there was one case in the LIR and another in the SLAR analyses. In the former case, the only difference with the best model was that the second-best did not include mortality. Given that it makes sense to consider mortality in a real-life scenario, the model with the lowest QAIC was in accordance with being the best one. In the latter case, the third model was the best-fitting and the fourth model was the second best. Again, the best-fitting suggests being the most logical because permanent association (or preferred companions) occurred to some extent (i.e., long-term associations among adult females) in the targeted population. Finally, analyses on the social structure of animals that spend most of its time submerged, such as beaked whales (Tyack et al., 2006), should be inferred with caution. However, we believe that the findings obtained from surface data should reflect, in a general way, the species social system.

To further assess the socioecology of deep-diving species within an evolutionary approach, future studies should combine photo-id analyses with genomics and/or biotelemetry (e.g., Aguilar de Soto et al., 2012; Abecassis et al., 2015; Visser et al., 2021). Although challenging, targeting several individuals of the same group would help clarify these elusive species' matrilineal kinship. Comprehensive studies, such as the present one, allow incrementing our knowledge on the social behaviour of beaked whales and identifying resident populations. This information is necessary to better understand, manage and protect such cryptic species from increasing anthropogenic disturbances for which they are vulnerable.

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

Ethical review and approval was not required for the animal study because we used photographic-identification data that are based on photographs of wild animals (i.e., a non-invasive method).

AUTHOR CONTRIBUTIONS

FA and AD conceived the study and validated the dataset (matches). AB, AD, RF, AS, LB, and FA compiled the photographic data. AB, AD, RF, and EH prepared the dataset. AB and MF performed the analyses. FA contributed to its interpretation. AB and FA led the writing of the manuscript. All authors contributed with data, made significant contributions to the drafts, and approved it 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.2022.809902/full#supplementary-material

REFERENCES

Abecassis, M., Polovina, J., Baird, R. W., Copeland, A., Drazen, J. C., Domokos, R., et al. (2015). Characterising a foraging hotspot for short-finned pilot whales and Blainville's beaked whales located off the west side of Hawai'i Island by using tagging and oceanographic data. *PLoS One* 10:e0142628. doi: 10.1371/journal.pone.0142628

Aguilar de Soto, N., Madsen, P. T., Tyack, P., Arranz, P., Marrero, J., et al. (2012). No shallow talk: Cryptic strategy in the vocal communication of Blainville's beaked whales. *Mar. Mamm. Sci.* 28, E75–E92. doi: 10.1111/j.1748-7692.2011.00495.x

Alves, F., Alessandrini, A., Servidio, A., Mendonça, A. S., Hartman, K. L., Prieto, R., et al. (2019). Complex biogeographical patterns support an ecological connectivity network of a large marine predator in the north-east Atlantic. *Divers. Distrib.* 25, 269–284. doi: 10.1111/ddi.12848

Alves, F., Ferreira, R., Fernandes, M., Halicka, Z., Dias, L., and Dinis, A. (2018). Analysis of occurrence patterns and biological factors of cetaceans based on long-term and fine-scale data from platforms of opportunity: Madeira Island as a case study. *Mar. Ecol.* 39:e12499. doi: 10.1111/maec.12499

Alves, F., Quérouil, S., Dinis, A., Nicolau, C., Ribeiro, C., Freitas, L., et al. (2013). Population structure of short-finned pilot whales in the oceanic archipelago of Madeira based on photo-identification and genetic analyses: Implications for conservation. *Aquat. Conserv.: Mar. Freshw. Ecosyst.* 23, 758–776. doi: 10.1002/aqc.2332

Augusto, J. F., Frasier, T. R., and Whitehead, H. (2017). Characterizing alloparental care in the pilot whale (*Globicephala melas*) population that summers off Cape Breton, Nova Scotia, Canada. *Mar. Mamm. Sci.* 33, 440–456. doi: 10.1111/mms.12377

Bailey, H., and Thompson, P. (2006). Quantitative analysis of bottlenose dolphin movement patterns and their relationship with foraging: Movement patterns and foraging. *J. Anim. Ecol.* 75, 456–465. doi: 10.1111/j.1365-2656.2006.01066.x

Baird, R. W. (2019). "Behavior and ecology of not-so-social odontocetes: Cuvier's and Blainville's beaked whales," in *Ethology and Behavioral Ecology of Odontocetes*, ed. B. Würsig (Cham: Springer International Publishing), 305–329. doi: 10.1007/978-3-030-16663-2_14

Baird, R. W., and Whitehead, H. (2000). Social organisation of mammal-eating killer whales: group stability and dispersal patterns. *Can. J. Zool.* 78, 2096–2105. doi: 10.1139/z00-155

Barrat, A., Barthelemy, M., Pastor-Satorras, R., and Vespignani, A. (2004). The architecture of complex weighted networks. *Proc. Natl. Acad. Sci.* 101, 3747–3752. doi: 10.1073/pnas.0400087101

Bejder, L., Fletcher, D., and Bräger, S. (1998). A method for testing association patterns of social animals. *Anim. Behav.* 56, 719–725. doi: 10.1006/anbe.1998.0802

Berger, V., Reichert, S., Lahdenperä, M., Jackson, J., Htut, W., and Lummaa, V. (2021). The elephant in the family: costs and benefits of elder siblings on younger offspring life-history trajectory in a matrilineal mammal. *J. Anim. Ecol.* 2021:13573. doi: 10.1111/1365-2656.13573

Borgatti, S. P. (2002). *NetDraw: Graph Visualization Software*. Harvard: Analytic Technologies.

Bose, S., Forrester, T. D., Brazeal, J. L., Sacks, B. N., Casady, D. S., and Wittmer, H. U. (2017). Implications of fidelity and philopatry for the population structure of female black-tailed deer. *Behav. Ecol.* 28, 983–990. doi: 10.1093/beheco/arx047

Burnham, K. P., and Anderson, D. R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. New York, NY: Springe-Verlag.

Cairns, S. J., and Schwager, S. J. (1987). A comparison of association indices. *Anim. Behav.* 35, 1454–1469. doi: 10.1016/S0003-3472(87)80018-0

Carroll, E. L., McGowen, M. R., McCarthy, M. L., Marx, F. G., Aguilar, N., Dalebout, M. L., et al. (2021). Speciation in the deep: genomics and morphology reveal a new species of beaked whale *Mesoplodon eueu*. *Proc. R. Soc. B* 288:20211213. doi: 10.1098/rspb.2021.1213

Claridge, D. E. (2006). *Fine-scale distribution and habitat selection of beaked whales. M.Sc. thesis*. Aberdeen: University of Aberdeen.

Clutton-Brock, T. H. (1989). Mammalian mating systems. *Proc. Royal Soc. Lond. B* 236, 339–372. doi: 10.1098/rspb.1989.0027)

Connor, R. C., Smolker, R. A., and Richards, A. F. (1992). Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). *Proc. Natl. Acad. Sci.* 89, 987–990. doi: 10.1073/pnas.89.3.987

Connor, R. C., Wells, R. S., Mann, J., and Read, A. J. (2000). "The bottlenose dolphin: social relationships in a fission-fusion society," in *Cetacean Societies*, eds J. Mann, R. C. Connor, P. L. Tyack, and H. Whitehead (London: University of Chicago Press).

Dinis, A., Marques, R., Dias, L., Sousa, D., Gomes, C., Abreu, N., et al. (2017). Site Fidelity of Blainville's Beaked Whale (*Mesoplodon densirostris*) off Madeira Island (Northeast Atlantic). *Aquat. Mamm.* 43, 387–390. doi: 10.1578/AM.43.4.2017.387

Duijns, S., Anderson, A. M., Aubry, Y., Dey, A., Flemming, S. A., Francis, C. M., et al. (2019). Long-distance migratory shorebirds travel faster towards their breeding grounds, but fly faster post-breeding. *Sci. Rep.* 9:9420. doi: 10.1038/s41598-019-45862-0

Farine, D. R. (2013). Animal social network inference and permutations for ecologists in R using *asnipe*. *Methods Ecol. Evol.* 4, 1187–1194. doi: 10.1111/2041-210X.12121

Farine, D. R., and Carter, G. G. (2022). Permutation tests for hypothesis testing with animal social network data: Problems and potential solutions. *Methods Ecol. Evol.* 13, 144–156. doi: 10.1111/2041-210X.13741

Farine, D. R., and Whitehead, H. (2015). Constructing, conducting and interpreting animal social network analysis. *J. Anim. Ecol.* 84, 1144–1163. doi: 10.1111/1365-2656.12418

Fedutin, I. D., Filatova, O. A., Mamaev, E. G., Burdin, A. M., and Hoyt, E. (2015). Occurrence and social structure of Baird's beaked whales, *Berardius bairdii*, in the Commander Islands, Russia. *Mar. Mamm. Sci.* 31, 853–865. doi: 10.1111/mms.12204

Fernandez, M., Alves, F., Ferreira, R., Fischer, J.-C., Thake, P., Nunes, N., et al. (2021). Modeling fine-scale cetaceans' distributions in oceanic islands: Madeira Archipelago as a case study. *Front. Mar. Sci.* 8:688248. doi: 10.3389/fmars.2021.688248

Foerster, S., McLellan, K., Schroepfer-Walker, K., Murray, C. M., Krupenye, C., Gilby, I. C., et al. (2015). Social bonds in the dispersing sex: partner preferences among adult female chimpanzees. *Anim. Behav.* 105, 139–152. doi: 10.1016/j.anbehav.2015.04.012

Geldmacher, J., van den Bogaard, P., Hoernle, K., and Schmincke, H.-U. (2000). The ^{40}Ar/^{39}Ar age dating of the Madeira Archipelago and hotspot track (eastern North Atlantic). *Geochem. Geophys. Geosystems* 1:1008. doi: 10.1029/1999GC000018

Gero, S., Gordon, J., and Whitehead, H. (2015). Individualised social preferences and long-term social fidelity between social units of sperm whales. *Anim. Behav.* 102, 15–23. doi: 10.1016/j.anbehav.2015.01.008

Ginsberg, J. R., and Young, T. P. (1992). Measuring association between individuals or groups in behavioural studies. *Anim. Behav.* 44, 377–379. doi: 10.1016/0003-3472(92)90042-8

Gowans, S., Whitehead, H., and Hooker, S. K. (2001). Social organisation in northern bottlenose whales (*Hyperoodon ampullatus*): not driven by deep-water foraging. *Anim. Behav.* 62, 369–377. doi: 10.1006/anbe.2001.1756

Gowans, S., Würsig, B., and Karczmarski, L. (2007). The Social Structure and Strategies of Delphinids: Predictions Based on an Ecological Framework. *Adv. Mar. Biol.* 53, 195–294. doi: 10.1016/S0065-2881(07)53003-8

Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* 28, 1140–1162. doi: 10.1016/S0003-3472(80)80103-5

Hartman, K. L., Fernandez, M., Wittich, A., and Azevedo, J. M. N. (2015). Sex differences in residency patterns of Risso's dolphins (*Grampus griseus*) in the Azores: causes and management implications. *Mar. Mamm. Sci.* 31, 1153–1167. doi: 10.1111/mms.12209

Hartman, K. L., Visser, F., and Hendriks, A. J. E. (2008). Social structure of Risso's dolphins (*Grampus griseus*) at the Azores: A stratified community based on highly associated social units. *Can. J. Zool.* 86, 294–306. doi: 10.1139/Z07-138

He, P., Maldonado-Chaparro, A. A., and Farine, D. R. (2019). The role of habitat configuration in shaping social structure: a gap in studies of animal social complexity. *Behav. Ecol. Sociobiol.* 73:9. doi: 10.1007/s00265-018-2602-7

Hinde, R. A. (1976). Interactions, Relationships and Social Structure. *Man* 11, 1–17. doi: 10.2307/2800384

Hooker, S. K., de Soto, N. A., Baird, R. W., Carroll, E. L., Claridge, D., Feyrer, L., et al. (2019). Future directions in research on beaked whales. *Front. Mar. Sci.* 5:514. doi: 10.3389/fmars.2018.00514

Hoppitt, W. J. E., and Farine, D. R. (2018). Association indices for quantifying social relationships: how to deal with missing observations of individuals or groups. *Anim. Behav.* 136, 227–238. doi: 10.1016/j.anbehav.2017.08.029

Kappeler, P. M. (2019). A framework for studying social complexity. *Behav. Ecol. Sociobiol.* 73:13. doi: 10.1007/s00265-018-2601-8

Koening, A., Scarry, C. J., Wheeler, B. C., and Borries, C. (2013). Variation in grouping patterns, mating systems and social structure: what socio-ecological models attempt to explain. *Philos. Trans. R. Soc. B* 368:20120348. doi: 10.1098/rstb.2012.0348

Le Boeuf, B. J. (1991). "Pinniped mating systems on land, ice and in the water: Emphasis on the Phocidae," in *The Behaviour of Pinnipeds*, ed. D. Renouf (Dordrecht: Springer), doi: 10.1007/978-94-011-3100-1_2

Li, S., and Rosso, M. (2021). Lack of knowledge threatens beaked whales. *Science* 371:791. doi: 10.1126/science.abg8922

Lukas, D., and Clutton-Brock, T. (2018). Social complexity and kinship in animal societies. *Ecol. Lett.* 21, 1129–1134. doi: 10.1111/ele.13079

Lusseau, D. (2007). Why are male social relationships complex in the doubtful sound bottlenose dolphin population? *PLoS One* 2:e348. doi: 10.1371/journal.pone.0000348

Lusseau, D., and Newman, M. E. J. (2004). Identifying the role that animals play in their social networks. *Proc. R. Soc. Lond. B* 271, S477–S481. doi: 10.1098/rsbl.2004.0225

Lusseau, D., Wilson, B., Hammond, P. S., Grellier, K., Durban, J. W., Parsons, K. M., et al. (2006). Quantifying the influence of sociality on population structure in bottlenose dolphins. *J. Anim. Ecol.* 75, 14–24. doi: 10.1111/j.1365-2656.2005.01013.x

Martins, A. M., Amorim, A. S. B., Figueiredo, M. P., Souza, R. J., Mendonça, A. P., Bashmachnikov, I. L., et al. (2007). *Sea surface temperature (AVHRR, MODIS) and ocean colour (MODIS) seasonal and interannual variability in the Macaronesian islands of Azores, Madeira, and Canaries*. Florence: SPIE Remote Sensing. doi: 10.1117/12.738373

McSweeney, D. J., Baird, R. W., and Mahaffy, S. D. (2007). Site Fidelity, Associations, and Movements of Cuvier's (*Ziphius cavirostris*) and Blainville's (*Mesoplodon densirostris*) Beaked Whales Off the Island of Hawai'i. *Mar. Mamm. Sci.* 23, 666–687. doi: 10.1111/j.1748-7692.2007.00135.x

Morales, J. M., Moorcroft, P. R., Matthiopoulos, J., Frair, J. L., Kie, J. G., Powell, R. A., et al. (2010). Building the bridge between animal movement and population dynamics. *Philos. Trans. R. Soc. B* 365, 2289–2301. doi: 10.1098/rstb.2010.0082

Pearson, H. C. (2011). Sociability of female bottlenose dolphins (*Tursiops* spp.) and chimpanzees (*Pan troglodytes*): Understanding evolutionary pathways toward social convergence. *Evol. Anthropol.* 20, 85–95. doi: 10.1002/evan.20296

Rendell, L., Cantor, M., Gero, S., Whitehead, H., and Mann, J. (2019). Causes and consequences of female centrality in cetacean societies. *Philos. Trans. R. Soc. B* 374:20180066. doi: 10.1098/rstb.2018.0066

Ritter, F., and Brederlau, B. (1999). Behavioural observations of dense beaked whales (*Mesoplodon densirostris*) off La Gomera, Canary Islands (1995-1997). *Aquat. Mamm.* 25, 55–61.

Robbins, J., Rosa, L. D., Allen, J. M., Mattila, D. K., Secchi, E. R., Friedlaender, A. S., et al. (2011). Return movement of a humpback whale between the Antarctic Peninsula and American Samoa: A seasonal migration record. *Endanger. Species Res.* 13, 117–121. doi: 10.3354/esr00328

Schreier, A. L., and Swedell, L. (2009). The fourth level of social structure in a multi-level society: ecological and social functions of clans in hamadryas baboons. *Am. J. Primatol.* 71, 948–955. doi: 10.1002/ajp.20736

Shuster, S. M., and Wade, M. J. (2003). *Mating systems and strategies*. Princeton: Princeton University Press.

Suárez, C.R. (2018). *Abundance estimate, survival and site fidelity patterns of Blainville's (Mesoplodon densirostris) and Cuvier's (Ziphius cavirostris) beaked whales off El Hierro (Canary Islands). M.Sc. thesis*. Scotland: University of Saint Andrews.

Sutherland, W. J. (1998). The importance of behavioural studies in conservation biology. *Anim. Behav.* 56, 801–809. doi: 10.1006/anbe.1998.0896

Tyack, P. L., Johnson, M., Aguilar Soto, N., Sturlese, A., and Madsen, P. T. (2006). Extreme diving of beaked whales. *J. Exp. Biol.* 209, 4238–4253. doi: 10.1242/jeb.02505

Tyack, P. L., Zimmer, W. M. X., Moretti, D., Southall, B. L., Claridge, D. E., Durban, J. W., et al. (2011). Beaked whales respond to simulated and actual navy sonar. *PLoS One* 6:e17009. doi: 10.1371/journal.pone.0017009

Visser, F., Merten, V. J., Bayer, T., Oudejans, M. G., de Jonge, D. S. W., Puebla, O., et al. (2021). Deep-sea predator niche segregation revealed by combined cetacean biologging and eDNA analysis of cephalopod prey. *Sci. Adv.* 7:eabf5908. doi: 10.1126/sciadv.abf5908

Weiss, M. N., Ellis, S., and Croft, D. P. (2021). Diversity and consequences of social network structure in toothed whales. *Front. Mar. Sci.* 8:688842. doi: 10.3389/fmars.2021.688842

Whitehead, H. (1995). Investigating structure and temporal scale in social organisations using identified individuals. *Behav. Ecol.* 6, 199–208. doi: 10.1093/beheco/6.2.199

Whitehead, H. (1996). Babysitting, dive synchrony, and indications of alloparental care in sperm whales. *Behav. Ecol. Sociobiol.* 38, 237–244. doi: 10.1007/s002650050238

Whitehead, H. (1999). Testing association patterns of social animals. *Anim. Behav.* 57, F26–F29. doi: 10.1006/anbe.1999.1099

Whitehead, H. (2001). Analysis of animal movement using opportunistic individual identifications: Application to Sperm Whales. *Ecology* 82, 1417–1432. doi: 10.2307/2679999

Whitehead, H. (2008). *Analysing animal societies: quantitative methods for vertebrate social analysis*. Chicago: University of Chicago Press.

Whitehead, H. (2009). SOCPROG programs: analysing animal social structures. *Behav. Ecol. Sociobiol.* 63, 765–778. doi: 10.1007/s00265-008-0697-y

Whitehead, H., Bejder, L., and Ottensmeyer, A. C. (2005). Testing association patterns: issues arising and extensions. *Anim. behav.* 69:e1. doi: 10.1016/j.anbehav.2004.11.004

Wilson, E. O. (1975). *Sociobiology: the new synthesis*. Cambridge, MA: Belknap Press.

Würsig, B., and Jefferson, T. (1990). Methods of photo-identification for small cetaceans. *Rep. Int. Whal. Comm.* Sp. Issue 12, 43–52.

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frontiers in Marine Science

SYSTEMATIC REVIEW
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The Status of Marine Megafauna Research in Macaronesia: A Systematic Review

Ashlie J. McIvor[1,2]*, Collin T. Williams[3], Filipe Alves[1,4], Ana Dinis[1,4], Miguel P. Pais[5,6] and João Canning-Clode[1,7]

[1] MARE – Marine and Environmental Sciences Centre, Regional Agency for the Development of Research (ARDITI), Funchal, Portugal, [2] Faculdade de Ciências, Universidade de Lisboa, Lisbon, Portugal, [3] Red Sea Research Center, Division of Biological and Environmental Science and Engineering, King Abdullah University of Science and Technology, Thuwal, Saudi Arabia, [4] Oceanic Observatory of Madeira (OOM), Funchal, Portugal, [5] MARE – Marine and Environmental Sciences Centre, Faculdade de Ciências, Universidade de Lisboa, Lisbon, Portugal, [6] Departamento de Biologia Animal, Faculdade de Ciências, Universidade de Lisboa, Lisbon, Portugal, [7] Smithsonian Environmental Research Center, Edgewater, MD, United States

Edited by:
Guillermo Luna-Jorquera,
Universidad Católica del Norte, Chile

Reviewed by:
Natascha Wosnick,
Federal University of Paraná, Brazil
Boris Michael Culik,
GEOMAR Helmholtz Centre for Ocean Research Kiel, Helmholtz Association of German Research Centres (HZ), Germany

***Correspondence:**
Ashlie J. McIvor
ashlie.mcivor@mare-centre.pt

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Marine megafauna serve valuable ecological and economical roles globally, yet, many species have experienced precipitous population declines. The significance of marine megafauna is particularly evident in Macaronesia, a complex of oceanic archipelagos in the Northeast Atlantic Ocean. Macaronesian islands provide important habitats for marine megafauna species, in turn supporting considerable regional economic activity (e.g., ecotourism and fisheries). Despite this, concerted efforts to manage marine megafauna throughout Macaronesia have been limited. This systematic review provides the first description of the trends in marine megafauna research in this unique insular ecosystem, to provide a better understanding of taxa-specific research needs and future directions for conservation. We identified and validated 408 peer-reviewed publications until 2021 following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) criteria. Literature was dominated by marine mammal research conducted in the northern archipelagos (Azores, Madeira, and Canary Islands) and marine turtle research conducted in Cabo Verde. Much less research focused on large-bodied fish, especially in Madeira and Canary Islands, leaving some of the most vulnerable species regionally data deficient. Research across scientific disciplines focused more on biological studies than management and policy, and anthropogenic impacts were quantified more frequently on mammals or turtles and less on fishes. By identifying gaps in our knowledge of megafauna in relation to threats faced by these organisms, we offer taxa-specific recommendations for future research direction. Although, overall our results indicate that determining population level connectivity should be a major research priority among many marine megafauna species as this information is vital to numerous management strategies, including marine protected areas. In this review, we present a basis of understanding of the current work in Macaronesia, highlighting critical data gaps that are urgently needed to guide the next steps toward establishing conservation priorities for marine megafauna in the region.

Keywords: Atlantic, insular systems, marine mammal, sea turtle, elasmobranch, conservation, predators, large fish

INTRODUCTION

Marine megafauna are broadly defined by their large size and important ecological functions, including animals such as mammals, large fishes, and sea turtles (Moleón et al., 2020; Pimiento et al., 2020). Most notably, marine megafauna are key components to their environment as they help shape ecosystems (and the related functional processes), many of which are considered ecosystem engineers and act as sentinels for ecosystem health (Bossart, 2006). For example, baleen whales contribute to the horizontal transfer of limiting nutrients throughout the water column (Roman et al., 2014), and stingrays alter the benthic morphology as bioturbators which increase localized nutrient fluxes (Lohrer et al., 2004). Moreover, many species of megafauna are considered apex and meso-predators across pelagic and coastal food-webs (Temple et al., 2018). The loss or depletion of such species may limit their current ecological impacts (Pimiento et al., 2020), and potentially result in trophic cascades with consequent loss of community structure and dynamics (Heithaus et al., 2008; Kiszka et al., 2015) and subsequent nutrient cycling (Burkholder et al., 2013). In addition to the biological and ecological consequences of megafauna extirpation, commercial and social relationships also rely on marine megafauna as a source of income in terms of fisheries (Morato, 2012; González et al., 2020; Martinez-Escauriaza et al., 2021) and ecotourism (O'Connor et al., 2009; Mazzoldi et al., 2019; Gonzáles-Mantilla et al., 2021).

Despite their commercial and ecological importance, many species of marine megafauna are of high conservation concern, of which nearly one-third are considered at risk of extinction (Pimiento et al., 2020; Dulvy et al., 2021). This is primarily due to the shared k-selected life history traits that these groups possess, notably high longevity, slow growth, late maturity, and low fecundity (Temple et al., 2018). The increase of waterborne anthropogenic activities has led to an increase in potential threats to marine megafauna, notably fisheries, marine traffic, pollution, and climate change (Halpern et al., 2008). The threats associated with humans often overlap with ecologically important areas for marine megafauna, consequently, a multitude of species have been impacted globally which continues to rapidly intensify (McCauley et al., 2015). Without protective measures, international cooperation, and management of threatened species, marine megafauna populations are expected to face global, local, and functional extinction within the next century (McCauley et al., 2015; Pimiento et al., 2020).

Successful conservation is dependent on quantifying certain biological aspects of marine megafauna, such as species distributions, habitat use, and connectivity (Sequeira et al., 2019). Yet, there are many challenges associated with conservation and research for these threatened groups, such as low detectability and encounter rates, in addition to the high costs associated with accessing the, often remote, marine environment which they inhabit (Afonso et al., 2020). Furthermore, the wide-scale migratory nature of many marine megafauna has made it challenging to acquire descriptive information for many species, and as such, their decline or loss may go unnoticed due to lack of knowledge and poor management (He et al., 2017; Temple et al., 2018). Insular systems, such as oceanic island systems, are particularly vulnerable regions that warrant increased attention as marine megafauna are often in closer proximity to anthropogenic threats (Fernández-Palacios et al., 2021). Management strategies for marine megafauna in these systems are largely based upon existing research conducted on these organisms. Consequently, there is a need to identify research areas lacking in such knowledge to help provide actionable conservation goals and better manage marine megafauna groups within oceanic insular ecosystems.

In this context, this review specifically focuses on the status of marine megafauna research in the Macaronesia region. Macaronesia lies in the Northeast Atlantic Ocean and is historically composed of four oceanic archipelagos of volcanic origin, in decreasing order of latitude: the Azores, Madeira, Canary Islands, and Cabo Verde. The northern archipelagos of the Azores, Madeira and Canary Islands are interconnected by oceanic currents and are considered temperate or sub-tropical, whereas Cabo Verde is considered a tropical ecosystem (Spalding et al., 2007). The Macaronesian biogeographic unit has been subject to years of some debate where, depending on the taxa of study, archipelagos have either been subdivided or grouped into smaller and distinct ecoregions (e.g., Lloris et al., 1991; Spalding et al., 2007). For example, the most recent study proposed the complete exclusion of Cabo Verde based on a multi-taxon approach to redefine the region (i.e., coastal fishes, invertebrates and macroalgae; Freitas et al., 2019c). Owing to the migratory nature of many marine megafauna species, Macaronesia is herein considered inclusive of all four archipelagos. Although there are taxa specific reviews on an archipelago scale (e.g., Das and Afonso, 2017), and few throughout the region (e.g., Valente et al., 2019; Cartagena-Matos et al., 2021), the current study presents the first comprehensive multi-taxa review across Macaronesia. Collecting information on such a wide-scale enables an assessment of current marine megafauna research status including gaps among archipelagos and key taxa.

The combination of high regional diversity and lack of comprehensive understanding of marine megafauna calls for a synthesized documentation of the research conducted in the region as a crucial step toward establishing conservation priorities for Macaronesia. The main objectives of this study were to (I) quantify the relative magnitude of research that has been conducted on key marine megafauna groups in Macaronesia, (II) compare the trends of research among the Macaronesian archipelagos, and (III) describe the advances and future direction of marine megafauna research within Macaronesia. Finally, this review aims to contribute in guiding future research, management, and evidence-based conservation of vital taxonomic groups for the marine ecosystem of Macaronesia.

GENERAL METHODOLOGY

This study followed the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA; Moher et al., 2016) guidelines (**Figure 1**). All analyses were performed after the characterization of suitable studies (**Supplementary Table 1**).

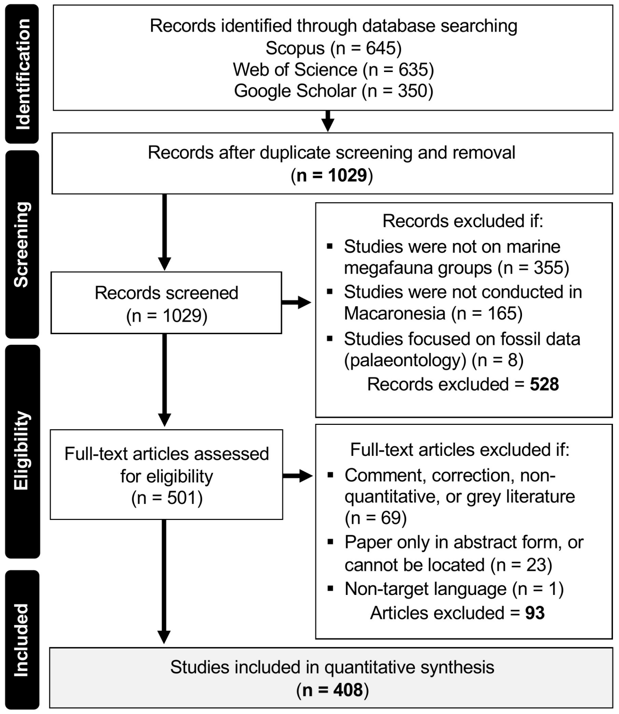

FIGURE 1 | Flow diagram of the Preferred Reporting Items for Systematic Reviews (PRISMA; Moher et al., 2016) methodology and selection process used, indicating the number (n) of studies included in this review. The bold numbers are key numerical values associated with the number of studies included in the review.

TABLE 1 | Search terms used to locate and acquire relevant literature for the systematic review in English, Portuguese (PT), and Spanish (SP).

Search terms	Translation
Marine mammals	
"marine mammal*" OR baleen* OR dolphin* OR whale* OR porpoise* OR cetacean* OR pinniped* OR seal*	**PT:** golfinho, baleia, foca **SP:** delfín, ballena, foca
Chondrichthyes	
"Elasmobranch*" OR shark* OR stingray* OR skate* OR Chondrichthyes* OR chimera*	**PT:** tubarão, raia **SP:** tiburón, mantarraya
Osteichthyes	
"predatory fish*" OR "mobile predator*" OR "game fish*" OR "sport fish*" OR "billfish*" OR sailfish* OR marlin* OR swordfish* OR scombrid* OR tuna*	**PT:** peixe-agulha, peixe-espada, pesca desportiva **SP:** pez espada, marlines, pez vela, pesca deportiva
Sea turtles	
turtle* AND (marine* OR sea* OR ocean*)	**PT:** tartaruga marinha **SP:** tortuga marina

Search terms were combined with a location search using TITLE-ABS-KEY (Macaronesia OR Azores* OR "Canary Islands*" OR Madeira* OR "Cape Verde*" OR "Cabo Verde*").*

TABLE 2 | Inclusion and exclusion criteria for literature in the systematic review.

Inclusion criteria	Exclusion criteria
The study focuses on marine megafauna, i.e., marine mammals, sea turtles, chondrichthyes, and large bodied game fish	The study was conducted on marine birds, or on non-target fish species
The study was conducted in Macaronesia, or the analyses were performed on data derived from the Macaronesian region	The study tagged or reported marine megafauna outside of Macaronesia which was later detected in Macaronesian waters
	The literature is a comment paper, or erratum/corrigendum paper, or only available in abstract form
The literature is in English, Portuguese, or Spanish	Reviews that do not provide quantitative analysis/data (e.g., descriptive books with no extractable data)
	The study of fossils (paleontology)

Searches were conducted in English, Portuguese, and Spanish using SciVerse Scopus[1], Thompson's ISI Web of Science[2], and Google Scholar[3] databases (**Table 1**). Results from Google Scholar that exceeded 100 publications were capped at 10 pages, owing to the negligible chance of finding further relevant publications past the 10th results page (Cartagena-Matos et al., 2021). Peer-reviewed research published between 1900 and February 2021 was included to assess general temporal trends. Literature published prior to 1970 was excluded from detailed analysis (i.e., scientific discipline, methodology, general taxa, and anthropogenic impacts) due to the uncertainty of peer-review. Additionally, all gray literature post 1970 and publications in a non-target language were fully excluded. This process provided 1,029 publication records, after removal of duplications.

A screening process was conducted based on a set criterion to filter appropriate studies (**Table 2**). Initially, titles and abstracts were screened for inclusion categories, resulting in 501 publications considered for full-text screening, of which 408 publications were included for full analysis. Validation of every decision to include or exclude a specific paper was confirmed by at least two authors to ensure all appropriate literature was included. The details of the retained literature for this systematic review can be found in the **Supplementary Material**.

Data Analysis

Data from publications that passed through all inclusion criteria was extracted using ArcGIS Survey123 (detailed description can be found in **Supplementary Table 2**). The collected data categorized publications by year of publication, author affiliation, archipelago, depth of the surveyed area, research theme (i.e., biology, or management and policy), primary methodology (e.g., extractive, observational, experimental, etc.), primary taxa (i.e., marine mammals, osteichthyes, chondrichthyes, or marine turtles), and if assessed, the type of anthropogenic impact investigated. Although some marine birds might be considered

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[1] https://www.scopus.com

[2] https://webofknowledge.com

[3] https://scholar.google.com

marine megafauna, these were excluded for the purpose of this analyses and review. All parameters were compiled into a singular database of marine megafauna research in Macaronesia (**Supplementary Table 3**). For the purposes of comparative assessment, publications that had data from more than one archipelago were represented by each individual archipelago when describing research trends over time (**Figures 2–5**; i.e., single study with data from Madeira and Canary Islands will be represented twice). Original graphical representations and statistical analysis were conducted in R version 4.0.3 (R Core Team, 2020). A linear regression model was fitted to the quantity of publications per year to test for significant trends in publications over time (R base package), excluding 2021 as it was an incomplete year. The threshold for statistical significance was $p \leq 0.05$.

RESULTS

Scientific publications investigating marine megafauna in Macaronesia have significantly increased over time ($r^2 = 0.66$; $p < 0.001$), reaching a peak annual output of 50 publications per year between 2019 and 2020 [maximum recorded annual publications per archipelago: Azores: 15 (2020); Madeira: 12 (2019); Canary Islands: 19 (2019); Cabo Verde: 10 (2019)] (**Figure 2**). Although, current trends of marine megafauna research within Macaronesia are highly variable among archipelagos. The majority of regional studies have been conducted solely in the Azores (33%), followed by the Canary Islands (30%), Cabo Verde (17%), and Madeira (10%). In addition, 10% of studies were conducted in more than one archipelago, and 3% included data from all Macaronesia (**Figure 2**). Of the studies that were conducted in more than one archipelago ($n = 30$), the majority included data derived from both the Azores and other archipelagos ($n = 23$; Azores-Madeira = 16; Azores-Canary Islands = 10; Azores-Cabo Verde = 2[4]). Studies that incorporated data from the Canary Islands and Madeira, and Canary Islands and Cabo Verde were least common ($n = 4$, respectively). From the total number of publications, 79% had at least one author affiliated to a research institution at the archipelago of study. According to our analysis, most publications (68%) were from sea-level or above (i.e., boat, shore, and desk-based). Of the 32% of studies that investigated marine megafauna at depth, 16% collected data from the first 30 m, 6% from between 31 and 200 m, 18% from depths below 200 m, and 65% did not define the depth investigated.

The primary taxa of research conducted in the Azores, Madeira, and the Canary Islands were marine mammals (51%, 51%, and 56%, respectively; **Figure 2**), followed by chondrichthyans (29%, 21%, and 18%, respectively), and an equivalent research output for marine turtles in the Canary Islands (18%). Relative trends in turtle research per archipelago appeared to increase with decreasing latitude (Azores: 8%, Madeira: 17%, Canary Islands: 18%, Cabo Verde: 43%). Research output on large-bodied osteichthyes received the third-most level of relative research effort in the Azores and Cabo Verde (12% and 14%, respectively), yet few studies were found in Madeira and Canary Islands (10 and 8%, respectively). Contrasting trends were observed in Cabo Verde, where the primary output was turtle research, followed by marine mammal (33%), osteichthyan, and chondrichthyan research (10%). Additionally, relative patterns of research effort by archipelago were not consistent among all taxa (**Figure 3**). The majority of research on marine mammals, chondrichthyes, and osteichthyes has been conducted in the Azores archipelago, with a similar, yet fewer number of studies on marine mammals having been conducted in the Canary Islands. Marine turtles have received more research attention in Cabo Verde than any other archipelago in Macaronesia.

Research across scientific disciplines was not evenly distributed, with more biological studies ($n = 346$ *c.f.* 62) than management and policy publications. The majority of biological research was conducted within the sub-disciplines of biodiversity and behavior yet was highly variable among taxa (**Figure 4**). Biological studies involving marine mammal research was composed mainly of pathological studies (19%), followed by population (18%), and biodiversity assessments (16%). There were less marine mammal publications focusing on life history (1%) and none on reproduction, similar to chondrichthyan research (1%, respectively). Chondrichthyan research was dominated by biodiversity research (34%), followed by trophic ecology (11%), whereas osteichthyan research had primarily behavioral (25%), and biochemical (17%) related studies. Within the sub-disciplines of osteichthyan research, there were no available publications on either reproductive of pathological assessments. Marine turtle research was predominantly focused on biochemistry studies (23%), pathology (14%), and genetic assessments (11%), with no publications on behavior or taxonomy, and few on their life history (1%). Within management and policy related sub-disciplines, the majority of marine mammal, chondrichthyan, and osteichthyan research was based on fisheries (38%, 62%, and 56%, respectively), whereas marine turtle research focused on environmental impacts assessments (EIAs; 47%). There were few publications on EIAs or marine protected areas (MPAs) for either chondrichthyes (5% and 6%, respectively) or osteichthyes (5% and 6%, respectively).

The number of sub-disciplines investigated within the primary thematic lines (i.e., biological studies; management and policy) have increased considerably over the past two decades (2000–2020; **Figure 5**). Biological studies, specifically biodiversity research, appears to be the earliest occurring sub-discipline per taxa, and is also one of the fastest growing research themes for marine mammal, chondrichthyan, and osteichthyan research. Marine mammal research on pathology, behavior and movement have seen recent increases in publication output, whereas chondrichthyan and osteichthyan trophic ecology have also shown recent increases. Marine turtle research has increased in almost all sub-disciplines in the past decade, especially within biochemistry, movement, and population ecology. Management and policy related disciplines have lagged in comparison with the first publications for marine mammal and osteichthyan research surfacing in 2003, then in 2010 for chondrichthyes, and 2011

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[4] Sum of individual products are greater than that of the total due to instances where data were derived from more than two archipelagos.

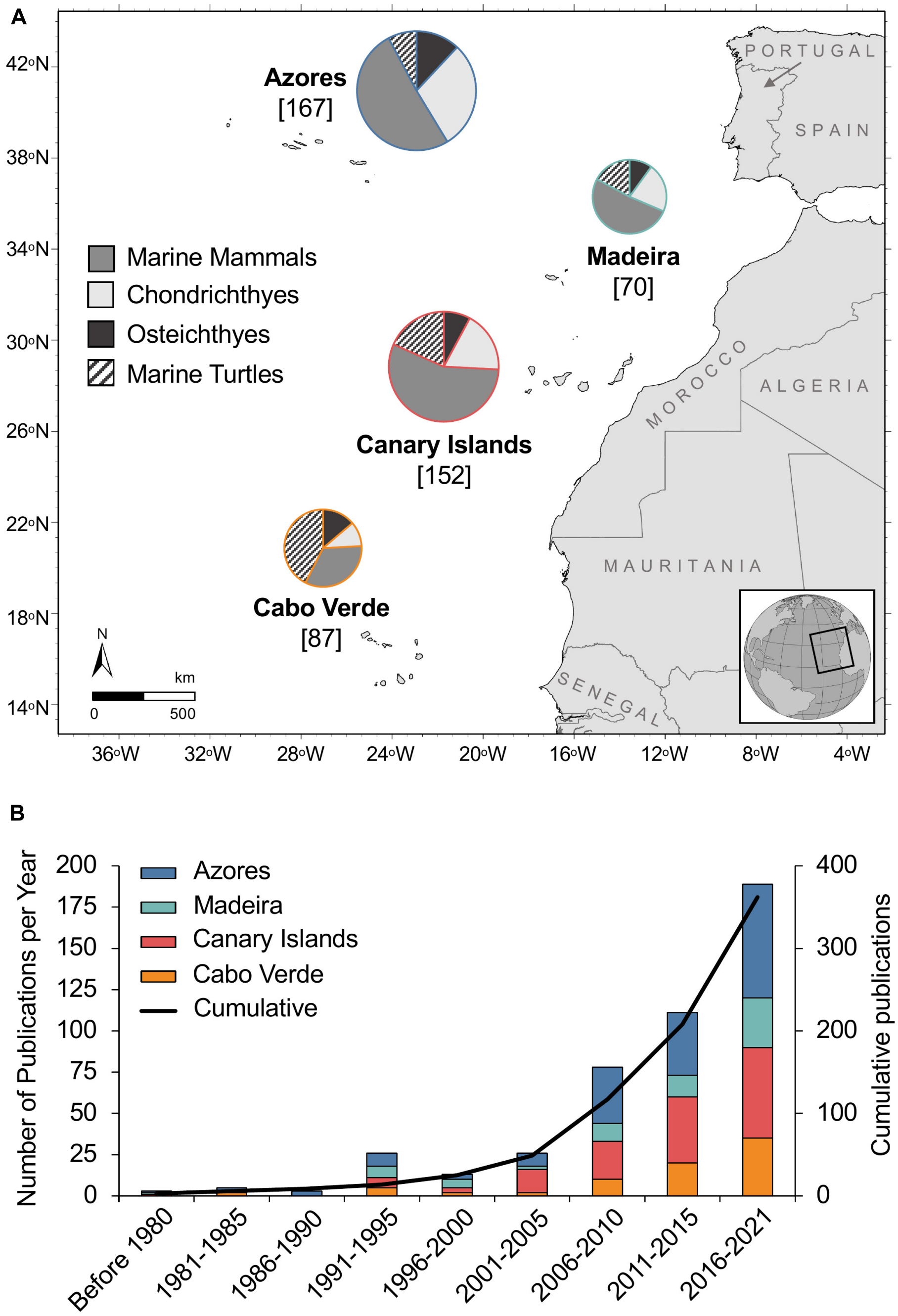

FIGURE 2 | Quantitative representation of reviewed publications by Macaronesian archipelago in relation to **(A)** composition of focal taxa (size of chart scaled to relative number of publications) and **(B)** publication trends over time.

for marine turtles. Research into MPAs has seen the most recent increase in publications for all taxa, except for osteichthyes. Notable increases in publication output have recently been observed in EIA research for osteichthyes and marine turtles, and in fisheries research for chondrichthyes.

The majority of publications did not attempt to quantify anthropogenic impacts (73%). Of the publications that quantified risk to the focal taxa, most focused on fishing related impacts, followed by marine pollutants and maritime traffic (**Figure 6**). Specifically, the majority of impacts assessments in marine mammal and chondrichthyan research focused on fishing related impacts, whereas osteichthyan and marine turtle research had a greater emphasis on impacts from marine pollution. Papers which assessed the impacts of pollution and climate change in Macaronesia were primarily focused on marine turtles, while the majority of marine traffic research was conducted in

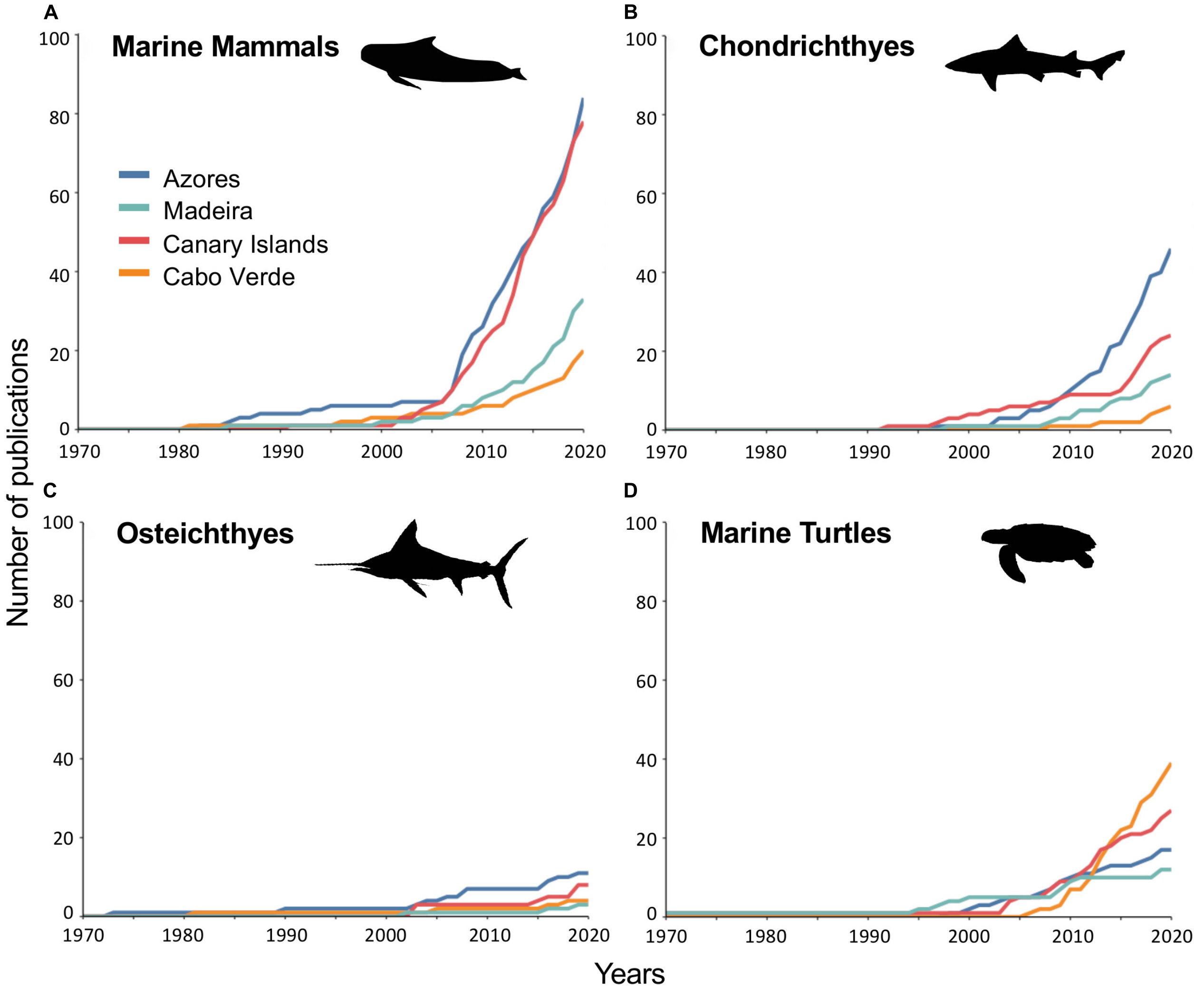

FIGURE 3 | Cumulative number of publications in marine megafauna research per archipelago through time: **(A)** marine mammals, **(B)** chondrichthyes, **(C)** large-bodied osteichthyes, and **(D)** marine turtles. Silhouettes derived from Phylopic (http://phylopic.org).

relation to marine mammals. Overall, anthropogenic impacts were quantified more frequently in publications that focused on marine mammals or marine turtles, and less likely in fish (**Figure 6**).

DISCUSSION

This study provides the first quantitative representation of relative trends in marine megafauna research throughout Macaronesia. Research output has increased annually, yet the reviewed studies are currently dominated by marine mammal research in the northern archipelagos (Azores, Madeira, and Canary Islands) and by marine turtle research in Cabo Verde. There is less fish-related research, especially within the Canary Islands and Cabo Verde, leaving some of the most vulnerable species regionally data deficient (Pimiento et al., 2020; Dulvy et al., 2021; **Supplementary Table 4** and **Supplementary Figure 1**). The majority of research is conducted from boats/land, and only 24% of research explored depths >30 m, highlighting a serious knowledge gap regarding pelagic and deep-sea ecology in this oceanic system. Although overfishing and direct harvesting are commonly referred to as the main global anthropogenic threats to marine megafauna (McCauley et al., 2015; Dulvy et al., 2021), our findings reveal that other significant threats (e.g., marine pollutants, climate change, etc.; **Figure 6**) remain largely unexplored in Macaronesia and require further research attention to fully-understand their impacts across marine megafauna taxa.

Marine Mammals

Macaronesia hosts a variety of resident marine mammals [e.g., short-finned pilot whale *Globicephala macrorhynchus* (Alves et al., 2013; Servidio et al., 2019), common bottlenose dolphin *Tursiops truncatus* (Dinis et al., 2016), and Mediterranean monk seal *Monachus monachus* (Pires et al., 2008)] as well as migratory species [e.g., rough-toothed dolphin *Steno bredanensis* (Steiner, 1995; Alves et al., 2018) and Bryde's whale *Balaenoptera edeni*

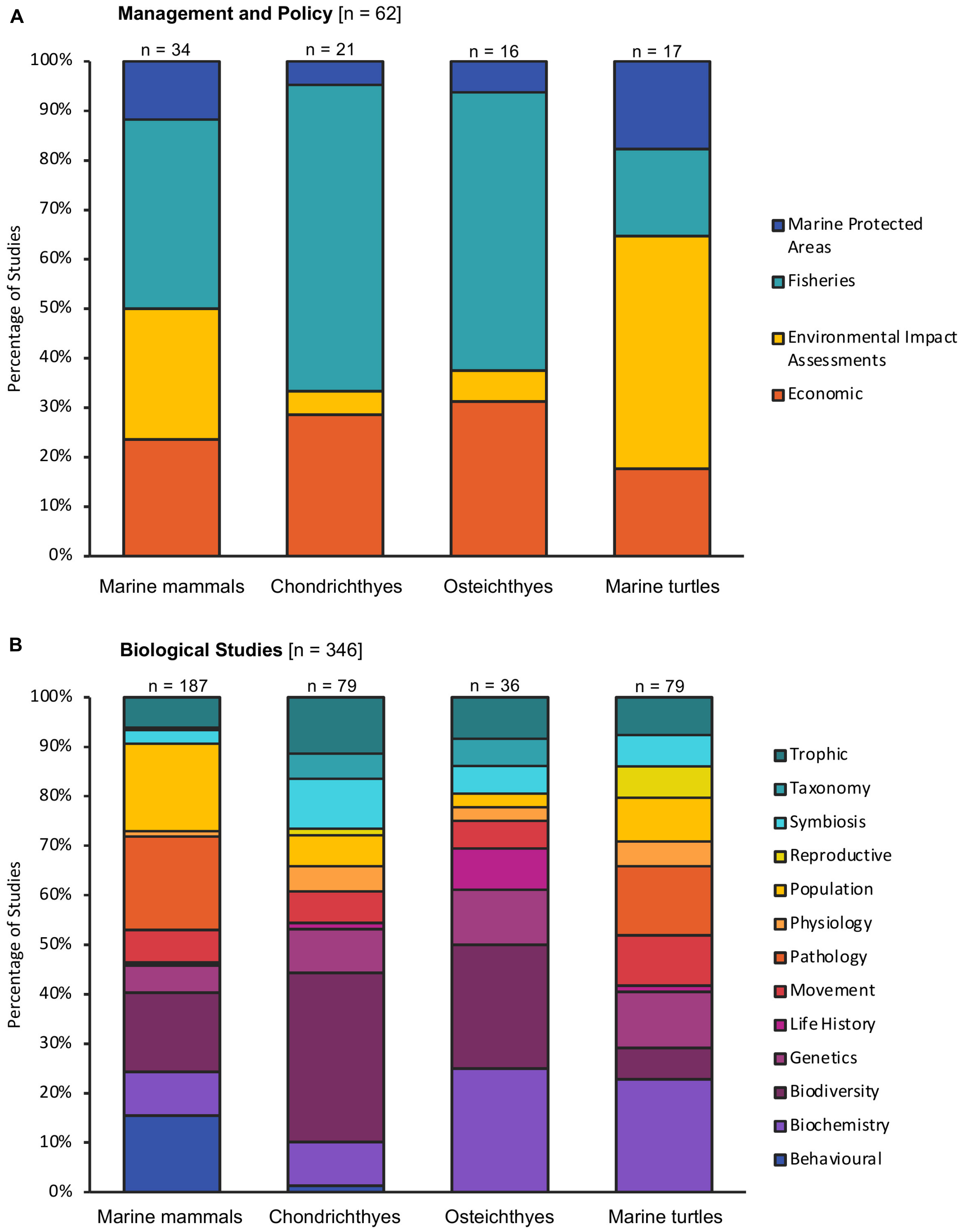

FIGURE 4 | Trends of sub-disciplines among reviewed papers corresponding to: **(A)** management and policy and **(B)** biological studies.

(Ferreira et al., 2021)]. Marine mammals are typically seen as charismatic animals that receive a lot of support from the public and conservation entities, which often refer to them as flagship species (Mazzoldi et al., 2019). There has been a corresponding shift in perspectives of marine mammals from a consumptive to an ecological resource. Following the end of industrial whaling in the Azores and Madeira (1984 and 1981, respectively; Brito, 2008; Mazzoldi et al., 2019), cetacean eco-tourism has become an important regional industry that has promoted their conservation (Mazzoldi et al., 2019). However, the expansion of anthropogenic activities in Macaronesia brings with it associated pressures that may require novel management strategies.

The majority of research in Macaronesia has been conducted in the Azores and Canary Islands. Marine mammal research

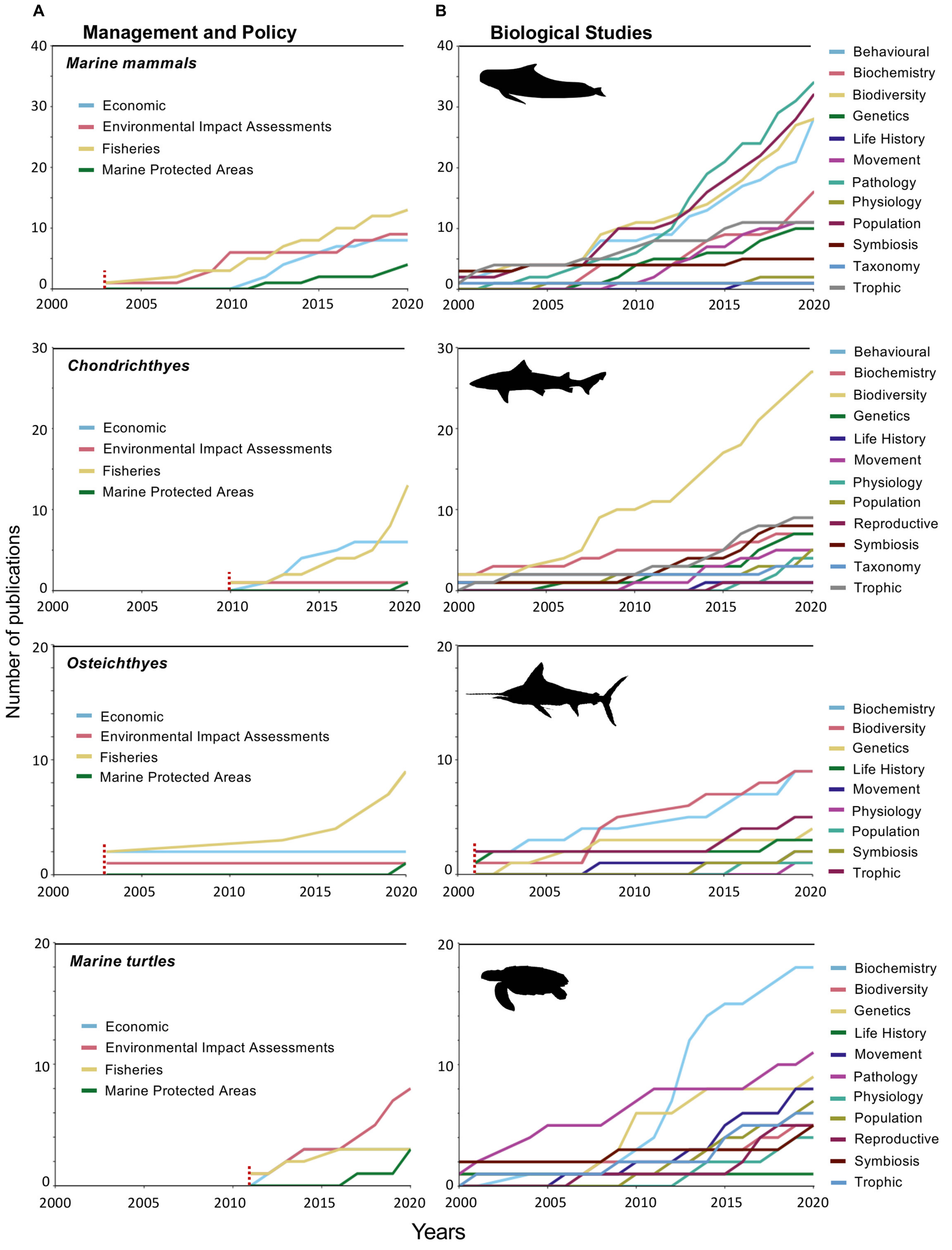

FIGURE 5 | Sub-topic evolution of **(A)** management and policy, and **(B)** biological studies per marine megafauna group, over the past two decades (2000–2020). Dashed red line indicates the first research article published within the respective topic. Note differences in scale per taxa.

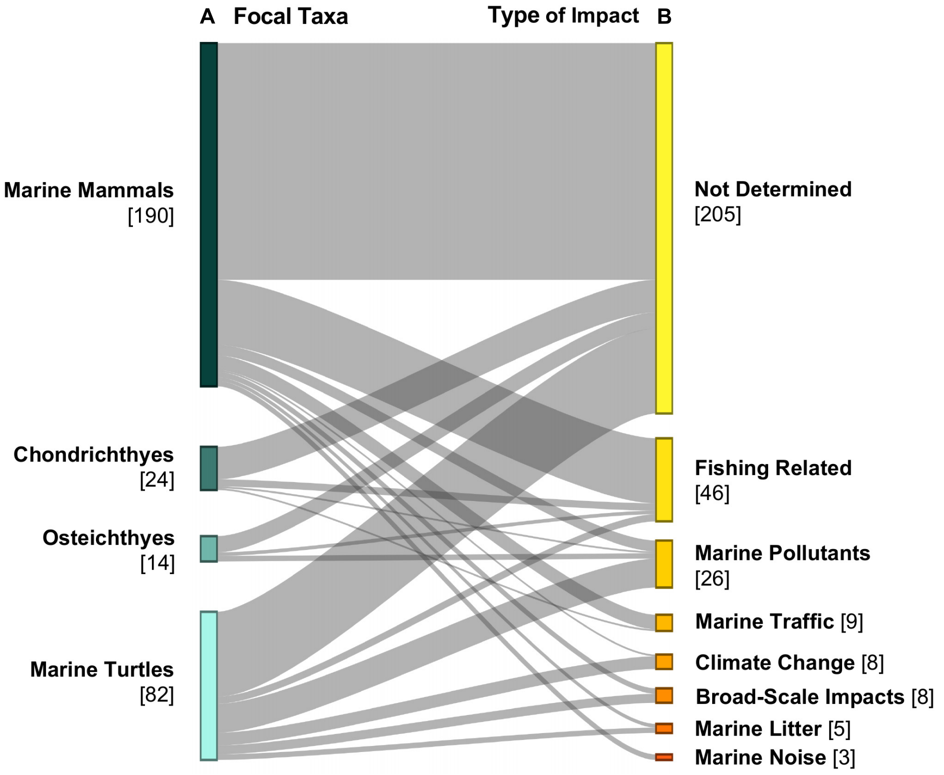

FIGURE 6 | Sankey diagram depicting **(A)** the number of publications that quantify **(B)** anthropogenic impacts on Macaronesia marine megafauna in relation to the focal taxa of study.

is the main research output for the Azores, Madeira, and the Canary Islands, and second largest output in Cabo Verde. Early exploitation of marine mammals in Macaronesia allowed preliminary research to grow (e.g., sperm whales *Physeter macrocephalus* in the Azores; Clarke et al., 1993) and has been steadily increasing since the 1980s. The primary focus of cetacean research in Macaronesia has been biodiversity/biogeography studies, population assessments [i.e., abundance and distribution (Alves et al., 2015; Wenzel et al., 2020)], and pathological research [e.g., necropsy/clinical reports, virology (Fernández et al., 2017)]. The high volume of pathological research is related to established stranding networks throughout Macaronesia, for which the majority has been conducted in the Canary Islands. In line with previous research, our review highlighted species specific biases in which research primarily focused on three main species (i.e., short-beaked common dolphin *Delphinus delphis,* sperm whale, and common bottlenose dolphin; Cartagena-Matos et al., 2021).

Although marine mammals have received the most research attention among marine megafauna regionally, certain fields of study remain unrefined. There is a distinct lack of ecological research surrounding species such as the pygmy (*Kogia breviceps*) and dwarf (*Kogia sima*) sperm whale, or beaked whales (Ziphiidae). This is not surprising as many of these species are elusive and difficult to study, and most of the known information comes from stranding-related necropsy reports (McAlpine, 2018). We also found a paucity of peer reviewed research on basic biological aspects of the Critically Endangered Mediterranean monk seal *Monachus monachus* (e.g., diet, movement, pollutants; European Mammal Assessment Team, 2007). The Mediterranean monk seal formerly inhabited the whole of Macaronesia (Monod, 1948; Machado, 1979; Hernandez, 1986; Silva et al., 2009; Brito, 2012; González, 2015), yet is now confined to the Madeiran Archipelago with a single population of ∼20 individuals (Karamanlidis et al., 2005; de Larrinoa et al., 2021). Without adequate information available for certain marine mammal species in Macaronesia, population declines and threats may go undocumented and ineffective species protections may be enacted. Across all marine mammals, population estimates, migratory patterns, and abundance estimates, which underpin many conservation strategies, are currently limited in Cabo Verde and Madeira (**Figure 3**). Understanding species connectivity is another important component of conservation, yet within Macaronesia this information remains scarce. For example, short-finned pilot whale and bottlenose dolphin population structuring is evident between the Azores, Madeira, and Canary Islands (Alves et al., 2019; Dinis et al., 2021), yet has not been expanded to include Cabo Verde (Hazevoet et al., 2010; Correia et al., 2020).

The main potential threats to cetaceans in northern Macaronesia include vessel collision (e.g., Canary Islands; Ritter and Panigada, 2018) and intensive whale watching throughout the Azores, Madeira, and Canary Islands (Arranz et al., 2021a,b;

Sambolino et al., 2022a). Other indirect or difficult to quantify threats, such as by-catch and overfishing, could also pose risks to this taxa, and are of greater concern in Cabo Verde (Visser et al., 2011; Lopes et al., 2016). The increase in marine-based anthropogenic activities is reflected as an increase of pressures faced by marine mammals (Fais et al., 2016; Cunha et al., 2017; Ritter et al., 2019; Schoeman et al., 2020; Sambolino et al., 2022b). This is echoed throughout the literature and has pushed research efforts to investigate the impacts of bycatch, pollutants, and marine traffic, yet future research should also focus on climate induced impacts (Sousa et al., 2021).

Successful conservation of marine mammals in Macaronesia will rely heavily upon a population-level understanding of their ecology and biology. Connectivity and biogeographical patterns of large delphinids and whales among the Macaronesian archipelagos should be prioritized, as managing migratory species often relies upon multi-national cooperation. Facilitating such cooperation requires robust data on species connectivity to guide protections within Economic Exclusion Zones (EEZs) and the international waters in between (Correia et al., 2020; Ferreira et al., 2021). This in turn requires an increased research effort in Macaronesia's offshore areas to attain reliable estimates of species richness and abundance of marine mammals, which may currently be underestimated (Valente et al., 2019; Correia et al., 2020; Cartagena-Matos et al., 2021).

Chondrichthyes

Chimeras, sharks, skates, and rays are especially vulnerable to exploitation owing to their specific life history traits and are experiencing precipitous worldwide declines (Dulvy et al., 2021). Among all megafauna groups, sharks are expected to be most impacted by the decline of taxonomic and functional diversity following species loss (Pimiento et al., 2020). Macaronesia hosts a diverse array of pelagic and demersal species, many of which are of high conservation concern, such as the shortfin mako shark *Isurus oxyrinchus* and angelshark *Squatina squatina*. Species composition differs between archipelagos, except for elasmobranch communities in the Azores and Madeira which are similarly dominated by deep-water Squaliformes (Das and Afonso, 2017). There are very few highly migratory species shared between Cabo Verde and the other Macaronesian archipelagos (Das and Afonso, 2017). Cabo Verde, which exhibits distinct biogeographic features (Floeter et al., 2008; Freitas et al., 2019c), supports a more coastal, tropical elasmobranch assemblage than its temperate counterparts (Wirtz et al., 2013). The majority of chondrichthyan species in Macaronesia are non-migratory, and species richness appears to decrease with latitude (Das and Afonso, 2017).

Within Macaronesia, Cabo Verde and Madeira have the least amount of research conducted on chondrichthyans, with alarmingly no information available for batoids other than within species checklists (Wirtz et al., 2008, 2013; Biscoito et al., 2018; Freitas et al., 2019c) and landings data (Martínez-Escauriaza et al., 2020). The Azores is considered a marine biodiversity hotspot (Afonso et al., 2020), to which many chondrichthyan studies have focused on biogeography and biodiversity, movement, and trophic ecology of the species that utilize local seamounts (Kukuev and Pavlov, 2008; Das and Afonso, 2017). Similar to other archipelagos, the majority of chondrichthyan research from the Azores has primarily focused on sharks and less on batoids or chimeras. Shark-based tourism in the Azores, which in 2014 was estimated to be worth over USD $2 million (Torres et al., 2017), may have facilitated the increase of research effort and long-term datasets from this archipelago. Thus, potential declines in elasmobranchs are more likely to be noticed in the Azores compared to other archipelagos, such as Madeira, where there is very little information on the abundance and distribution of elasmobranchs (Correia et al., 2016). The majority of information available on chondrichthyans from Madeira is derived from commercial fisheries, primarily focusing on species distribution records, check-lists, and taxonomy of deep-water sharks (e.g., Freitas et al., 2017; Biscoito et al., 2018; Stefanni et al., 2021). The Canary Islands have been identified as a unique stronghold for the Critically Endangered angelshark (Barker et al., 2016; Morey et al., 2019) which has led to the increase in chondrichthyan research from the archipelago. Information on elasmobranchs in Cabo Verde is scant, representing merely ∼1% of the reviewed studies.

Many basic biological questions relevant to fisheries management remain unanswered regarding the life-history, reproduction, and drivers of distribution of many chondrichthyes in the region. For example, the scarcity of research conducted on batoids from Madeira and Cabo Verde, with only recent advancements from the Canary Islands (see Tuya et al., 2021), remains a particularly concerning hindrance to the management of these species. Furthermore, there is some evidence of pupping and potential nursery grounds in Macaronesia [e.g., blue shark *Prionace glauca,* Azores (Vandeperre et al., 2014, 2016); smooth hammerhead shark *Sphyrna zygaena*, Azores (Santos et al., 1995; Das and Afonso, 2017) and Madeira (Freitas and Biscoito, 2018); angelshark, Canary Islands (Meyers et al., 2017; Jiménez-Alvarado et al., 2020)], yet there is little information generally on biologically sensitive areas, including nursery grounds, inshore and offshore aggregation, and deep-water skate and ray egg deposition sites. Fisheries-related research only represents 6% of the total research effort in Macaronesia, yet is an essential component to managing populations as there is little evidence that currently legal fisheries are sustainable without adequate baseline information and bycatch statistics (Hareide et al., 2007; EASME, 2017). For example, there is an absence of detailed information regarding species distribution and spatial overlap with regional fisheries, such as those targeting black scabbardfish *Aphanopus carbo* (Veiga et al., 2013), which may further increase the vulnerability of biologically sensitive sites to fisheries. Moreover, inconsistencies between the catch and landing of sharks (i.e., unreported or misreported discards) have been documented in the Azores (Machete et al., 2011; Das and Afonso, 2017) and the Canaries (Pajuelo et al., 2010), yet have not been investigated in Madeira.

Overfishing has been identified as a global driver of extinction for more than one-third of chondrichthyan species (Dulvy et al., 2021), and is likely the largest threat in Macaronesia. Although shark bycatch rates are considered relatively low (Bordalo-Machado and Figueiredo, 2009), they often include species of conservation concern, specifically deep-sea sharks such as the Portuguese dogfish *Centroscymnus coelolepis*, leaf-scale gulper shark *Centrophorus squamosus*, and kitefin shark *Dalatias licha* (Holley and Marchal, 2004; Ramos et al., 2013; Campos et al., 2019), and pelagic sharks (i.e., blue shark and shortfin mako shark). Other factors that may impact coastal chondrichthyan species, such as the angelshark, include pollution and habitat destruction (Das and Afonso, 2017; Jiménez-Alvarado et al., 2020).

Spatial protections often rely upon knowledge of a species' connectivity patterns, information which is currently unavailable for many Macaronesian chondrichthyans. Accordingly, future chondrichthyan research should seek to investigate population structuring and movement patterns across various spatial scales throughout Macaronesia. Moreover, the lack of regional monitoring of fisheries may limit future research efforts, as baseline information needed to examine population trends through time may be unavailable. Establishing regional fisheries observer programs may be one way to address current knowledge gaps for chondrichthyans in certain Macaronesian archipelagos. Observer programs can yield robust estimates of bycatch and discards (e.g., the Azorean Fisheries Observer Program)[5], which could be valuable in understanding the impacts of longline fisheries on deep-sea sharks. Despite this, there are inherent limitations in the types of information that can be determined through observer programs, and the establishment of such programs may be particularly challenging in Cabo Verde given the numerous international fleets that fish their waters (Coelho et al., 2020; González et al., 2020). Further research may be required to propose technical improvements to fishing gear that can minimize the catch of non-target chondrichthyan species, as little has been done to investigate economically viable alternatives in the region. Overall, our findings indicate a pressing need for future investigations of chondrichthyan abundance, distribution and connectivity to inform fishing regulations and implement effective MPAs (Dulvy et al., 2021).

Osteichthyes

The osteichthyan megafauna of Macaronesia is primarily composed of large-bodied tunas (i.e., *Thunnus* spp.) and billfish (i.e., Xiphiidae and Istiophoridae) which are both highly migratory predators. Tunas are a commercially important fisheries resource in the waters of Macaronesia, including albacore tuna *Thunnus alalunga*, yellowfin tuna *Thunnus albacares*, Atlantic bluefin tuna *Thunnus thynnus*, and bigeye tuna *Thunnus obesus*. With the exception of bigeye tuna (Vulnerable; Collette et al., 2021), all other species have recently been re-classified as Least Concern by the IUCN Red List of Endangered Species (**Supplementary Table 4**) owing to decades of reduced catch quotas and successful enforcement in the Atlantic. Billfish are another economically important group regionally and are targeted by commercial and recreational fishers throughout Macaronesia, notably the Atlantic blue marlin *Makaira nigricans*, white marlin *Kajikia albida*, broadbill swordfish *Xiphias gladius*, Atlantic sailfish *Istiophorus albicans*, roundscale spearfish *Tetrapturus georgii*, and the longbill spearfish *Tetrapturus pfluegeri*.

Within this species group, our review only yielded 31 relevant papers, showing that more work has been conducted solely on tunas than on billfish (62 *c.f.* 16%; excluding species checklists). The vast majority of work in Macaronesia has been conducted in the Azores, followed by the Canary Islands, Cabo Verde, and Madeira. Tuna and billfish research have mainly focused on biochemical analysis and genetic work to identify population dynamics, reproductive biology, and to define stock boundaries. This work has been supported by an increase in telemetry studies to understand spatio-temporal connectivity of delineated stocks (Arrizabalaga et al., 2008; Braun et al., 2019). Stock assessment needs appear to be the primary driver for most research conducted on large-bodied osteichthyes in the region. The larger quantity of tuna literature may be due in part to their heavy exploitation and the subsequent efforts to assess population dynamics and reproductive biology in the greater Atlantic. Most work has concentrated on Atlantic bluefin and bigeye tuna in an attempt to identify population differentiation, mixing rates, and natal origins. Of the 14 publications available for billfish from Macaronesia, nine were inclusions in biodiversity assessments and only two quantified tissue contamination in broadbill swordfish. The remaining two relevant papers investigated the movements and connectivity estimates of broadbill swordfish off the Azores, and estimated fishing intensity and spatial use for commercial fleets on the Madeira-Tore seamounts. All non-biodiversity/check-list publications were from the Azores, with the exception of the latter publication in Madeiran waters.

Contrary to the quantity of bluefin tuna work from the Pacific and the south and northwest Atlantic, very few ecological studies have been conducted on tuna movements, reproduction, and foraging ecology from the northeast Atlantic (Azores, Madeira, and Canary Islands; Romero et al., 2021). To date, our knowledge on the spawning periods and locations of Atlantic bluefin tuna in Macaronesian waters is limited, although potential spawning grounds may occur in the waters between the Azores and Madeira, and to the east of the Canary Islands (Natale et al., 2020). Moreover, Cabo Verde has also been suggested to be a spawning area for yellowfin tuna (Kitchens et al., 2018), yet there is very little information available from this archipelago. Nevertheless, fundamental questions regarding stock structure and natal origins within mixing hotspots remain. Despite six species of billfish found throughout Macaronesia, the broadbill swordfish was the only species with dedicated research attention which is most likely owed to their commercial value. There were no publications identified in this review on roundscale spearfish, longbill spearfish, or Atlantic sailfish within Macaronesia.

There were not a sufficient number of studies to examine the specific anthropogenic impacts on this group, yet fisheries exploitation is expected to be the greatest threat to declines of tuna and billfish. Recreational fishing may also have undocumented impacts, as some species are typically landed for personal consumption in Macaronesia (e.g., Atlantic blue marlin; Martinez-Escauriaza et al., 2021), yet there is limited information regarding recreational fishing industries throughout the region. Attention must be given to the roundscale spearfish

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[5] www.popaobserver.org

(Data Deficient; Collette et al., 2011), as there have been frequent misclassification of this species in white marlin and longbill spearfish (Beerkircher et al., 2009), which has hindered catch data and population estimates throughout its range.

There is a general lack of information on tunas and billfish in Macaronesia, with strong regional and species biases among what little research is available. Ascertaining primary biological data, such as population structure and life history parameters, would be a logical first step toward adequately managing this species group in Macaronesia. Significant uncertainty surrounds stock delimitations for many species, and more information is needed to understand which Macaronesian archipelagos share stocks of each species. Further examinations of life history characteristics among Macaronesian fish stocks could determine if variation occurs within the region and enable tailored management strategies for each stock. Although establishing fishery regulations for such migratory species is inherently challenging, ongoing research programs (e.g., the Atlantic Ocean Tuna Tagging Program)[6] demonstrate that recovery of Atlantic stocks of historically overfished large pelagic fish species is possible. With many fundamental biological questions currently unanswered future research on osteichthyan megafauna in Macaronesia describing connectivity and life history patterns between archipelagos will likely have a great impact on future management and protections for these species.

Marine Turtles

Six species of marine turtles are known to occur in Macaronesia, the most common being the loggerhead turtle, *Caretta caretta*. The summer occurrence of loggerhead turtles in the Azores, Madeira and Canaries is largely associated with the pelagic phase of the western-Atlantic rookery that feed in oceanic waters (Bolten et al., 1993, 1998; Bjorndal et al., 2000). There are latitudinal correlations between Macaronesian distributions and the natal origin of loggerhead turtles, where those found in the Azores and Madeira typically represent turtles from Florida (United States), and those in Canary Islands from Mexico (Monzón-Argüello et al., 2009). Nesting of the North East Atlantic subpopulation occurs in Cabo Verde and represents the third largest nesting population of loggerhead turtles worldwide (Marco et al., 2011, 2012), with the majority of females (i.e., 60–65%) nesting in Boa Vista Island (Marco et al., 2012). There is evidence of dispersal of Cape Verdean juveniles into northern waters of Macaronesia (Monzón-Argüello et al., 2010c). Hawksbill *Eretmochelys imbricata* and green turtles *Chelonia mydas* have also been documented nesting in Cabo Verde, but more notably use the area for foraging (Monzón-Argüello et al., 2010a,b; Marco et al., 2011). These two species have additionally been recorded in the Azores (Santos et al., 2010), Madeira, and the Canary Islands, albeit relatively less prevalent (Fretey, 2001). Leatherback turtles *Dermochelys coriacea* have been documented in all Macaronesian archipelagos (Doyle et al., 2008; Marco et al., 2011; Correia et al., 2019). Occasional migrations of Olive ridley *Lepidochelys olivacea* have been documented in Madeira, Canary Islands, and Cabo Verde (Fretey, 2001; Marco et al., 2011; Carrillo and Alcántara, 2014; Barcelos et al., 2021), in addition to Kemp's ridley turtles *Lepidochelys kempii* in the Azores and Madeira archipelagos (Brongersma, 1972; Bolten and Martins, 1990; Santos et al., 2010).

The majority of turtle research in Macaronesia has been conducted in Cabo Verde, closely followed by the Canary Islands, with relatively fewer studies from the Azores and Madeira (**Figure 3**). This largely is a result of the regional nesting of the North East Atlantic subpopulation of loggerhead turtles in Cabo Verde, and the long-term monitoring efforts from local NGOs and other environmental agencies in this archipelago (e.g., Turtle Foundation, in 2008; Maio Biodiversity Foundation, in 2010). In the Canary Islands, the majority of research has been conducted on dead or stranded turtles, whereas in Cabo Verde research is conducted on nesting individuals. Turtle research in Madeira and the Azores has primarily targeted juveniles in pelagic waters where they forage (Freitas et al., 2018, 2019a). The quantity of turtle research appears to decrease with increasing latitude, most likely due to decreasing water temperatures (i.e., physiological constraints) and distance from the Cape Verdean rookery (i.e., decreased prevalence). The majority of initial publications focused on demographic research, although more recent research on turtles in Macaronesia have focused on biochemistry [e.g., stable isotopes (Raposo et al., 2019), pollutants and contaminants (Orós et al., 2013; Camacho et al., 2014)], and environmental impact assessments (Marco et al., 2021).

There is considerably less research available for hawksbill, Kemp's and Olive Ridley sea turtles relative to other species, as they are less prevalent in the region and thus more challenging to study. Moreover, little information is currently available on the physiology and reproductive ecology of sea turtles in Macaronesia. This is particularly important, as higher environmental temperatures are expected with climate change, which may reduce hatching success, hatchling fitness (Laloë et al., 2014; Santidrián Tomillo et al., 2014; Martins et al., 2020), and increased sporadic nesting events (Carreras et al., 2018) in areas of previously low to no nesting activity (e.g., loggerhead turtles in Malaga, Spain; Gonzalez-Paredes et al., 2021), but also increase parasite abundance (Brunner and Eizaguirre, 2016). There is little information on the causes of the increase in parasite prevalence in Cabo Verde, and the functional links between environmental changes, contaminants, or population density on viral transmission (Lockley et al., 2020; Farrell et al., 2021).

Parasites can be vectors of virus transmission (Greenblatt et al., 2005; Bunkley-Williams et al., 2008; Jones et al., 2016) and have been shown to be correlated with feeding ecology, reproductive success and population dynamics (Lockley et al., 2020), posing as a population level threat. Currently, sea turtle infection has been described in Cabo Verde (Sarmiento-Ramírez et al., 2010; Stiebens et al., 2013), Madeira (Valente et al., 2009), and Canary Islands (Orós et al., 2004; Alfaro et al., 2008). Moreover, among marine megafauna, sea turtles are unique in that they nest on land. This behavior facilitates important ecological connections between terrestrial and marine systems, but also exposes sea turtles to a suite of anthropogenic pressures (Hamann et al., 2010; Pimiento et al., 2020). Wildlife watching tourism (Marco et al., 2021) and the implementation of several

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[6] www.iccat.int

environmental protection organizations in Cabo Verde has significantly decreased poaching pressures (Marco et al., 2012, 2021), yet the mass increase in tourism has resulted in a host of other anthropogenic threats such as habitat modification, light pollution (Silva et al., 2017), and beach traffic (Aguilera et al., 2019). In the Azores, Madeira, and Canary Islands, where sea turtle nesting is not known to occur, fisheries and marine litter remain the largest threats to sea turtles, in addition to climate change (Ferreira et al., 2001, 2011; Vandeperre, 2020).

The need to better understand the biological responses of sea turtles to rapid climate change (Hamann et al., 2010) warrants considerable future research efforts throughout Macaronesia so that tailored regional management plans can be established for these organisms. Recently, the Azores has adopted a monitoring program (see COSTA project; Vandeperre, 2020) which is anticipated to result in an increase of scientific research, however, to the best of our knowledge, Madeira does not yet have a dedicated and funded monitoring program in place. The scarcity of long-term monitoring in the Azores and Madeira has made it challenging to document population estimates in the surrounding waters. Without this information it is impossible to identify climate driven changes in abundance and distribution of sea turtles throughout Macaronesia as a whole. In the Azores, Madeira, and Canary Islands specifically, many biological aspects of marine turtles are still unexplored, but future research should focus on immediately pressing areas of study such as documenting mortality rates and quantifying the effect of various pressures (e.g., climate change, fisheries interactions, and marine debris). In Cabo Verde, further investigation into parasite prevalence and mediation is paramount as turtle reproduction, demography, and survival may be significantly impacted.

FINAL REMARKS

The current study provides a comprehensive description of research conducted on marine megafauna in Macaronesia to-date, highlighting the limitations of our knowledge and areas of research that urgently need to be pursued. The literature discussed in this review reflects what is available to the wider scientific community, however, we acknowledge that there is a variety of unpublished works and reports that may not have been discussed owing to their omission in the search engines used. Data availability and accessibility varies between archipelagos (Valente et al., 2019), as such the reporting bias may impact the quantification of records within this review. There is a compelling need to make unpublished work more accessible and to subject regional reports to the peer-reviewed process so that the development of conservation strategies is backed by robust research. Secondly, the absence or presence of literature within the review may have been affected by language. Although searches were conducted in English, Portuguese, and Spanish, the English language may have overrepresented the number of publications which in turn could affect the number of representative publications per archipelago (Mongeon and Paul-Hus, 2016). Inconsistent or non-inclusive language remains a major barrier for regional managers to incorporate research findings into regulations, which may hinder coordinated conservation efforts. Lastly, differences in resource allocation may also play a large role in the output of publications in Macaronesia. Although European countries may be more likely to receive research investment, the majority of research quantified in this review was conducted in the Azores, whereas the least amount of literature was available from Madeira, despite being archipelagos of the same country. This may be a result of different investments and strategy in science from the regional governments, although the results and patterns found in our analysis are more likely to be affected by specific sampling and research effort in each archipelago and the establishment of particular research groups on those archipelagos.

Within Macaronesia, conservation of marine megafaunal groups requires coordinated actions among key stakeholders (i.e., researchers, policymakers, and non-governmental organizations), and in many cases, among national archipelagos. Regional stakeholder cooperation will likely be required to obtain baseline information for many species, which is essential to understand species population trends in addition to their movement and distribution patterns. Without such information, species-specific interactions with the anthropogenic threats or potential range-shifts in response to climate change scenarios cannot be fully quantified (Correia et al., 2020). The implementation of monitoring programs within and beyond national jurisdictions have the potential to significantly contribute to the integrated management of marine megafauna throughout Macaronesia. Tourism development in particular can increase scientific output through data acquisition (e.g., whale watching, sports fishing), but also increase the social and cultural value of marine megafauna to locals (e.g., shark-based tourism can provide a shift from a fisheries-based resource to a more profitable conservation-based resource; Vianna et al., 2011; Cisneros-Montemayor et al., 2013). Future conservation initiatives may benefit to focus on citizen science and ecosystem services based approaches to increase regional scientific knowledge. As the eco-tourism sectors of Macaronesian economies grow, so will the need for marine megafauna conservation.

While our findings represent the current status of marine megafauna research, the field continues to develop. Fundamentally, population level connectivity of marine megafauna species needs to be ascertained so that, among other management strategies, effective MPAs can be implemented, yet climate driven changes in abundance and distribution must also be considered to maintain protection. To prevent regional extirpation of vulnerable species, national and regional governments, and other relevant stakeholders must come together to optimize MPA designs using systematic conservation planning to meet common conservation objectives (Alves et al., 2022a; van Zinnicq et al., 2022). For example, although Madeira has much less research relative to the other archipelagos, it has the support of multiple stakeholders and has subsequently recently implemented Europe's largest MPA, the Selvagens Nature Reserve (Alves et al., 2022b). Critical data gaps identified in this review provide a path forward to better understand the marine megafauna within the complex island system of

Macaronesia, and aid in the development of regional, national, and international conservation strategies.

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

AM: conceptualization, methodology, formal analysis, investigation, data curation, writing – original draft, review and editing, and visualization. CW: data curation, validation, investigation, resources, and writing – review and editing. FA, AD, MP, and JC-C: writing – review and editing, supervision, and funding. All authors are responsible for and agreed to the publishing of the final version of the manuscript.

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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.2022.819581/full#supplementary-material

REFERENCES

Afonso, P., Fontes, J., Giacomello, E., Magalhães, M. C., Martins, H. R., Morato, T., et al. (2020). The azores: a mid-atlantic hotspot for marine megafauna research and conservation. *Front. Mar. Sci.* 6:826. doi: 10.3389/fmars.2019.00826

Aguilera, M., Medina-Suárez, M., Pinós, J., Liria, A., López-Jurado, L. F., and Benejam, L. (2019). Assessing the effects of multiple off-road vehicle (ORVs) tyre ruts on seaward orientation of hatchling sea turtles: implications for conservation. *J. Coast. Conserv.* 23, 111–119. doi: 10.1007/s11852-018-0641-x

Alfaro, A., Rees, A. F., Frick, M., Panagopoulou, A., and Williams, K. (2008). "Synopsis of infections in sea turtles caused by virus, bacteria and parasites: an ecological review," in *Proceedings of the 27th Annual Symposium on Sea Turtle Biology and Conservation NOAA Tech Memo*, Myrtle Beach.

Alves, F., Alessandrini, A., Servidio, A., Mendonça, A. S., Hartman, K. L., Prieto, R., et al. (2019). Complex biogeographical patterns support an ecological connectivity network of a large marine predator in the north-east Atlantic. *Divers. Distrib.* 25, 269–284. doi: 10.1111/ddi.12848

Alves, F., Dinis, A., Nicolau, C., Ribeiro, C., Kaufmann, M., Fortuna, C., et al. (2015). Survival and abundance of short-finned pilot whales in the archipelago of Madeira, NE Atlantic. *Mar. Mamm. Sci.* 31, 106–121. doi: 10.1111/mms.12137

Alves, F., Ferreira, R., Fernandes, M., Halicka, Z., Dias, L., and Dinis, A. (2018). Analysis of occurrence patterns and biological factors of cetaceans based on long-term and fine-scale data from platforms of opportunity: Madeira Island as a case study. *Mar. Ecol.* 39:e12499. doi: 10.1111/maec.12499

Alves, F., Rosso, M., Li, S., and Nowacek, D. P. (2022a). A sea of possibilities for marine megafauna. *Science* 375, 391–392. doi: 10.1126/SCIENCE.ABN6022

Alves, F., Monteiro, J. G., Oliveira, P., and Canning-Clode, J. (2022b). Portugal leads with Europe's largest marine reserve. *Nature* 601, 318–318. doi: 10.1038/D41586-022-00093-8

Alves, F., Quérouil, S., Dinis, A., Nicolau, C., Ribeiro, C., Freitas, L., et al. (2013). Population structure of short-finned pilot whales in the oceanic archipelago of Madeira based on photo-identification and genetic analyses: implications for conservation. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 23, 758–776. doi: 10.1002/aqc.2332

Arranz, P., de Soto, N. A., Madsen, P. T., and Sprogis, K. R. (2021a). Whale-watch vessel noise levels with applications to whale-watching guidelines and conservation. *Mar. Policy* 134:104776. doi: 10.1016/j.marpol.2021.104776

Arranz, P., Glarou, M., and Sprogis, K. R. (2021b). Decreased resting and nursing in short - finned pilot whales when exposed to louder petrol engine noise of a hybrid whale - watch vessel. *Sci. Rep.* 11:21195. doi: 10.1038/s41598-021-00487-0

Arrizabalaga, H., Pereira, J. G., Royer, F., Galuardi, B., Goñi, N., Artetxe, I., et al. (2008). Bigeye tuna (*Thunnus obesus*) vertical movements in the Azores Islands determined with pop-up satellite archival tags. *Fish. Oceanogr.* 17, 74–83. doi: 10.1111/j.1365-2419.2008.00464.x

Barcelos, L. M. D., Michielsen, G., Sérgio, B., Oliveira, S., and Barreiros, J. P. (2021). First record of the olive ridley sea turtle, *Lepidochelys olivacea* (Eschscholtz, 1829), in the azores islands, northeastern atlantic ocean (testudines, cheloniidae). *Herpetol. Notes* 14, 371–373.

Barker, J., Bertoli, A., Clark, M., Dulvy, N., Gordon, C., Hood, A., et al. (2016). *Angelshark Action Plan for the Canary Islands*. London: Zoological Society of London.

Beerkircher, L., Arocha, F., Barse, A., Prince, E., Restrepo, V., Serafy, J., et al. (2009). Effects of species misidentification on population assessment of overfished white marlin *Tetrapturus albidus* and roundscale spearfish *T. georgii*. *Endanger. Species Res.* 9, 81–90. doi: 10.3354/esr00234

Biscoito, M., Ribeiro, C., and Freitas, M. (2018). Annotated checklist of the fishes of the archipelago of Madeira (NE Atlantic): I-Chondrichthyes. *Zootaxa* 4429, 459–494. doi: 10.11646/zootaxa.4429.3.2

Bjorndal, K. A., Bolten, A. B., and Martins, H. R. (2000). Somatic growth model of juvenile loggerhead sea turtles *Caretta caretta*: duration of pelagic stage. *Mar. Ecol. Prog. Ser.* 202, 265–272. doi: 10.3354/meps202265

Bolten, A. B., Bjorndal, K. A., Martins, H. R., Dellinger, T., Biscoito, M. J., Encalada, S. E., et al. (1998). Transatlantic developmental migrations of loggerhead sea turtles demonstrated by mtDNA sequence analysis. *Ecol. Appl.* 8, 1–7. doi: 10.2307/2641306

Bolten, A. B., and Martins, H. R. (1990). Kemp's ridley captured in the Azores. *Mar. Turt. Newsl.* 48:23.

Bolten, A. B., Martins, H. R., Bjorndal, K. A., and Gordon, J. (1993). Size distribution of pelagic-stage loggerhead sea turtles (*Caretta caretta*) in the waters around the Azores and Madeira. *Arquipélago* 11, 49–54.

Bordalo-Machado, P., and Figueiredo, I. (2009). The fishery for black scabbardfish (*Aphanopus carbo* Lowe, 1839) in the Portuguese continental slope. *Rev. Fish Biol. Fish.* 19, 49–67. doi: 10.1007/s11160-008-9089-7

Bossart, G. D. (2006). Marine mammals as sentinel species for oceans and human health. *Oceanography* 19, 134–137. doi: 10.5670/oceanog.2006.77

Braun, C. D., Gaube, P., Afonso, P., Fontes, J., Skomal, G. B., Thorrold, S. R., et al. (2019). Assimilating electronic tagging, oceanographic modelling, and fisheries data to estimate movements and connectivity of swordfish in the North Atlantic. *ICES J. Mar. Sci.* 76, 2305–2317. doi: 10.1093/icesjms/fsz106

Brito, C. (2008). Assessment of catch statistics during the land-based whaling in Portugal. *Mar. Biodivers. Rec.* 1:e92. doi: 10.1017/s175526720700930x

Brito, C. (2012). "Portuguese sealing and whaling activities as contributions to understand early Northeast Atlantic environmental history of marine mammals," in *New Approaches to the Study of Marine Mammals*, eds A. Romero and E. O. Keith (London: InTech), 207–222. doi: 10.5772/54213

Brongersma, L. D. (1972). European Atlantic turtles. *Zool. Verh.* 121, 1–318.

Brunner, F. S., and Eizaguirre, C. (2016). Can environmental change affect host/parasite-mediated speciation? *Zoology* 119, 384–394. doi: 10.1016/j.zool.2016.04.001

Bunkley-Williams, L., Williams, E. H., Horrocks, J. A., Horta, H. C., Mignucci-Giannoni, A. A., and Poponi, A. C. (2008). New leeches and diseases for the hawksbill sea turtle and the West Indies. *Comp. Parasitol.* 75, 263–270. doi: 10.1654/4252.1

Burkholder, D. A., Heithaus, M. R., Fourqurean, J. W., Wirsing, A., and Dill, L. M. (2013). Patterns of top-down control in a seagrass ecosystem: could a roving apex predator induce a behaviour-mediated trophic cascade? *J. Anim. Ecol.* 82, 1192–1202. doi: 10.1111/1365-2656.12097

Camacho, M., Boada, L. D., Orós, J., López, P., Zumbado, M., Almeida-González, M., et al. (2014). Monitoring organic and inorganic pollutants in juvenile live sea turtles: results from a study of *Chelonia mydas* and *Eretmochelys imbricata* in Cape Verde. *Sci. Total Environ.* 481, 303–310. doi: 10.1016/j.scitotenv.2014.02.051

Campos, A., Lopes, P., Fonseca, P., Figueiredo, I., Henriques, V., Gouveia, N., et al. (2019). Portuguese fisheries in seamounts of Madeira-Tore (NE Atlantic). *Mar. Policy* 99, 50–57. doi: 10.1016/j.marpol.2018.10.005

Carreras, C., Pascual, M., Tomás, J., Marco, A., Hochsheid, S., Castillo, J. J., et al. (2018). Sporadic nesting reveals long distance colonisation in the philopatric loggerhead sea turtle (*Caretta caretta*). *Sci. Rep.* 8:1435. doi: 10.1038/s41598-018-19887-w

Carrillo, M., and Alcántara, E. (2014). *Programa de Seguimiento de la Tortuga boba (Caretta caretta) Para Evaluar el Estado de Conservación de la Especie en las Islas Canarias: Informe de las Campañas de Avistamiento de 2013*. Santa Cruz, CA: Observatorio Ambiental Granadilla.

Cartagena-Matos, B., Lugué, K., Fonseca, P., Marques, T. A., Prieto, R., Alves, F., et al. (2021). Trends in cetacean research in the Eastern North Atlantic. *Mamm. Rev.* 51, 436–453. doi: 10.1111/mam.12238

Cisneros-Montemayor, A. M., Barnes-Mauthe, M., Al-Abdulrazzak, D., Navarro-Holm, E., and Sumaila, U. R. (2013). Global economic value of shark ecotourism: implications for conservation. *Oryx* 47, 381–388. doi: 10.1017/S0030605312001718

Clarke, M. R., Martins, H. R., and Pascoe, P. (1993). The diet of sperm whales (*Physeter macrocephalus* Linnaeus 1758) off the Azores. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 339, 67–82. doi: 10.1098/rstb.1993.0005

Coelho, R., Macías, D., Ortiz de Urbina, J., Martins, A., Monteiro, C., Lino, P. G., et al. (2020). Local indicators for global species: pelagic sharks in the tropical northeast Atlantic, Cabo Verde islands region. *Ecol. Indic.* 110:105942. doi: 10.1016/j.ecolind.2019.105942

Collette, B., Amorim, A. F., Boustany, A., Carpenter, K. E., de Oliveira Leite, N. Jr., Fox, W., et al. (2011). Tetrapturus georgii. *IUCN Red List Threat. Species* 2011:e.T170333A6752763.

Collette, B. B., Boustany, A., Fox, W., Graves, J., Juan Jorda, M., and Restrepo, V. (2021). Thunnus obesus. *IUCN Red List Threat. Species* 2021:e.T21859A46912402. doi: 10.2305/IUCN.UK.2021-2.RLTS.T21859A46912402.en

Correia, A. M., Gandra, M., Liberal, M., Valente, R., Gil, Á., Rosso, M., et al. (2019). A dataset of cetacean occurrences in the Eastern North Atlantic. *Sci. Data* 6:177. doi: 10.1038/s41597-019-0187-2

Correia, A. M., Gil, Á, Valente, R. F., Rosso, M., Sousa-Pinto, I., and Pierce, G. J. (2020). Distribution of cetacean species at a large scale - connecting continents with the Macaronesian archipelagos in the eastern North Atlantic. *Divers. Distrib.* 26, 1234–1247. doi: 10.1111/ddi.13127

Correia, J., Morgado, F., and Erzini, K. (2016). Elasmobranch landings in the Portuguese commercial fishery from 1986 to 2009. *Arquipélago* 33, 81–109.

Cunha, I., Freitas, L., Alves, F., Dinis, A., Ribeiro, C., Nicolau, C., et al. (2017). Marine traffic and potential impacts towards cetaceans within the Madeira EEZ. *J. Cetacean Res. Manag.* 16, 17–28.

Das, D., and Afonso, P. (2017). Review of the diversity, ecology, and conservation of elasmobranchs in the Azores region, Mid-North Atlantic. *Front. Mar. Sci.* 4:354. doi: 10.3389/fmars.2017.00354

de Larrinoa, P. F., Baker, J. D., Cedenilla, M. A., Harting, A. L., Haye, M. O., Muñoz, M., et al. (2021). Age-specific survival and reproductive rates of Mediterranean monk seals at the Cabo Blanco Peninsula, West Africa. *Endanger. Species Res.* 45, 315–329. doi: 10.3354/ESR01134

Dinis, A., Alves, F., Nicolau, C., Ribeiro, C., Kaufmann, M., Cañadas, A., et al. (2016). Bottlenose dolphin *Tursiops truncatus* group dynamics, site fidelity, residency and movement patterns in the Madeira Archipelago (North-East Atlantic). *Afr. J. Mar. Sci.* 38, 151–160. doi: 10.2989/1814232X.2016.1167780

Dinis, A., Molina, C., Tobeña, M., Sambolino, A., Hartman, K., Fernandez, M., et al. (2021). Large-scale movements of common bottlenose dolphins in the Atlantic: dolphins with an international courtyard. *PeerJ* 9:e11069. doi: 10.7717/peerj.11069

Doyle, T. K., Houghton, J. D. R., O'Súilleabháin, P. F., Hobson, V. J., Marnell, F., Davenport, J., et al. (2008). Leatherback turtles satellite-tagged in European waters. *Endanger. Species Res.* 4, 23–31. doi: 10.3354/esr00076

Dulvy, N. K., Pacoureau, N., Rigby, C. L., Pollom, R. A., Jabado, R. W., Ebert, D. A., et al. (2021). Overfishing drives over one-third of all sharks and rays toward a global extinction crisis. *Curr. Biol.* 31, 4773–4787.e8. doi: 10.1016/j.cub.2021.08.062

EASME (2017). *Realising the Potential of the Outermost Regions for Sustainable Blue Growth*. Available online at: https://ec.europa.eu/regional_policy/sources/policy/themes/outermost-regions/pdf/rup_2017/rup_sust_blue_growth_exec_en.pdf (accessed July 2020).

European Mammal Assessment Team (2007). Monachus Monachus. *IUCN Red List Threat. Species* 2007:e.T13653A4305994.

Fais, A., Lewis, T. P., Zitterbart, D. P., Álvarez, O., Tejedor, A., and AguilarSoto, N. (2016). Abundance and distribution of sperm whales in the canary islands: can sperm whales in the archipelago sustain the current level of ship-strike mortalities? *PLoS One* 11:e0150660. doi: 10.1371/journal.pone.0150660

Farrell, J. A., Yetsko, K., Whitmore, L., Whilde, J., Eastman, C. B., Ramia, D. R., et al. (2021). Environmental DNA monitoring of oncogenic viral shedding and genomic profiling of sea turtle fibropapillomatosis reveals unusual viral dynamics. *Commun. Biol.* 4:565. doi: 10.1038/s42003-021-02085-2

Fernández, A., Sierra, E., Díaz-Delgado, J., Sacchini, S., Sánchez-Paz, Y., Suárez-Santana, C., et al. (2017). Deadly acute decompression sickness in risso's dolphins. *Sci. Rep.* 7:13621. doi: 10.1038/s41598-017-14038-z

Fernández-Palacios, J. M., Kreft, H., Irl, S. D. H., Norder, S., Ah-Peng, C., Borges, P. A. V., et al. (2021). Scientists' warning – the outstanding biodiversity of islands is in peril. *Glob. Ecol. Conserv.* 31:e01847. doi: 10.1016/j.gecco.2021.e01847

Ferreira, R., Dinis, A., Badenas, A., Sambolino, A., Marrero-Pérez, J., Crespo, A., et al. (2021). Bryde's whales in the North-East Atlantic: new insights on site fidelity and connectivity between oceanic archipelagos. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 31, 2938–2950. doi: 10.1002/aqc.3665

Ferreira, R., Martins, H., Silva, A., and Bolten, A. (2001). Impact of swordfish fisheries on sea turtles in the Azores. *Arquipelago* 18A, 75–79.

Ferreira, R. L., Martins, H. R., Bolten, A. B., Santos, M. A., and Erzini, K. (2011). Influence of environmental and fishery parameters on loggerhead sea turtle by-catch in the longline fishery in the Azores archipelago and implications for conservation. *J. Mar. Biol. Assoc. U.K.* 91, 1697–1705. doi: 10.1017/S0025315410000846

Floeter, S. R., Rocha, L. A., Robertson, D. R., Joyeux, J. C., Smith-Vaniz, W. F., Wirtz, P., et al. (2008). Atlantic reef fish biogeography and evolution. *J. Biogeogr.* 35, 22–47. doi: 10.1111/j.1365-2699.2007.01790.x

Freitas, C., Caldeira, R., and Dellinger, T. (2019a). Surface behavior of pelagic juvenile loggerhead sea turtles in the eastern North Atlantic. *J. Exp. Mar. Biol. Ecol.* 510, 73–80. doi: 10.1016/j.jembe.2018.10.006

Freitas, R., Mendes, T. C., Almeida, C., Melo, T., Villaça, R. C., Noguchi, R., et al. (2019b). Reef fish and benthic community structures of the Santa Luzia Marine Reserve in the Cabo Verde islands, eastern central Atlantic Ocean. *Afr. J. Mar. Sci.* 41, 177–190. doi: 10.2989/1814232X.2019.1616613

Freitas, R., Romeiras, M., Silva, L., Cordeiro, R., Madeira, P., González, J. A., et al. (2019c). Restructuring of the 'Macaronesia' biogeographic unit: a marine multi-taxon biogeographical approach. *Sci. Rep.* 9:15792. doi: 10.1038/s41598-019-51786-6

Freitas, C., Caldeira, R., Reis, J., and Dellinger, T. (2018). Foraging behavior of juvenile loggerhead sea turtles in the open ocean: from lévy exploration to area-restricted search. *Mar. Ecol. Prog. Ser.* 595, 203–215. doi: 10.3354/meps12581

Freitas, M., and Biscoito, M. (2018). "Madeira Island (NE Atlantic), a nursery area for smooth hammerhead shark, *Sphyrna zygaena* (Linnaeus, 1758)?," in *Proceedings of the 22nd Annual European Elasmobranch Association Meeting*, Peniche. doi: 10.13140/RG.2.2.36767.41129

Freitas, M., Vieira, S., Costa, L., Delgado, J., Biscoito, M., and González, J. A. (2017). First records of *Chimaera opalescens* (Holocephali: Chimaeriformes: Chimaeridae) from Madeira and north-west African coast. *Acta Ichthyol. Piscat.* 47, 81–84. doi: 10.3750/AIEP/02114

Fretey, J. (2001). *Biogeography and Conservation of Marine Turtles of the Atlantic Coast of Africa. Biogéographie et Conservation des Tortues Marines de la Côte Atlantique de l'Afrique*. CMS Technical Series Publication 6. Bonn: UNEP, 429.

Gonzáles-Mantilla, P. G., Gallagher, A. J., León, C. J., and Vianna, G. M. S. (2021). Challenges and conservation potential of shark-diving tourism in the Macaronesian archipelagos. *Mar. Policy* 131:104632. doi: 10.1016/j.marpol.2021.104632

González, J. A., Monteiro, C. A., Correia, S., Lopes, E., Almeida, N., Martins, A., et al. (2020). Current and emerging small-scale fisheries and target species in Cabo Verde, with recommendations for pilot actions favouring sustainable development. *Cybium Int. J. Ichthyol.* 44, 355–371. doi: 10.26028/cybium/2020-444-006

González, L. M. (2015). Prehistoric and historic distributions of the critically endangered Mediterranean monk seal (*Monachus monachus*) in the eastern Atlantic. *Mar. Mamm. Sci.* 31, 1168–1192. doi: 10.1111/mms.12228

Gonzalez-Paredes, D., Fernández-Maldonado, C., Grondona, M., Martínez-Valverde, R., and Marco, A. (2021). The westernmost nest of a loggerhead sea turtle, *Caretta caretta* (Linnaeus 1758), registered in the Mediterranean Basin. *Herpetol. Notes* 14, 907–912.

Greenblatt, R. J., Quackenbush, S. L., Casey, R. N., Rovnak, J., Balazs, G. H., Work, T. M., et al. (2005). Genomic variation of the fibropapilloma-associated marine turtle herpesvirus across seven geographic areas and three host species. *J. Virol.* 79, 1125–1132. doi: 10.1128/jvi.79.2.1125-1132.2005

Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., et al. (2008). A global map of human impact on marine ecosystems. *Science* 319, 948–952. doi: 10.1126/science.1149345

Hamann, M., Godfrey, M. H., Seminoff, J. A., Arthur, K., Barata, P. C. R., Bjorndal, K. A., et al. (2010). Global research priorities for sea turtles: informing management and conservation in the 21st century. *Endanger. Species Res.* 11, 245–269. doi: 10.3354/esr00279

Hareide, N., Carlson, J., Clarke, M., Clarke, S., Ellis, J., Fordham, S., et al. (2007). *European Shark Fisheries: a Preliminary Investigation into Fisheries, Conversion Factors, Trade Products, Markets and Management Measures*. Galway: European Elasmobranch Association, 71.

Hazevoet, C. J., Monteiro, V., López, P., Varo-cruz, N., Torda, G., Berrow, S., et al. (2010). Recent data on whales and dolphins (Mammalia : Cetacea) from the Cape Verde Islands, including records of four taxa new to the archipelago. *Zool. Caboverdiana* 1, 75–99.

He, F., Zarfl, C., Bremerich, V., Henshaw, A., Darwall, W., Tockner, K., et al. (2017). Disappearing giants: a review of threats to freshwater megafauna. *WIREs Water* 4:e1208. doi: 10.1002/wat2.1208

Heithaus, M. R., Frid, A., Wirsing, A. J., and Worm, B. (2008). Predicting ecological consequences of marine top predator declines. *Trends Ecol. Evol.* 23, 202–210. doi: 10.1016/j.tree.2008.01.003

Hernandez, E. (1986). "Historical data of the mediterranean monk seal in the canary islands and notes for its future reintroduction," in *Proceedings of the 1st Expert Meeting on the Mediterranean Monk Seal*, (Strasbourg: Convention on the Conservation of European Wildlife and Natural Habitats), 1–11.

Holley, J. F., and Marchal, P. (2004). Fishing strategy development under changing conditions: examples from the French offshore fleet fishing in the North Atlantic. *ICES J. Mar. Sci.* 61, 1410–1431. doi: 10.1016/j.icesjms.2004.08.010

Jiménez-Alvarado, D., Meyers, E. K. M., Caro, M. B., Sealey, M. J., and Barker, J. (2020). Investigation of juvenile angelshark (*Squatina squatina*) habitat in the Canary Islands with recommended measures for protection and management. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 30, 2019–2025. doi: 10.1002/aqc.3337

Jones, K., Ariel, E., Burgess, G., and Read, M. (2016). A review of fibropapillomatosis in Green turtles (*Chelonia mydas*). *Vet. J.* 212, 48–57. doi: 10.1016/j.tvjl.2015.10.041

Karamanlidis, A. A., Pires, R., Neves, H. C., and Santos, C. (2005). Habitat of the endangered Mediterranean monk seal (*Monachus monachus*) at São Lourenço-Madeira. *Aquat. Mamm.* 29, 400–403. doi: 10.1578/01675420360736596

Kiszka, J. J., Heithaus, M. R., and Wirsing, A. J. (2015). Behavioural drivers of the ecological roles and importance of marine mammals. *Mar. Ecol. Prog. Ser.* 523, 267–281. doi: 10.3354/meps11180

Kitchens, L. L., Rooker, J. R., Reynal, L., Falterman, B. J., Saillant, E., and Murua, H. (2018). Discriminating among yellowfin tuna *Thunnus albacares* nursery areas in the Atlantic Ocean using otolith chemistry. *Mar. Ecol. Prog. Ser.* 603, 201–213. doi: 10.3354/meps12676

Kukuev, E. I., and Pavlov, V. P. (2008). The first case of mass catch of a rare frill shark *Chlamydoselachus anguineus* over a seamount of the Mid-Atlantic Ridge. *J. Ichthyol.* 48, 676–678. doi: 10.1134/S0032945208080158

Laloë, J. O., Cozens, J., Renom, B., Taxonera, A., and Hays, G. C. (2014). Effects of rising temperature on the viability of an important sea turtle rookery. *Nat. Clim. Change* 4, 513–518. doi: 10.1038/nclimate2236

Lloris, D., Rucabado, J., and Figueroa, H. (1991). Biogeography of the Macaronesian ichthyofauna (the Azores, Madeira, the Canary islands, Cape Verde and the african enclave). *Bol. Mus. Munic. Funchal* 43, 191–241.

Lockley, E. C., Fouda, L., Correia, S. M., Taxonera, A., Nash, L. N., Fairweather, K., et al. (2020). Long-term survey of sea turtles (*Caretta caretta*) reveals correlations between parasite infection, feeding ecology, reproductive success and population dynamics. *Sci. Rep.* 10:18569. doi: 10.1038/s41598-020-75498-4

Lohrer, A. M., Thrush, S. F., and Gibbs, M. M. (2004). Bioturbators enhance ecosystem function through complex biogeochemical interactions. *Nature* 431, 1092–1095. doi: 10.1038/nature03042

Lopes, K., Passos, L., Rodrigues, J. G., Koenen, F., Stiebens, V., Székely, T., et al. (2016). Sea turtle, shark, and dolphin bycatch rates by artisanal and semi-industrial fishers in maio Island, Cape Verde. *Chelonian Conserv. Biol.* 15, 279–288. doi: 10.2744/CB-1213.1

Machado, A. J. M. (1979). *Os Lobos Marinhos (Género Monachus, Fleming 1822)*. Cascais: Museu do Mar, Unidade de Mamalogia.

Machete, M., Morato, T., and Menezes, G. (2011). Experimental fisheries for black scabbardfish (*Aphanopus carbo*) in the Azores, Northeast Atlantic. *ICES J. Mar. Sci.* 68, 302–308. doi: 10.1093/icesjms/fsq087

Marco, A., Abella, E., Liria-Loza, A., Martins, S., López, O., Jiménez-Bordón, S., et al. (2012). Abundance and exploitation of loggerhead turtles nesting in Boa Vista island, Cape Verde: the only substantial rookery in the eastern Atlantic. *Anim. Conserv.* 15, 351–360. doi: 10.1111/j.1469-1795.2012.00547.x

Marco, A., Abella-Pérez, E., Monzón-argüello, C., Martins, S., Araújo, S., and López Jurado, L. F. (2011). The international importance of the archipelago of Cape Verde for marine turtles, in particular the loggerhead turtle *Caretta caretta*. *Zool. Caboverdiana* 2, 1–11.

Marco, A., Martins, S., Martín-Rábano, A., Lopes, S., Clarke, L. J., and Abella, E. (2021). Risk assessment of wildlife-watching tourism in an important endangered loggerhead turtle rookery. *Endanger. Species Res.* 45, 195–207. doi: 10.3354/ESR01130

Martínez-Escauriaza, R., Hermida, M., Villasante, S., Gouveia, L., Gouveia, N., and Pita, P. (2020). Importance of recreational shore angling in the archipelago of madeira, Portugal (Northeast Atlantic). *Sci. Mar.* 84, 331–341. doi: 10.3989/scimar.05046.30A

Martinez-Escauriaza, R., Pita, P., de Gouveia, M. L. F., Gouveia, N. M. A., Teixeira, E., de Freitas, M., et al. (2021). Analysis of big game fishing catches of blue marlin (*Makaira nigricans*) in the madeira archipelago (Eastern Atlantic) and factors that affect its presence. *Sustainability* 13:8975. doi: 10.3390/su13168975

Martins, S., Silva, E., Abella, E., de Santos Loureiro, N., and Marco, A. (2020). Warmer incubation temperature influences sea turtle survival and nullifies the benefit of a female-biased sex ratio. *Clim. Change* 163, 689–704. doi: 10.1007/s10584-020-02933-w

Mazzoldi, C., Bearzi, G., Brito, C., Carvalho, I., Desiderà, E., Endrizzi, L., et al. (2019). From sea monsters to charismatic megafauna: changes in perception and use of large marine animals. *PLoS One* 14:e0226810. doi: 10.1371/journal.pone.0226810

McAlpine, D. F. (2018). "Pygmy and dwarf sperm whales: *Kogia breviceps* and *K. sima*," in *Encyclopedia of Marine Mammals*, eds H. Thewissen, B. Würsig, and W. F. Perrin (Cambridge, MA: Academic Press), 786–788. doi: 10.1016/b978-0-12-804327-1.00209-0

McCauley, D. J., Pinsky, M. L., Palumbi, S. R., Estes, J. A., Joyce, F. H., and Warner, R. R. (2015). Marine defaunation: animal loss in the global ocean. *Science* 347:1255641. doi: 10.1126/science.1255641

Meyers, E. K. M., Tuya, F., Barker, J., Jiménez Alvarado, D., Castro-Hernández, J. J., Haroun, R., et al. (2017). Population structure, distribution and habitat use of the Critically Endangered Angelshark, *Squatina squatina*, in the Canary Islands. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 27, 1133–1144. doi: 10.1002/aqc.2769

Moher, D., Shamseer, L., Clarke, M., Ghersi, D., Liberati, A., Petticrew, M., et al. (2016). Preferred reporting items for systematic review and meta-analysis protocols (PRISMA-P) 2015 statement. *Syst. Rev.* 4:1. doi: 10.1186/2046-4053-4-1

Moleón, M., Sánchez-Zapata, J. A., Donázar, J. A., Revilla, E., Martín-López, B., Gutiérrez-Cánovas, C., et al. (2020). Rethinking megafauna. *Proc. R. Soc. B Biol. Sci.* 287:20192643. doi: 10.1098/rspb.2019.2643

Mongeon, P., and Paul-Hus, A. (2016). The journal coverage of web of science and scopus: a comparative analysis. *Scientometrics* 106, 213–228. doi: 10.1007/s11192-015-1765-5

Monod, T. (1948). *Le Phoque Moine Dans l'Atlantique*, Vol. 34, ed. A. Nobre (Porto: Imprensa Portuguesa), 7–19.

Monzón-Argüello, C., López-Jurado, L. F., Rico, C., Marco, A., López, P., Hays, G. C., et al. (2010a). Evidence from genetic and Lagrangian drifter data for transatlantic transport of small juvenile green turtles. *J. Biogeogr.* 37, 1752–1766. doi: 10.1111/j.1365-2699.2010.02326.x

Monzón-Argüello, C., Rico, C., Marco, A., López, P., and López-Jurado, L. F. (2010b). Genetic characterization of eastern Atlantic hawksbill turtles at a foraging group indicates major undiscovered nesting populations in the region. *J. Exp. Mar. Biol. Ecol.* 387, 9–14. doi: 10.1016/j.jembe.2010.03.004

Monzón-Argüello, C., Rico, C., Naro-Maciel, E., Varo-Cruz, N., López, P., Marco, A., et al. (2010c). Population structure and conservation implications for the loggerhead sea turtle of the Cape Verde Islands. *Conserv. Genet.* 11, 1871–1884. doi: 10.1007/s10592-010-0079-7

Monzón-Argüello, C., Rico, C., Carreras, C., Calabuig, P., Marco, A., and López-Jurado, L. F. (2009). Variation in spatial distribution of juvenile loggerhead turtles in the eastern Atlantic and western Mediterranean Sea. *J. Exp. Mar. Biol. Ecol.* 373, 79–86. doi: 10.1016/j.jembe.2009.03.007

Morato, T. (2012). Description of environmental issues, fish stocks and fisheries in the EEZs around the Azores and Madeira. *Eur. Commun.* 63, 3–54. Available online at: https://stecf.jrc.ec.europa.eu/documents/43805/465474/Item+6.2+Report+Morato_Azores_Madeira.pdf

Morey, G., Barker, J., Hood, A., Gordon, C., Bartolí, A., Meyers, E. K. M., et al. (2019). Squatina squatina. *IUCN Red List Threat. Species* 2019:e.T39332A117498371. doi: 10.2305/IUCN.UK.2019-1.RLTS.T39332A117498371.en

Natale, A. D., Macias, D., and Cort, J. L. (2020). Atlantic bluefin tuna fisheries: temporal changes in the exploitation pattern, feasibility of sampling, factors that can influence our ability to understand spawning structure and dynamics. *Collect. Vol. Sci. Pap. ICCAT* 76, 354–388.

O'Connor, S., Campbell, R., Cortez, H., and Knowles, T. (2009). *Whale Watching Worldwide: Tourism Numbers, Expenditures and Expanding Economic Benefits; a Special Report from the International Fund for Animal Welfare*. Yarmouth MA: International Fund for Animal Welfare.

Orós, J., Calabuig, P., and Déniz, S. (2004). Digestive pathology of sea turtles stranded in the Canary Islands between 1993 and 2001. *Vet. Rec.* 155, 169–174. doi: 10.1136/vr.155.6.169

Orós, J., Monagas, P., Calabuig, P., Luzardo, O. P., and Camacho, M. (2013). Pansteatitis associated with high levels of polychlorinated biphenyls in a wild loggerhead sea turtle *Caretta caretta*. *Dis. Aquat. Organ.* 102, 237–242. doi: 10.3354/dao02550

Pajuelo, J. G., González, J. A., and Santana, J. I. (2010). Bycatch and incidental catch of the black scabbardfish (*Aphanopus* spp.) fishery off the Canary Islands. *Fish. Res.* 106, 448–453. doi: 10.1016/j.fishres.2010.09.019

Pimiento, C., Leprieur, F., Silvestro, D., Lefcheck, J. S., Albouy, C., Rasher, D. B., et al. (2020). Functional diversity of marine megafauna in the Anthropocene. *Sci. Adv.* 6:eaay7650. doi: 10.1126/sciadv.aay7650

Pires, R., Neves, H. C., and Karamanlidis, A. A. (2008). The critically endangered mediterranean monk seal *Monachus monachus* in the archipelago of Madeira: priorities for conservation. *Oryx* 42, 278–285. doi: 10.1017/S0030605308006704

R Core Team (2020). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Ramos, H., Silva, E., and Gonçalves, L. (2013). *Reduction of Deep-Sea Sharks' by-Catches in the Portuguese Long-Line Black Scabbard Fishery*. Final Report to the European Commission MARE/2011/06 (SI2.602201). Horta: seaExpert, Lda.

Raposo, C., Patrício, A. R., Catry, P., Dellinger, T., and Granadeiro, J. P. (2019). Evidence for trophic differences between live and bycatch oceanic juvenile loggerhead sea turtles. *Mar. Biol.* 166:29. doi: 10.1007/s00227-019-3466-8

Ritter, F., de Soto, N. A., and Martín, V. (2019). "Towards ship strike mitigation in the canary Islands," in *Proceedings of the Annual Scientific Committee Meeting Held in Nairobi in 2019* (Cambridge: International Whaling Commission).

Ritter, F., and Panigada, S. (2018). Collisions of vessels with cetaceans- the underestimated threat. *World Seas Environ. Eval.* III, 531–547. doi: 10.1016/B978-0-12-805052-1.00026-7

Roman, J., Estes, J. A., Morissette, L., Smith, C., Costa, D., McCarthy, J., et al. (2014). Whales as marine ecosystem engineers. *Front. Ecol. Environ.* 12, 377–385. doi: 10.1890/130220

Romero, J., Catry, P., Hermida, M., Neves, V., Cavaleiro, B., Gouveia, L., et al. (2021). Tunas off northwest Africa: the epipelagic diet of the bigeye and Skipjack tunas. *Fish. Res.* 238:105914. doi: 10.1016/j.fishres.2021.105914

Sambolino, A., Alves, F., Fernandez, M., Krakauer, A. B., Ferreira, R., and Dinis, A. (2022a). Spatial and temporal characterization of the exposure of island-associated cetacean populations to whale-watching in Madeira Island (NE Atlantic). *Reg. Stud. Mar. Sci.* 49:102084. doi: 10.1016/j.rsma.2021.102084

Sambolino, A., Ortega-Zamora, C., González-Sálamo, J., Dinis, A., Cordeiro, N., Canning-Clode, J., et al. (2022b). Determination of phthalic acid esters and di(2-ethylhexyl) adipate in fish and squid using the ammonium formate version of the QuEChERS method combined with gas chromatography mass spectrometry. *Food Chem.* 380:132174. doi: 10.1016/J.FOODCHEM.2022.132174

Santidrián Tomillo, P., Oro, D., Paladino, F. V., Piedra, R., Sieg, A. E., and Spotila, J. R. (2014). High beach temperatures increased female-biased primary sex ratios but reduced output of female hatchlings in the leatherback turtle. *Biol. Conserv.* 176, 71–79. doi: 10.1016/j.biocon.2014.05.011

Santos, M. A., Martins, H. R., and Santos, R. S. (2010). "Reptilia," in *A List of the Terrestrial and Marine Biota From the Azores*, eds P. A. V. Borges, A. Costa, R. Cunha, R. Gabriel, V. Gonçalves, and A. F. Martins (Cascais: Principia Editora), 344.

Santos, R. S., Hawkins, S., Monteiro, L. R., Alves, M., and Isidro, E. J. (1995). Marine research, resources and conservation in the Azores. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 5, 311–354. doi: 10.1002/aqc.3270050406

Sarmiento-Ramírez, J. M., Abella, E., Martín, M. P., Tellería, M. T., López-Jurado, L. F., Marco, A., et al. (2010). *Fusarium solani* is responsible for mass mortalities in nests of loggerhead sea turtle, *Caretta caretta*, in Boavista, Cape Verde. *FEMS Microbiol. Lett.* 312, 192–200. doi: 10.1111/j.1574-6968.2010.02116.x

Schoeman, R. P., Patterson-Abrolat, C., and Plön, S. (2020). A global review of vessel collisions with marine animals. *Front. Mar. Sci.* 7:292. doi: 10.3389/fmars.2020.00292

Sequeira, A. M. M., Hays, G. C., Sims, D. W., Eguíluz, V. M., Rodríguez, J. P., Heupel, M. R., et al. (2019). Overhauling ocean spatial planning to improve marine megafauna conservation. *Front. Mar. Sci.* 6:639. doi: 10.3389/fmars.2019.00639

Servidio, A., Pérez-Gil, E., Pérez-Gil, M., Cañadas, A., Hammond, P. S., and Martín, V. (2019). Site fidelity and movement patterns of short-finned pilot whales within the Canary Islands: evidence for resident and transient populations. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 29, 227–241. doi: 10.1002/aqc.3135

Silva, E., Marco, A., da Graça, J., Pérez, H., Abella, E., Patino-Martinez, J., et al. (2017). Light pollution affects nesting behavior of loggerhead turtles and predation risk of nests and hatchlings. *J. Photochem. Photobiol. B Biol.* 173, 240–249. doi: 10.1016/j.jphotobiol.2017.06.006

Silva, M. A., Brito, C., Santos, S. V., and Barreiros, J. P. (2009). Historic and recent occurrences of pinnipeds in the Archipelago of the Azores. *Mammalia* 73, 60–62. doi: 10.1515/MAMM.2009.008

Sousa, A., Alves, F., Arranz, P., Dinis, A., Fernandez, M., González García, L., et al. (2021). Climate change vulnerability of cetaceans in Macaronesia: insights from a trait-based assessment. *Sci. Total Environ.* 795:148652. doi: 10.1016/j.scitotenv.2021.148652

Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdaña, Z. A., Finlayson, M., et al. (2007). Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *Bioscience* 57, 573–583. doi: 10.1641/B570707

Stefanni, S., Catarino, D., Ribeiro, P. A., Freitas, M., Menezes, G. M., Neat, F., et al. (2021). Molecular systematics of the long-snouted deep water dogfish (Centrophoridae, Deania) with implications for identification, taxonomy, and conservation. *Front. Mar. Sci.* 7:588192. doi: 10.3389/fmars.2020.588192

Steiner, L. (1995). Rough-toothed dolphin, *Steno bredanensis*: a new species record for the Azores, with some notes on behaviour. Arquipelago. *Life Mar. Sci.* 13A, 125–127.

Stiebens, V. A., Merino, S. E., Roder, C., Chain, F. J. J., Lee, P. L. M., and Eizaguirre, C. (2013). Living on the edge: how philopatry maintains adaptive potential. *Proc. R. Soc. B Biol. Sci.* 280:20130305. doi: 10.1098/rspb.2013.0305

Temple, A. J., Kiszka, J. J., Stead, S. M., Wambiji, N., Brito, A., Poonian, C. N. S., et al. (2018). Marine megafauna interactions with small-scale fisheries in the southwestern Indian Ocean: a review of status and challenges for research and management. *Rev. Fish Biol. Fish.* 28, 89–115. doi: 10.1007/s11160-017-9494-x

Torres, P., Bolhão, N., Tristão da Cunha, R., Vieira, J., and Rodrigues, A. (2017). Dead or alive: the growing importance of shark diving in the Mid-Atlantic region. *J. Nat. Conserv.* 36, 20–28. doi: 10.1016/j.jnc.2017.01.005

Tuya, F., Aguilar, R., Espino, F., Bosch, N. E., Meyers, E. K. M., Jiménez-Alvarado, D., et al. (2021). Differences in the occurrence and abundance of batoids across an oceanic archipelago using complementary data sources: implications for conservation. *Ecol. Evol.* 11, 16704–16715. doi: 10.1002/ece3.8290

Valente, A. L., Delgado, C., Moreira, C., Ferreira, S., Dellinger, T., Pinheiro De Carvalho, M. A. A., et al. (2009). Helminth component community of the loggerhead sea turtle, caretta caretta, from madeira archipelago, Portugal. *J. Parasitol.* 95, 249–252. doi: 10.1645/GE-1519.1

Valente, R., Correia, A. M., Gil, Á, González García, L., and Sousa-Pinto, I. (2019). Baleen whales in Macaronesia: occurrence patterns revealed through a bibliographic review. *Mamm. Rev.* 49, 129–151. doi: 10.1111/mam.12148

van Zinnicq, M. P. M., Guttridge, T. L., Smukall, M. J., Adams, V. M., Bond, M. E., Burke, P. J., et al. (2022). Using movement models and systematic conservation planning to inform marine protected area design for a multi-species predator community. *Biol. Conserv.* 266:109469. doi: 10.1016/J.BIOCON.2022.109469

Vandeperre, F. (2020). *COSTA Project-COnsolidating Sea Turtle Conservation in the Azores*. Horta: University of the Azores.

Vandeperre, F., Aires-da-Silva, A., Lennert-Cody, C., Serrão Santos, R., and Afonso, P. (2016). Essential pelagic habitat of juvenile blue shark (*Prionace glauca*) inferred from telemetry data. *Limnol. Oceanogr.* 61, 1605–1625. doi: 10.1002/lno.10321

Vandeperre, F., Aires-da-Silva, A., Santos, M., Ferreira, R., Bolten, A. B., Serrao Santos, R., et al. (2014). Demography and ecology of blue shark (*Prionace glauca*) in the central North Atlantic. *Fish. Res.* 153, 89–102. doi: 10.1016/j.fishres.2014.01.006

Veiga, N., Moura, T., and Figueiredo, I. (2013). Spatial overlap between the leafscale gulper shark and the black scabbardfish off Portugal. *Aquat. Living Resour.* 26, 343–353. doi: 10.1051/alr/2013070

Vianna, G., Meeuwig, J. J., and Pannell, D. J. (2011). *The Socio-Economic Value of the Shark-Diving Industry in Fiji*. Perth: University of Western Australia.

Visser, F., Hartman, K. L., Rood, E. J. J., Hendriks, A. J. E., Zult, D. B., Wolff, W. J., et al. (2011). Risso's dolphins alter daily resting pattern in response to whale watching at the Azores. *Mar. Mamm. Sci.* 27, 366–381. doi: 10.1111/j.1748-7692.2010.00398.x

Wenzel, F. W., Broms, F., López-Suárez, P., Lopes, K., Veiga, N., Yeoman, K., et al. (2020). Humpback whales (*Megaptera novaeangliae*) in the cape verde islands: migratory patterns, resightings, and abundance. *Aquat. Mamm.* 46, 21–31. doi: 10.1578/AM.46.1.2020.21

Wirtz, P., Brito, A., Falcón, J. M., Freitas, R., Fricke, R., Monteiro, V., et al. (2013). The coastal fishes of the Cape Verde Islands - New records and an annotated check-list: (Pisces). *Spixiana* 36, 113–142.

Wirtz, P., Fricke, R., and Biscoito, M. J. (2008). The coastal fishes of Madeira Island - New records and an annotated check-list. *Zootaxa* 1715, 1–26. doi: 10.11646/zootaxa.1715.1.1

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Tracing Seal Predation Back to the Source Colony of Their Penguin Prey: A Trace Element and Stable Isotope Analysis

Sarah-Lena Reinhold[1,2], Simon D. Goldsworthy[1,2], John P.Y. Arnould[3], Bronwyn M. Gillanders[1], Sean D. Connell[1] and Rebecca R. McIntosh[4]*

[1] Southern Seas Ecology Laboratories, University of Adelaide, School of Biological Sciences, Adelaide, SA, Australia, [2] South Australian Research and Development Institute (SARDI), Aquatic Sciences, West Beach, SA, Australia, [3] School of Life and Environmental Sciences, Deakin University, Burwood, VIC, Australia, [4] Conservation Department, Phillip Island Nature Parks, Cowes, VIC, Australia

Edited by:
Patrick Jodice,
United States Geological Survey (USGS), United States

Reviewed by:
Luis Cardona,
University of Barcelona, Spain
Andrea Walters,
University of Tasmania, Australia

***Correspondence:**
Sarah-Lena Reinhold
sarah-lena.reinhold@adelaide.edu.au

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Marine predators recovering from historic, commercial, over-harvesting can create conservation challenges when they prey on vulnerable species. Pinniped predation of seabirds presents one such challenge and identifying the source colonies experiencing seal predation are needed to inform conservation management and decision planning. Here, we present a novel application of stable isotope and trace element techniques to identify the source colony of little penguins (*Eudyptula minor*) predated by long-nosed fur seals (*Arctocephalus forsteri*). We created baseline biochemical 'feather-prints' from feathers for six major breeding colonies across south-east Australia to compare with feathers from predated penguins recovered from seal scats. Feeding trials of captive seals confirmed that digestion of penguin feathers did not compromise stable isotope (δ^{13}C and δ^{15}N) or trace element (Al, Ti, Sr and Mg) signatures. The resulting biochemical 'feather-prints' were found to be robust in being correctly classified to local sites (78%) and broader regions (85%). The distinguishing 'feather-prints' appeared to be driven by industrial inputs from land, colony-specific foraging patterns and potentially proximity to oceanographic systems (i.e. upwelling). Here, we show that 46-70% of predated feathers were assigned to 'local' penguin colonies. We consider that the regional penguin abundances and the proximity of their colonies to seal sites, as well as demographic-specific foraging patterns may shape their contribution to seal diet at local, regional and inter-regional scales. This diagnostic tool is powerful, having broad applications identifying seabird colonies at greatest risk to pinniped predation and informing targeted, site-specific, conservation effort.

Keywords: wildlife conflict management, predator-prey interaction, feathers, stable isotope analysis, trace element analysis, little penguin *Eudyptula minor*, long-nosed fur seal, *Arctocephalus forsteri*

INTRODUCTION

Many pinniped populations are undergoing sustained growth after being heavily depleted by commercial harvest between the late 1800s and early 1900s (Ling, 1999; Magera et al., 2013; Roman et al., 2015; Goldsworthy et al., 2019b). Whilst the resurgence of these top-predators represent significant conservation outcomes and are to be celebrated, they come with new challenges in understanding the importance of healthy predator populations in restoring ecosystem function and their top-down effects on their prey, including seabirds (Marshall et al., 2016). The effect of higher trophic predators (such as pinnipeds and other marine mammals) on the behaviour, distribution or abundance of their prey is also influenced by how vulnerable the prey species are to other natural or anthropogenic threats (Hunter and Price, 1992; Matson and Hunter, 1992; Hunt Jr et al., 2002). Seabirds are considered the most threatened group of birds in the world, experiencing natural and anthropogenic stressors in both their terrestrial and marine environments (Croxall et al., 2012; Dias et al., 2019) with populations globally declining by >70% since 1950 (Paleczny et al., 2015). Penguins (family Spheniscidae) provide a prime example of physiologically unique (flightless) seabirds vulnerable to both terrestrial and marine predation (Xavier and Trathan, 2020), with 10 of the 18 recognized penguin species listed as either vulnerable or endangered on the *ICUN Red List 2021*. At the lowest end of the penguin size range, little penguins (*Eudyptula minor*), averaging 30 cm in length and 1 kg in body mass, have a slower swimming speed than other penguin species (Bethge et al., 1997), potentially increasing their vulnerability to seal predation. Little penguins also share a sympatric breeding distribution with the long-nosed fur seal (*Arctocephalus forsteri*); co-occurring on offshore islands from the southwest coast of Western Australia, across the southern coast (including Tasmania) and up the eastern coast of mainland Australia (as far north as South Solitary Island), and on to New Zealand and the Chatham Islands (Marchant and Higgins, 1990) where penguins also breed.

Recent population declines in little penguins (hereafter penguin), a component of the long-nosed fur seal diet, has exacerbated social tensions around the recovery of the native long-nosed fur seal. Ancestral *A. forsteri* established populations on New Zealand and Australian coasts in the last million years (Kirkwood and Goldsworthy, 2013). Also known as the New Zealand fur seal, we prefer to use the vernacular name 'long-nosed fur seal' in Australia, as fishers and other community sectors argue incorrectly that the long-nosed fur seal is not native to Australia (Shaughnessy et al., 2015). In the last 2-3 decades, the population size of this species across south-eastern Australia (New South Wales – Tasmania) has been increasing (Shaughnessy et al., 2015; S. Reinhold et al., unpubl. data). Misperceptions of the 'introduced' status of long-nosed fur seals have in-part driven calls to cull this native top predator in Australia.

Predation of seabirds occurs amongst many seal species (Antarctic fur seals (*Arctocephalus gazella)*: (Visser et al., 2008); Cape fur seals (*Arctocephalus pusillus*): (Du Toit et al., 2004); leopard seals (*Hydrurga leptonyx*): (Ainley et al., 2005); South American sea lions (*Otaria flavescens*): (Rey et al., 2012); New Zealand sea lions (*Phocarctos hookeri*): (Morrison et al., 2016), and long-nosed fur seals (Page et al., 2005). In South Australia, penguin remains have been detected in 0-40% of long-nosed fur seal scats (Page et al., 2005; Goldsworthy et al., 2019a) with the variance attributed to potential differences in site-specific and age-class related predation patterns. In 2006-08, 30% of long-nosed fur seal scats from Kanowna Island, in Central Bass Strait, Victoria, showed evidence of penguin predation (Hoskins et al., 2017). Recently, however, seven hot spots of penguin predation (>30% of scats with penguin remains) have been detected across south-eastern Australia, four of which occur in Bass Strait (S. Reinhold et al., unpubl. data).

Bass Strait, the shallow continental shelf area between mainland Australia and Tasmania, is a key region for Australian seabirds, supporting a large proportion of breeding populations of at least 11 species (Ross et al., 1995), including 82% of Australia's little penguin population. On a global scale, this marine area is considered a region of low primary productivity (Gibbs et al., 1986; Gibbs et al., 1991) that occurs at the confluence of three main ocean currents; the East Australian Current (EAC), South Australian Current (SAC) and sub-Antarctic surface water (SASW). The latter two represent key sources of primary productivity, as do the Bonney Upwelling and west Tasmanian upwelling that disperse nutrient rich water into west Bass Strait (Middleton et al., 2007; Middleton and Bye, 2007; Kämpf, 2015).

In Bass Strait, during pre-moult, foraging adult penguins undertake an intensive foraging bout that lasts approximately three weeks – likely accessing prey in nutrient rich waters (i.e. areas of upwelling). This pre-moult foraging period is critical for adult penguins to increase their body mass to sustain the upcoming three week period of fasting during moult (Gales et al., 1988). Post-moult foraging also entails an extended offshore foraging period that serves to re-plenish fasting penguins in the lead up to the breeding season (McCutcheon et al., 2011). Consequently, moulted penguin feathers retain the biochemical signatures of the environmental conditions (i.e. different sources of primary production) and anthropogenic contaminants, also described as bottom-up influences, experienced by penguins during the pre-moult foraging period (Hobson and Clark, 1992; Finger et al., 2015; Kowalczyk et al., 2015). In St Kilda (Port Phillip Bay, Victoria) for example, trace metal concentrations in penguin feathers have been linked to varying levels of industrialisation adjacent to penguin foraging zones (Finger et al., 2015). Similarly, stable carbon isotopes ($\delta^{13}C$) from penguin feathers have been used to provide insight into the relative contributions of different production sources in a trophic network (Hobson et al., 1994; Cherel and Hobson, 2007). By contrast, nitrogen ($\delta^{15}N$) serves as an indicator of consumer trophic position (Vanderklift and Ponsard, 2003). Combined, trace element and stable isotope signatures in feathers therefore provide a biochemical map of bottom-up factors (toxicants, primary productivity and trophic positioning) for penguins using different pre-moult foraging zones. Hence, the potential exists to compare between penguin feathers recovered from long-nosed fur seal scats and moulted penguin feathers (Fromant et al., 2020). Complimentary to the highly synchronised life stages of penguins across Bass Strait, the different levels of coastal industrialisation and sources of primary productivity entering this system (EAC in the east and Antarctic upwelling in the west) (Gibbs et al., 1986; Gibbs et al., 1991), suggest that Bass Strait may be a good candidate for detecting biochemical variation (in feathers) between penguin colonies using different pre-moult foraging zones.

Feathers have been consistently recovered from long-nosed fur seal scats where penguin predation occurs. In terrestrial systems, predator-prey relationships have successfully been explored using stable isotope signatures from the hair of wild deer, compared to the deer hair retrieved from the scats of wolves where their ranges overlap (Derbridge et al., 2012). Similarly, we aim to develop biochemical techniques that can identify the source colony of predated penguin feathers recovered from long-nosed fur seal scats. Using a combination of stable isotope and trace element techniques, this research aims to (1) develop a biochemical map as a baseline of 'feather-prints' – using moulted feathers from penguin colonies across Western, Central and Eastern Bass Strait and Port Phillip Bay, (2) use these 'feather-prints' to determine the scale of differentiation as either colony or region specific (or both), and (3)use the baseline 'feather-prints' to infer the source colony and/or region of predated feathers in long-nosed fur seal scats.

MATERIALS AND METHODS

Sample Collection

Every year, between November and March, adult penguins in Bass Strait experience three, highly synchronised, life stages in the lead up to the breeding season; (1) pre-moult foraging (Nov-Jan), (2) a catastrophic moult during which all feathers are shed while individuals are on land (Feb-March), and (3) post-moult foraging (March-April) (Reilly and Cullen, 1981). We collected moulted feathers from penguin colonies across four regions; Western (Cape Nelson and Deen Maar Island), Central (Phillip Island, Kanowna Island and Rabbit Island) and Eastern Bass Strait (Gabo Island), and Port Phillip Bay (St. Kilda) to inform baseline biochemical 'feather-prints' (**Figure 1** and **Table 1**). Kanowna and Gabo Island feathers were opportunistically collected from satellite tracking retrieval procedures (feathers remaining on water-proof tape used to attach GPS data loggers were collected - separate study), whilst moulted feathers were collected for the other four sites. Trace element and stable isotope concentrations circulating in the blood at the time of moult are thought to be a combination of what has been consumed in the weeks of pre-moult feeding and a remobilisation of chemical sequestration from internal tissues (Furness et al., 1986; Bearhop et al., 2000). The blood supply to feathers ceases after formation of the new feathers. Therefore, the data presented from feathers moulted in 2019 are an indication of 2018/19 pre-moult foraging

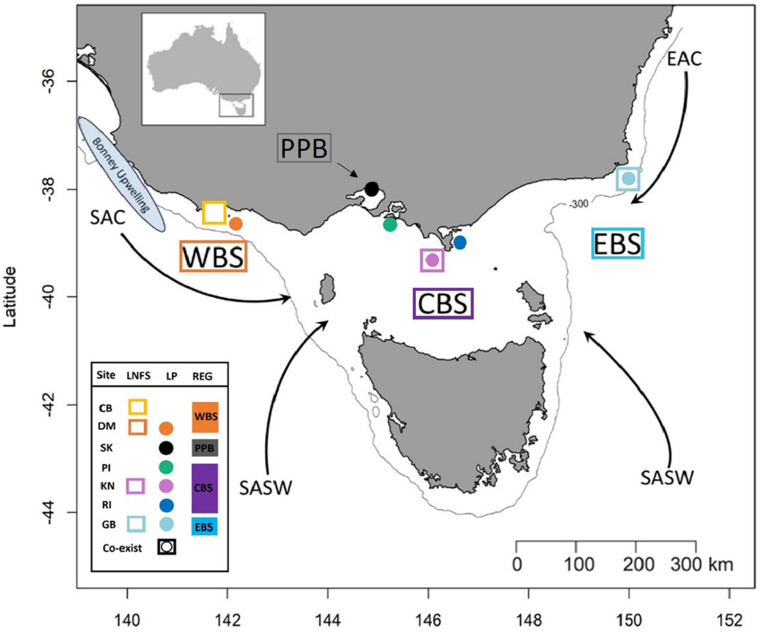

FIGURE 1 | Simplified representation of the four sampling regions and the major water masses influencing those regions. Western Bass Strait (WBS); Port Phillip Bay (PPB); Central Bass Strait (CBS); Eastern Bass Strait (EBS); Cape Bridgewater (CB); Deen Maar Island (DM); St. Kilda (SK); Phillip Island (PI); Kanowna Island (KN); Rabbit Island (RI); Gabo Island (GB); South Australian Current (SAC); Sub-Antarctic Surface Water (SASW); and East Australian Current (EAC) from Sandery and Kämpf (2007). Circles indicate sampled penguin colonies, squares represent sample sites of scats of long-nosed fur seals and squares with circles represent locations where both species co-exist. The solid line indicates the location of the 300m isobath.

TABLE 1 | Collection locations, seasons and sample sizes for Moulted Feathers (MF) and Scat Feathers (SF) retrieved from little penguin colonies and scats of long-nosed fur seals respectively.

Region of sample	Site	Lat, Lon	Sample	Time sampled	Feathers sampled (*n*)
Western Bass Strait	Cape Bridgewater	- 38.3956, 141.4065	SF	Nov-Dec 2018	11
	Cape Nelson	-38.4042, 141.5615	MF	March 2019	7
	Deen Maar Island	-38.4161, 142.0038	MF	March 2019	7
Pt. Phillip Bay	St. Kilda	- 37.5101, 144.5762	MF	March 2019	14
Central Bass Strait	Phillip Island	-38.5111, 145.1496	MF	Feb-March 2019	14
	Kanowna Island	-39.1548, 146.3104	SF	Oct-Dec 2018	10
	Kanowna Island	-39.1548, 146.3104	MF	Oct-Dec 2018	14
	Rabbit Island	-38.9111, 140.50937	MF	March 2019	14
Eastern Bass Strait	Gabo Island	-37.5649, 149.9133	SF	Oct-Dec 2018	16
	Gabo Island	-37.5649, 149.9133	MF	Oct-Dec 2018	14

at all sites (**Figure 2** and **Table 1**). Between October and November 2018, we randomly sampled fresh scats from three long-nosed fur seal sites across northern Bass Strait (**Table 1**). Feathers are metabolically inert after formation and, hence, penguin feathers retrieved from long-nosed fur seal scats collected between April 2018 and up to February 2019 reflect the biochemical signatures of pre-moult foraging of penguins during 2018 (**Figure 2**). Overall, penguin feathers were evident in 37 scats; Cape Bridgewater (Western Bass Strait) (*n*=11), Kanowna Island (Central Bass Strait) (*n*=10) and Gabo Island (Eastern Bass Strait) (*n*=16).

Feeding Trial

To investigate the biochemical effect of digestion on penguin feathers and subsequent comparability between moulted and scat feathers, three feeding trials were undertaken at Melbourne Zoo, between August and November 2018. Three long-nosed fur seals (*n* = 1 female, *n* = 3 male) and one Australian fur seal (female; *Arctocephalus pusillus doriferus*) were fed fish tightly stuffed with little penguin feathers (approx. 50g) from two penguin carcasses from Phillip Island that died naturally as a result of heat stress. Feeding occurred between 0900-1000 h on three separate occasions (a minimum of 10 days apart). Scats were then collected daily for 72 h and frozen at -20°C until analysed. Samples were soaked in warm water in individual plastic containers for at least 24 h and washed with tap water through a nested 1.0 mm sieve to extract digested feathers. Undigested feathers were also collected from the two penguin carcasses and used as a control for comparison to digested feathers. Due to sample size limitations, feathers originating from one carcass were used for trace element signature comparisons between digested and undigested feathers. Feathers from both penguin carcasses were utilised for stable isotope comparisons.

Sample Processing

The laboratory procedures described below were used to determine stable isotope and trace element signatures in penguin feathers recovered from the feeding trial, moulted feathers and predated feathers from long-nosed fur seal scats (**Table 1**).

Stable Isotope Analyses

We cleaned penguin feathers in 5ml teflon vials containing 2:1 chloroform:methanol solution (5 ml) using a sonic bath with vials immersed in water for 2 minutes. Two successive methanol rinses using the sonic bath (2 min per rinse) followed initial cleaning (Cherel et al., 2014). Feathers were then oven dried (60°C) for 48 hours and cut into small fragments. We packed ~0.4mg of feathers into pre-combusted tin capsules (Elemental Microanalysis 9x5mm C10-042) and determined carbon (13C/12C, δ^{13}C and nitrogen (15N/14N, δ^{15}N isotope ratios using a continuous flow ratio mass spectrometer (Nu Horizon,

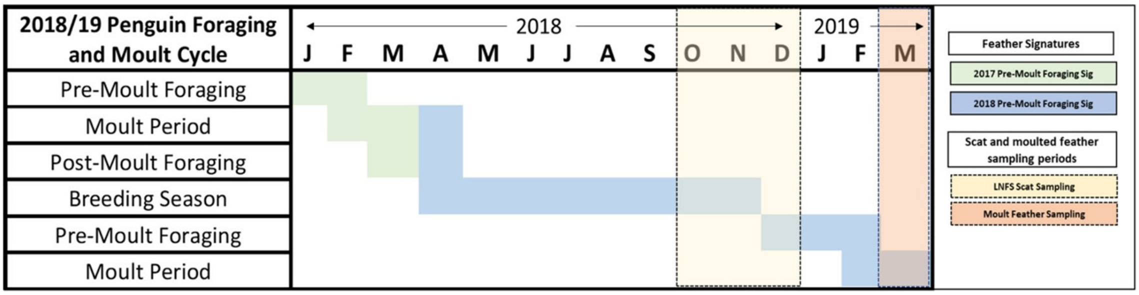

FIGURE 2 | Foraging and moult phenology of little penguins in Bass Strait. Blocks with horizontal lines correspond to the 2017 and 2018 pre-moult foraging signatures of feathers. Yellow and orange shaded blocks correspond to the sampling periods of seal scats and moulted penguin feathers respectively.

Wrexham, UK) coupled to an elemental analyser (EA3000, EuroVector, Pavia, Italy). Isotopic results are presented in δ notation relative to Vienna PeeDee Belemnite and the atmospheric abundance for $\delta^{13}C$ and $\delta^{15}N$, respectively (Coplen et al., 2006).

All samples where corrected for instrument drift and normalized according to reference values using in-house standards (*n*=25); glycine -31.2‰, glutamic acid -16.72‰ & triphenylamine (TPA) -29.2‰ calibrated against USGS and IAEA certified reference materials (USGS40, USGS 41, IAEA-2).

Trace Element Analysis

Penguin feathers were vigorously washed in Milli-Q water three times and then oven-dried at 45°C for 48 h with a resulting dry weight (dw) range of 1.9 – 5.4 mg dw (Finger et al., 2015). Whole feathers were initially digested in an aqua regia solution made up of (2.7ml 70% nitric acid (RCI Premium, ACI Labscan) and 0.3ml 37% hydrochloric acid (NORMAPURE, VWR CHEMICALS Analar) at 95°C for 12 h. Samples were then re-digested using 0.03 ml 69% nitric acid and diluted with Milli- Q water to a final volume of 3 mL (2% nitric concentration and ~1000ppb dilution). Feathers were assessed for concentrations of Lithium (Li), Boron (B), sodium (Na), magnesium (Mg), aluminium (Al), potassium (K), calcium (Ca), titanium (Ti), vanadium (V), cromium (Cr), manganese (Mn), iron (Fe), cobalt (Co), nickel (Ni), copper (Cu), zinc (Zn), arsenic (As), selenium (Se), strontium (Sr), cadmium (Cd), tin (Sn), antimony (Sb), barium (Ba), lead (Pb), and bismuth (Bi). Feathers were analysed at Adelaide Microscopy, University of Adelaide, with an Agilent 8900x ICP-MS/MS and limit of detection of 0.01 mg/kg. Trace elements Li, Cr, Ni, As, Cd, Sn, Sb, Pb and Bi were below the limit of detection (0.01 mg/kg) and therefore excluded from further analysis. Elements B, Na, Mg, Al, K, Fe, Sr, Se, Ti, V, Mn, Co and Ba exceeded the detection limits of the ICP-MS/MS for 100% of samples. A minimum of five procedural blanks were analysed per 60 samples and all results reported as mg/kg dry weight (dw). External machine precision (i.e. machine drift) was assessed by measuring 100ppb standards every 10 samples in the absence of Standard Reference Materials (SRM) for feather tissues.

Statistical Analyses

Feeding trial analysis of digested and undigested feathers were prioritised above the broader analysis of moulted and scat feathers to inform their biochemical comparability.

Feeding Trial

To determine whether long-nosed fur seal digestion altered the feather biochemical signatures, we performed paired t-tests for the undigested and digested feathers, for each stable isotope ($\delta^{13}C$ and $\delta^{15}N$) and trace element (B, Na, Mg, Al, K, Fe, Sr, Se, Sn, Ti, V, Mn, Co and Ba) detected. Significance was taken to be $p<0.05$ for all statistical analyses.

Moulted and Scat Feathers

Normality of distribution for each element and stable isotope was tested using the Shapiro Wilk test. Parametric assumptions were violated for Mg and $\delta^{15}N$ regardless of transformation type. Therefore, to apply a consistent statistical approach to all elements and stable isotopes for multivariate analyses, non-parametric tests were used. Biochemical signatures were compared between sites using a two-factor PERMANOVA design for each element and isotope individually and then all signatures combined (Anderson, 2001). Data were normalised prior to constructing resemblance matrices based on Euclidean distance dissimilarity and analysed using unrestricted permutation with 9999 random repeats. No significant differences were detected between the two sites sampled in Western Bass Strait, Deen Maar Island and Cape Nelson. Due to the close proximity of the sites and uniform Western Bass Strait regional representation, the seven samples from each site were pooled for comparison to the remaining five sites. Boxplots were used to display the median and lower (Q1) and upper (Q3) quartiles for each trace element and stable isotope per site. Outliers in the multivariate baseline data were identified using Principle Component Analysis (PCA) and feathers that were beyond a 95% confidence ellipse were excluded from further analysis (**Figure S1**). Multivariate data were then reduced to two-dimensions and visualized using canonical analysis of principal coordinates (CAP) (Anderson and Willis, 2003). Canonical axes (CAP1 and CAP2) represent linear combinations of the orthonormal principal coordinate axes that best discriminate feather biochemistry by site or region. Vector diagrams in each canonical plot show the influence of individual elements and stable isotopes to sample positioning in multivariate space. The relative length and direction of each vector correspond to its discriminatory ability.

Signatures of feathers collected from scats were added to the CAP plot as unknown samples and leave-one-out cross validation was used to classify a source colony based on the multi-elemental signals of each scat feather sample. Accurate source colony allocations of scat feathers relies on the assumption that all possible colony sources across Bass Strait and Port Phillip Bay have been included in the baseline data set (Campana, 1999). All statistical analyses were executed using R version 4.2.3 (R Core Team, 2020) and PRIMER (v. 7.0.13; Auckland, NZ).

RESULTS

Feeding Trial

No significant variation was detected among stable isotope signatures between undigested and digested feathers, from two penguin carcasses; $\delta^{13}C$ ($n = 3$, $t = 1.47$ $df = 2$, $P = 0.28$), ($n = 6$, $t = 0.74$, $df = 5$, $P = 0.49$), and $\delta^{15}N$ ($n = 3$, $t = 0.63$, $df = 2$, $P = 0.59$), ($n = 6$, $t = 0.92$, $df = 5$, $P = 0.40$) (**Figure 3**). Comparison of undigested and digested feathers from one carcass also yielded similar means for trace elements Mg ($t = -0.70$ $df = 6$, $P = 0.51$), Al ($t = -0.72$ $df = 6$, $P = 0.50$), Ti ($t = 0.94$ $df = 6$, $P = 0.38$), Sr ($t = 0.05$ $df = 6$, $P = 0.96$) (**Figure 4**). However, we did detect a significant difference ($P < 0.05$ for each) in B, Na, Fe, Cu, Zn, Se, V and Mn between undigested and digested feathers and we therefore excluded these from further analyses of penguin colony or seal scat feathers.

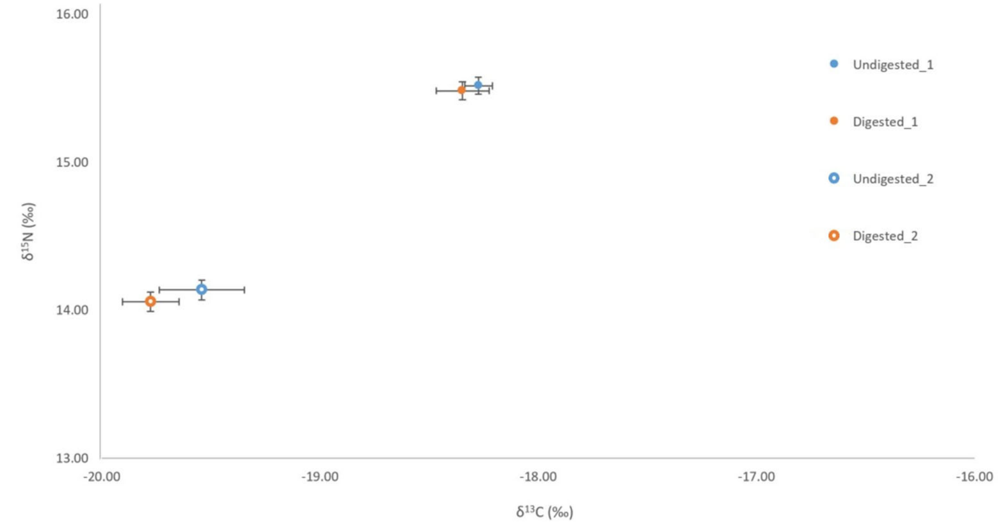

FIGURE 3 | Comparison of δ^{13}C and δ^{15}N signatures for undigested (penguin 1 *n*= 6, penguin 2 *n*=6) and digested (penguin 1 *n*= 3, penguin 2 *n*=3) feathers of little penguins consumed by captive Australian and long-nosed fur seals.

Penguin Baseline 'Feather-Prints'

Individual Chemistry Signatures

Trace element and stable isotope concentrations isolated for comparison with scat feathers for the six penguin locations sampled across four regions (Western, Central and Eastern Bass Strait, and Port Phillip Bay) are shown in the supplementary materials (**Table S1**). One-way MANOVA detected a significant difference in the distribution of mean stable isotope values and trace element concentrations in moulted feathers at both regional and site scales. Mean Ti concentrations in feathers showed the greatest difference between Western Bass Strait and other regions, with feathers containing on average 3.1, 5.4, and 8.3 times more Ti than feathers from Port Phillip Bay, Central and Eastern Bass Strait

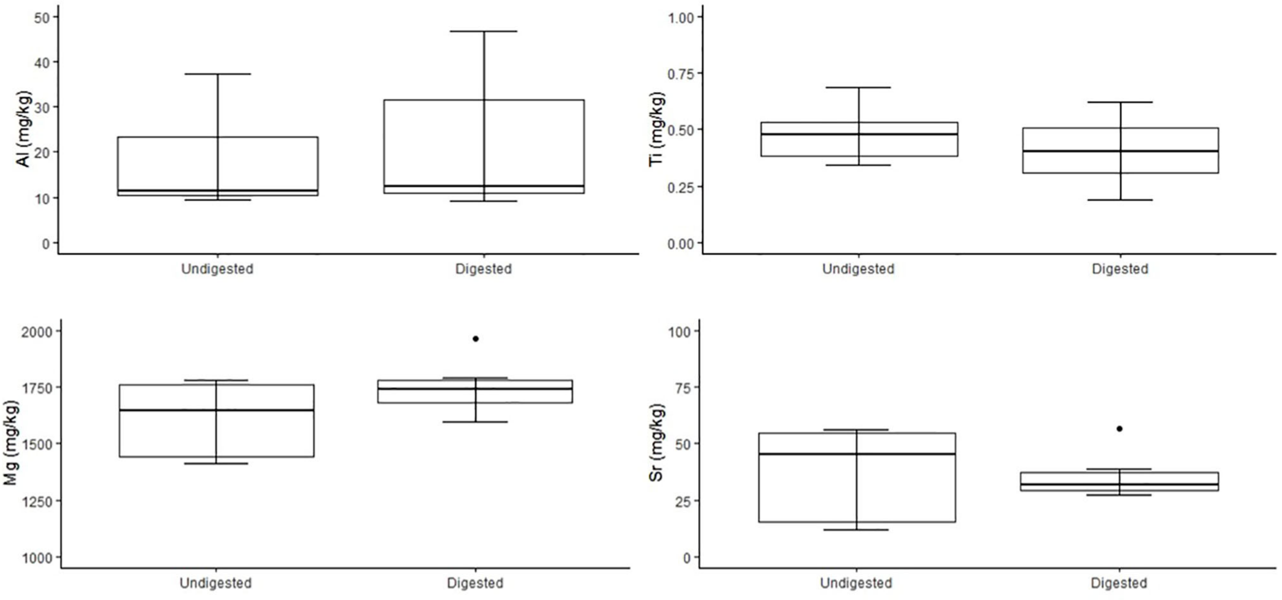

FIGURE 4 | Comparison of concentrations of trace elements Al, Ti, Mg and Sr (mg/kg dry weight) of undigested (*n* = 7) and digested (*n* = 7) feathers from carcass of *n* = 1 little penguin. Box plots display median values with box edges representing lower (Q1) and upper (Q3) quartiles, defined as the 25th and 75th percentiles, whiskers representing variability outside the upper and lower quartiles and dots representing outliers.

respectively. Similar mean Al concentrations were detected for feathers from Western Bass Strait sites and Port Phillip Bay (p = 0.52) with both regions demonstrating a minimum of Al levels two-fold higher than Central and Eastern Bass Strait sites (**Figure 5**). Western Bass Strait demonstrated similar Sr concentrations to all regions (p >0.05 for all) but significantly different Mg concentrations at a regional scale (p <0.05 for all). Port Phillip Bay δ^{15}N and δ^{13}C values differed significantly to all other regions (p = 0.00 for all) (**Figure S1, S2**), whilst regionally Western, Central and Eastern Bass Strait resulted in statistically similar values for both stable isotopes (p >0.05 for all). At a site level, Kanowna Island δ^{15}N values differed significantly to all sites (all p <0.05) with the exception of Gabo Island (p = 0.06). For δ^{13}C, Kanowna and Rabbit Island also differed (p = 0.00) but all other sites resulted in statistically similar values when compared to one another across the three Bass Strait regions (p >0.05 for all).

Multivariate Results

There was considerable variation in the elemental concentrations and stable isotope values in baseline feathers that resulted in biochemical differentiation at both regional and site-specific scales (**Figure 6**). With the exception of three feathers (1 per site; Deen Maar, Rabbit Island and Gabo Island), PCO analysis resulted in the distribution of all baseline feathers within the 95% confidence ellipse (**Figure S3**). Overall, CAP analysis resulted in regional classification success for 85% of baseline feathers and 78% at colony-specific scales (**Figure 6**). Western Bass Strait (93.3% *correct classification) and Port Phillip Bay (92.9% *) resulted in the highest correct classifications with dissimilarity measures predominantly driven by high Ti and δ^{15}N signatures respectively. Both regions also demonstrated high Al levels compared to baseline feather signatures from Central and Eastern Bass Strait (**Figure 5**). Central (82.1% *) and Eastern Bass Strait (76.9% *) baseline data shared similar Mg and Sr concentrations with δ^{13}C predominantly driving variation between the two regions. The relative length and direction of each vector corresponding to the discriminatory ability of each biochemical signature remained largely consistent between site and regional CAP comparisons. For sites, St. Kilda (92.9% *) resulted in the highest proportion of correct classifications (thereafter referred to as site or regional 'biochemical resolution') followed by Deen Maar Island (86.7% *), Kanowna Island (78.6% *), Rabbit Island (72.7% *), Gabo Island (69.2% *) and Phillip Island (64.3% *) (**Figure 6**).

Scat Feathers – Source Penguin Colony

All signatures of scat feathers overlapped with the baseline data of which 32.4% were assigned to penguins from Kanowna Island (Central Bass Strait), followed by 27.0% from Gabo Island (Eastern Bass Strait). Rabbit Island (Central Bass Strait), Deen Maar Island (Western Bass Strait) and Phillip Island (Central Bass Strait) each made up 18.9%, 13.5% and 8.1% of scat feathers respectively. St. Kilda (Port Phillip Bay) penguins however, remained undetected from the scats collected across the three regions in this study (**Figure 7**). Local penguin colonies accounted for 46-70% of predated feathers. These local colonies either (1) co-exist with the long-nosed fur seals we sampled or (2) occur in closest proximity, relative to other sampled colonies, to the sampled seal site (**Figure 8**).

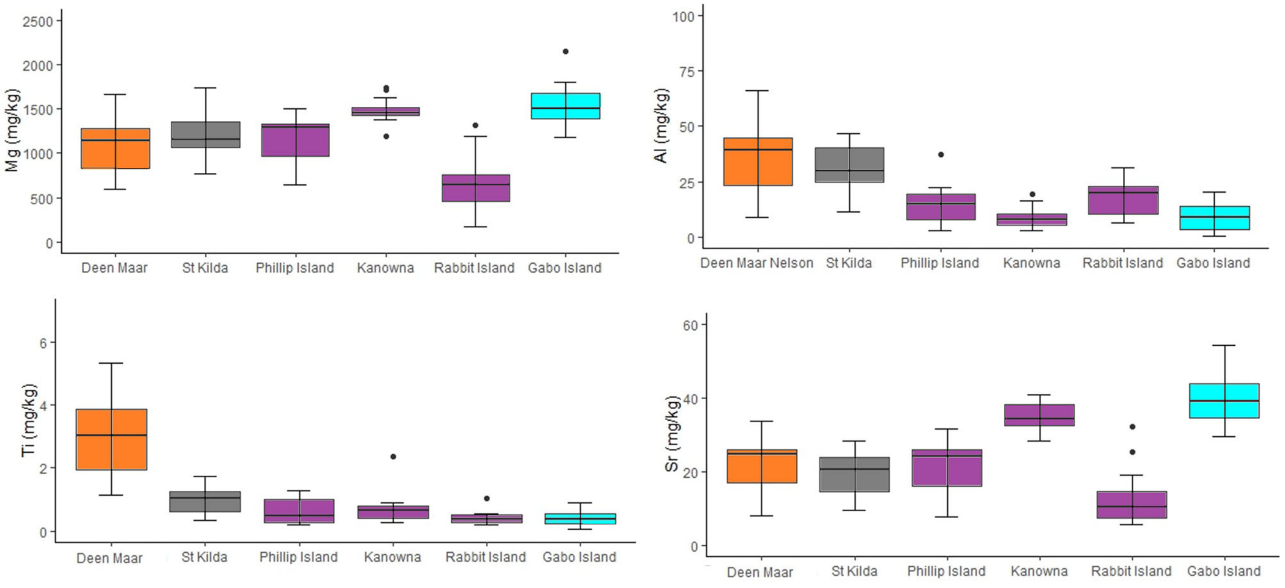

FIGURE 5 | Concentrations for trace elements Al, Ti, Mg and Sr (mg/kg dry weight) from moulted feathers of little penguins collected from Deen Maar Island and Cape Nelson (WBS), St. Kilda (PPB), Phillip Island (CBS), Kanowna Island (CBS), Rabbit Island (CBS) and Gabo Island (EBS). Box plots display median values with box edges representing lower (Q1) and upper (Q3) quartiles, defined as the 25th and 75th percentiles, whiskers representing variability outside the upper and lower quartiles and dots representing outliers. The Y-axis for each element differs and colors of box plots correspond to colors presented in **Figure 1**.

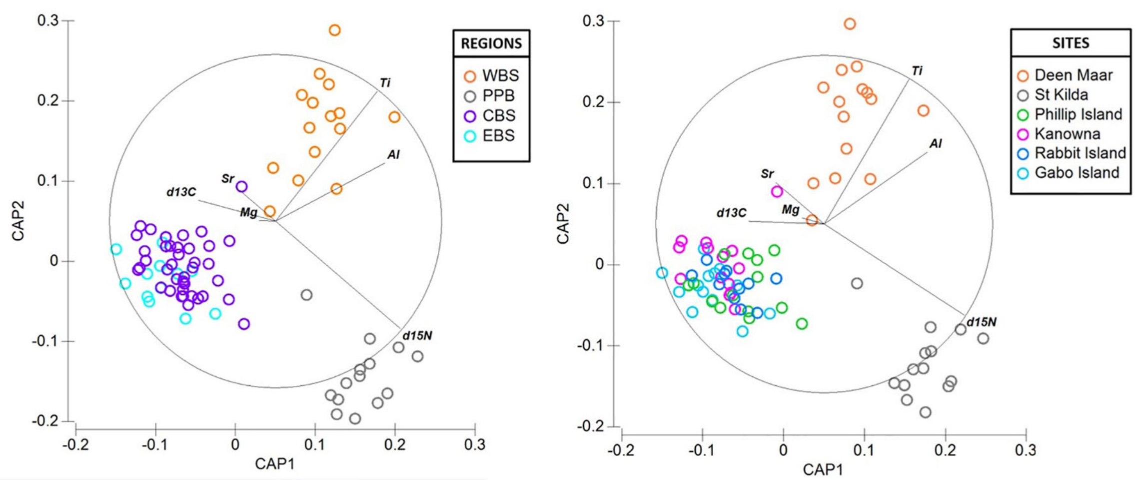

FIGURE 6 | Canonical variate plots of the multi-elemental and isotope chemistry of feathers of little penguins sampled across four regions; **(A)** Western (WBS), Central (CBS) and Eastern Bass Strait (EBS) and Port Phillip Bay (PPB) and **(B)** sites; Deen Maar Island, St. Kilda, Phillip Island, Kanowna Island, Rabbit Island and Gabo Island. Vector diagrams show the direction and weight of individual isotopes and elements to sample distribution.

The proportion of predated feathers assigned to regional and inter-regional penguin colonies, relative to the site of long-nosed fur seal scat collection, varied across the three regions (**Figure 7**). Whilst predated feathers from Western Bass Strait were exclusively detected in Cape Bridgewater (Western Bass Strait) scats, the remaining 54% of scat feathers resulted in the highest inter-regional diversity of penguins including Central Bass Strait colonies; Kanowna Island (27%) and Phillip Island (9%), as well as Eastern Bass Strait, Gabo Island (18%), feathers. Comparatively, scat feathers from Kanowna Island (Central Bass Strait) resulted in the highest occurrence of localised predation with 70% of feathers assigned to Kanowna Island penguins and the remaining 30%

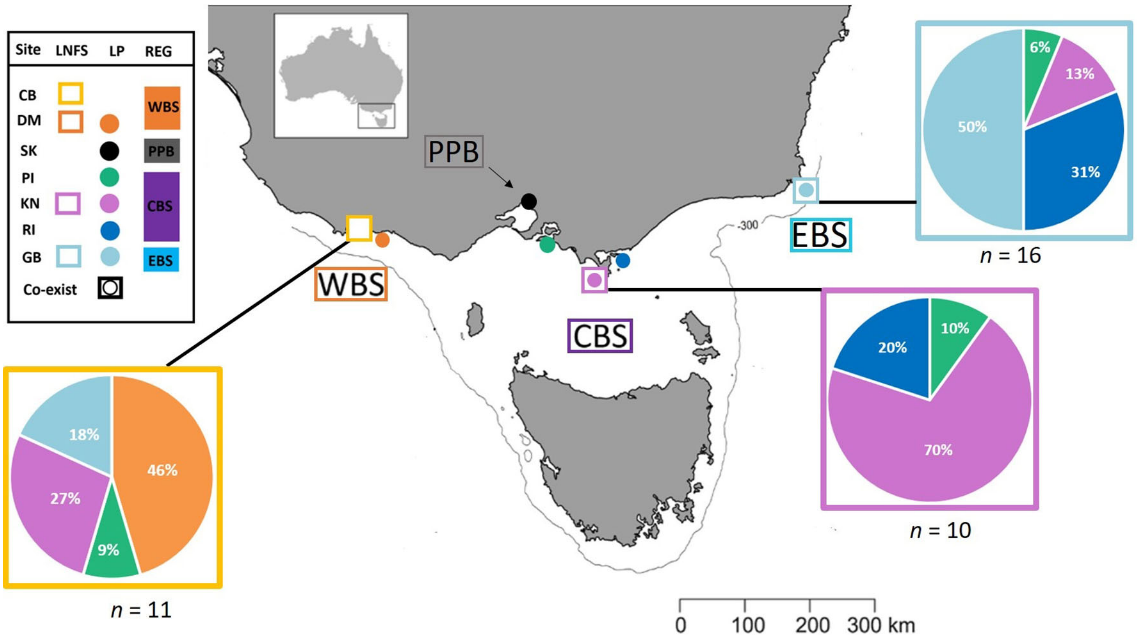

FIGURE 7 | Proportional (%) contribution of source-colonies assigned to little penguin feathers retrieved from scats of long-nosed fur seals. Plots show results of canonical variate analysis of baseline multi-elemental and isotope signatures from penguin colonies sampled across Western (WBS), Central (CBS) and Eastern Bass Strait (EBS), and Pt. Phillip Bay (PPB); Deen Maar Island and Cape Nelson (DM); St. Kilda (SK); Phillip Island (PI); Kanowna Island (KN); Rabbit Island (RI); Gabo Island (GB). Scats of long-nosed fur seals were sampled between October – November 2018.

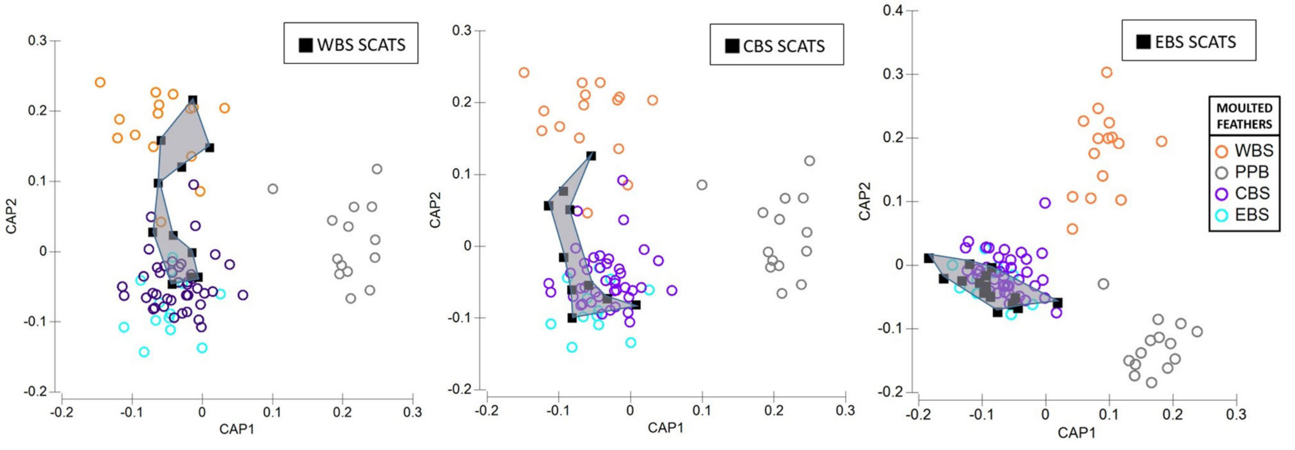

FIGURE 8 | Canonical variate plots of the multi-elemental and isotope chemistry of feathers sampled from colonies of little penguins across Western (WBS), Central (CBS), Eastern Bass Strait (EBS), and Pt. Phillip Bay (PPB) (indicated by circles). Squares with convex hulls represent feathers retrieved from long-nosed fur seal scats sampled from **(A)** Cape Bridgewater (WBS), **(B)** Kanowna Island (CBS) and **(C)** Gabo Island (EBS).

attributed to regional colonies; Rabbit Island (20%) and Phillip Island (10%) (**Figure 8**). Complimentary to the 50% of Gabo scat feathers allocated to local Gabo Island penguins, the remaining predated feathers were assigned to originating from inter-regional Central Bass Strait colonies; Rabbit Island (31%), Kanowna Island (13%) and Phillip Island (6%) (**Figure 8**).

DISCUSSION

This study was able to chemically discriminate moulted penguin feathers among sites across Bass Strait and Port Phillip Bay. Using these baseline data, moulted feathers were assigned to their known region or colony of origin with 85% and 78% accuracy, respectively. Variance in moulted feather signatures may reflect system-specific, bottom-up influences including foraging specialisation in areas of high productivity, as well as potential industrial and oceanographic factors within or adjacent to the respective penguin foraging zones.

Across the three regions sampled for long-nosed fur seal scats, 46-70% of feathers collected from scats indicated patterns of 'local' penguin predation. Inter-regional predation of penguins, relative to the site of long-nosed fur seal scat collection, were detected in Eastern and Western Bass Strait scats, while Central Bass Strait scats were solely assigned to 'local' and regional penguins. The latter was likely explained by a higher bioavailability of penguins in Central Bass Strait. In comparison, Western Bass Strait birds were predated at a localised scale only. Whereas St. Kilda penguins, known to forage exclusively in Port Phillip Bay and situated furthest from long-nosed fur seal sites (relative to other penguin colonies sampled in this study), remained undetected in all scats. Potential drivers shaping localised and inter-regional predation (or lack thereof) are described with reference to penguin colony proximity to seal sites, areas of high productivity and demographic-specific species foraging movements.

Baseline Signatures From Moulted Penguin Feathers

Results of feeding trials supported the biochemical comparability between baseline signatures from moulted and scat feathers. Arregui et al. (2018) also reported fin whale scats as a reliable indicator of prey consumption with unaltered stable isotope ratios of krill post transit along the digestive tract. The afore mentioned biochemical comparisons between wild deer hair and predated hair from the scats of wolves, further highlights the application of such methods across marine and terrestrial predator-prey relationships (Derbridge et al., 2012).

Across Bass Strait and Port Phillip Bay, moulted feathers from St. Kilda retained stable isotope and trace element signatures with the highest overall discriminatory resolution (92.9% correct classification). Key biochemical signatures discriminating moulted feathers from St. Kilda, included elevated δ^{15}N and Al levels. St. Kilda penguins are known to forage exclusively within PPB, specialising on juvenile anchovy and luminous bay squid with high δ^{15}N values (Preston et al., 2008; Chiaradia et al., 2012). Consistent with the findings of this study, Kowalczyk et al. (2015) detected high δ^{15}N levels in St. Kilda penguin feathers (**Table S1**). Finger et al. (2015) also detected elevated Aluminium (22% higher than this study), Arsenic and Mercury concentrations in St. Kilda penguins compared to other Central Bass Strait breeding sites (Phillip Island and Notch Island) (**Table S1**). Aluminum impairment in seabirds is mainly related to its disruptive effect on calcium homeostasis as well as phosphorus metabolism, ultimately leading to muscle weakness and decreased growth rates (Scheuhammer, 1987). Port Phillip Bay is host to the city of Melbourne's business district, and the restricted currents and wave action in the bay may act as a contamination hotspot for the heavy metals subsequently reflected in elevated levels amongst St. Kilda penguin feathers (Aly et al., 2013).

Elevated Al but also Ti concentrations discriminated moulted feathers from Western Bass Strait from penguin colonies in Central and Eastern Bass Strait. The bioaccumulation of anthropogenic and natural sources of both Ti and Al represent potential risks to seabirds such as penguins that forage at higher trophic levels (Scheuhammer, 1987; Finger et al., 2015; Walsh, 2018; Hauser-Davis et al., 2020). Titanium, which is often depleted in surface waters but elevated in deep water, and which can occur over a range of at least two orders of magnitude, has been described as a potential tracer of chemical transfer processes in open oceans (Dammshäuser et al., 2011). Penguin colonies from Western Bass Strait in this study are situated within the eastern bounds of the Bonney Upwelling system – an important source of transfer for deep and nutrient rich waters to the surface (Middleton and Bye, 2007). However, very little is known about the biological function of Ti and Al, or the biogeochemical processes (like coastal upwelling) that may control its distribution in the marine environment.

We highlight two local sources (~40km from Western Bass Strait penguin colonies) of potential industrial discharge for both Ti and Al; (1) the Portland Aluminium Smelter and (2) the commercial Port of Portland. Emissions from the Portland Aluminium Smelter, with a production capacity of 345,000 tonnes of Al per year, can enter coastal waters *via* contaminated particulate matter and effluent discharge that potentially biomagnify up the marine trophic food chain (Radhalakshmiet al., 2014; Sun et al., 2020). For Ti, potential local entry points within Western Bass Strait include transport *via* the mineral sands from the Port of Portland, from which titanium dioxide ($Ti0_2$) is derived (Force, 1991). In 2017, for example, approximately 490,000 tonnes of mineral sands were reported as imported/exported *via* the Port of Portland. In its nanoparticulate (matter between 1-100nm) form, $Ti0_2$ is used in a wide range of products (i.e. sunscreen, paints, cements, care cosmetics) and considered a contaminant of emerging concern - particularly for aquatic ecosystems (Weir et al., 2012; Shi et al., 2013; Hauser-Davis et al., 2020). Miller et al. (2012) demonstrated that relatively low levels of ultraviolet light, consistent with those found in nature, can induce toxicity of $Ti0_2$ nanoparticles to marine phytoplankton. However, very little is known about the potential effects of $Ti0_2$ travelling up the trophic chain.

In comparison to Western Bass Strait and Port Phillip Bay (93% and 92% correct classification, respectively), a higher level of biochemical homogeneity was detected between Central (82.1%) and Eastern Bass Strait (76.9%) sites (**Figure 6A**). This may reflect overlapping foraging zones and/or the confluence of currents meeting in Central Bass Strait reducing the discriminatory biochemical resolution between the two regions (Ridgway, 1997; Sandery and Kämpf, 2007). For example, oligotrophic, low nutrient waters from the East Australian Current (EAC) flow southward along the eastern edge of Bass Strait and the South Australian Current (SAC) advects warm water from the west that flows eastward through Bass Strait (Sandery and Kämpf, 2007). Pre-moult Eastern Bass Strait penguins at Gabo Island, unconstrained by chick feeding requirements, may travel along the EAC towards other sources of nutrient rich inputs into Central Bass Strait.

Overall, biochemical variation in moulted penguin feathers between the four regions provide baseline signatures at high spatial resolution that reflect variation in distance to areas of high productivity and consequent foraging strategies, as well as natural and potentially land derived anthropogenic sources of elevated contaminants. Interestingly, these baseline signatures also highlight the complexity of threats penguins encounter, including potential terrestrial sources of contaminants, at system-specific levels.

Bioavailability and Proximity Influences Predation Pressure

Both, long-nosed fur seals and penguins are highly mobile marine predators demonstrating vastly different foraging strategies which are broadly shaped by system-specific cycles of productivity and life history constraints (Page et al., 2005; Sidhu et al., 2012; Pelletier et al., 2014; Foo et al., 2019). Feathers originating from St. Kilda penguins were undetected from scats, likely explained by the specialised foraging that occurs from this colony throughout the year within the confines of Port Phillip Bay (Preston et al., 2008; Chiaradia et al., 2012). We note that long-nosed fur seals do not commonly within Port Phillip Bay. Furthermore, St. Kilda penguins have experienced a decline since their estimated peak population size of 1061 adults in 2015, with estimates of, 998 adults in 2016, 738 adults in 2017, and 694 adults in 2018 (F. Sperring, *unpublished data*). Overall, between 46-70% of predated feathers retrieved from scats across Bass Strait were assigned to 'local' penguins (**Figure 8**). Most likely, this reflects overlapping marine foraging zones for the animals with shared or close terrestrial habitat. Both species utilise epipelagic coastal waters, but the long-nosed fur seals also forage in offshore waters (Collins et al., 1999; Baylis et al., 2008; Salton et al., 2021). For example, Salton et al. (2021) recently tracked a sub-adult male fur seal from Montague Island, New South Wales, to the Nee Islets, in southern New Zealand. During our study, scat sampling occurred during the penguin-breeding season (Oct-Dec 2018) when adult penguins across Victoria typically make one-day foraging trips (Chiaradia, 1999), typically within a 30 km radius of their breeding site (Collins et al., 1999). Consequently, we can expect that local breeding penguins are more bioavailable to nearby long-nosed fur seals when constrained by mate and chick feeding requirements.

The highest level of localised predation was detected for Kanowna Island (Central Bass Strait), where predated feathers were solely allocated to Kanowna penguins (70%) or other colonies within the Central Bass Strait region (30%). Relative to Eastern and Western Bass Strait, Central Bass Strait has a greater abundance of penguins - proportionally increasing the bioavailability of Central Bass Strait penguins within the region (Dann pers comm). For both Central and Eastern Bass Strait, the proportion of different feather signatures found in the scats correlated to the proximity of source penguin colonies. Both regions displayed patterns of increased predation pressure on local, and then regional or inter-regional penguins, with proximity to seal sites. For example, in addition to the birds originating from Kanowna Island (70%), the proportional contribution of Rabbit Island (20%) and Phillip Island (10%) penguins to scats collected from Central Bass Strait correlated with the colonies proximity (~45km and ~120km respectively) to Kanowna Island. For Eastern Bass Strait, local penguins comprised 50% of predated birds. The remaining birds were assigned to inter-regional Central Bass Strait penguins; Rabbit (31%), Kanowna (13%) and Phillip Island (6%). These three colonies are located ~330km, ~370km and ~500km from Gabo Island, respectively. Overall, the largest proportion of scat feathers collected across Bass Strait originated from Kanowna and Gabo Island penguin colonies, the two largest penguin colonies co-existing with long-nosed fur seals (Reinhold, S. unpublished data). The combination of high penguin bioavailability in close proximity to seal sites may therefore place Kanowna and Gabo Island colonies at greater risk of seal predation. We note however, population level inferences about penguin colonies at greatest risk to seal predation require an increased sample size of scat feathers sampled across a broad temporal spectrum.

Species and Demographic-Specific Foraging Movements

While understanding where predatory events on penguins occur is beyond the scope of this study, the presence of inter-regional penguins in scats from Western and Eastern Bass Strait may reflect sexually immature penguins (<2yrs) which are more likely to demonstrate a more versatile foraging strategy that includes occurrence in these regions (Dann et al., 1992). Unlike breeding penguins, juveniles are more likely to travel further post-fledging and during penguin breeding months. However, the exclusive occurrence of Western Bass Strait penguins in scats from Western Bass Strait at Cape Bridgewater (46% of Western Bass Strait scats feathers) may suggest that juvenile as well as breeding birds from Western Bass Strait undertake more localised foraging strategies. The nutrient rich Bonney Upwelling system extends around the Western Bass Strait penguin colonies and provides an abundance of nearby food. This constrained spatial distribution of predated penguins from Western Bass Strait is consistent with dispersal patterns described for banded penguins from Western Bass Strait colonies (Norman et al., 2017). On average, banded penguins recovered from 20 colonies between Lorne and Portland (320km range) in Western Bass Strait moved ~38km from their original banding site (Norman et al., 2012). Phillip Island penguins also travel west post fledging, attributed to the access of nutrient-rich Bonney upwelling waters (Reilly and Cullen, 1982; Dann et al., 1992). Recoveries of flipper-banded first-year birds from Phillip Island indicate that they travel several hundred kilometers west between Warrnambool and Port MacDonnell, situated in the Bonney Upwelling 250km and 420 km from Phillip Island (Dann et al., 1992).

An equally plausible explanation for the occurrence of inter-regional (adult or juvenile) penguins in seal scats is long-distance movements by long-nosed fur seals (up to 220 km per day (Salton et al., 2021). Long-nosed fur seals retain prey for an estimated gut passage half time of 51 hours – prior to defecating scats (Fea and Harcourt, 1997). This represents the amount of time it takes for half the total of recovered prey remains to reappear in scats. Consequently, seals arriving from distant foraging grounds could still be digesting penguins sourced from inter-regional predation events upon their return to the site of scat collection. However, the proportional contribution of inter-regional penguins detected in this study should be considered as a minimum - as scats defecated at sea are likely to retain a higher proportion of hard-parts originating from prey, including penguin feathers, consumed in offshore waters.

CONCLUSION

This is the first study to develop a diagnostic tool for identifying seabird colonies at greatest risk to pinniped predation. Interestingly, the biochemical signatures that best discriminated between penguin colonies were shaped by system-specific dynamics including proximity to areas of high ocean productivity, human development, and industrialization, thus highlighting the inter-section of terrestrial and marine threats that penguins encounter. We propose future studies also explore the resilience of Hg concentrations in feathers to seal digestion, potentially enhancing the future biochemical resolution of colony-specific baselines.

Overall, seals were more likely to prey upon the penguins breeding in closest proximity to them, consistent with the constrained foraging patterns displayed by adult penguins during the breeding season – when the seal scats were collected. Region-specific predator-prey dynamics were likely tied to the proximity of penguin colonies to seals sites and the abundance or bioavailability of penguins. Meanwhile, inter-regional predator-prey dynamics may reflect variation in the dispersion of seals or juvenile penguins.

This study also suggests that penguin colonies may still be in decline despite a lack of seal predation. In such cases, other natural and anthropogenic stressors, for example industrialisation, shown here by heavy metal loads in feathers, may warrant further research to understand their contribution to population declines. As the factors that influence predation, or lack thereof, vary across regions and among local sites, this study highlights the value and importance of identifying the source colony of seabirds predated by pinnipeds to inform effective management efforts and outcomes.

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 Adelaide Animal Ethics Committee (S2017-106) and the Phillip Island Nature Park Animal Ethics Committee (2.2016).

AUTHOR CONTRIBUTIONS

S-LR, SG, BG, SC, and RM conceived and designed the study. S-LR, JA, and RM assisted with sample collection. S-LR wrote the manuscript, performed the laboratory processing and sample preparation, collected and analysed the data, and applied the statistical analyses. 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.2022.813106/full#supplementary-material

REFERENCES

Ainley, D. G., Ballard, G., Karl, B. J., and Dugger, K. M. (2005). Leopard Seal Predation Rates at Penguin Colonies of Different Size. *Antarctic Sci.* 17, 335–340. doi: 10.1017/S0954102005002750

Aly, W., Williams, I. D., and Hudson, M. D. (2013). Metal Contamination in Water, Sediment and Biota From a Semi-Enclosed Coastal Area. *Environ. Monitoring Assess.* 185, 3879–3895. doi: 10.1007/s10661-012-2837-0

Anderson, M. J. (2001). A New Method for Non-Parametric Multivariate Analysis of Variance. *Austral Ecol.* 26, 32–46. doi: 10.1111/j.1442-9993.2001.01070.pp.x

Anderson, M. J., and Willis, T. J. (2003). Canonical Analysis of Principal Coordinates: A Useful Method of Constrained Ordination for Ecology. *Ecology* 84, 511–525. doi: 10.1890/0012-9658(2003)084[0511:CAOPCA]2.0.CO;2

Arregui, M., Borrell, A., Víkingsson, G., Ólafsdóttir, D., and Aguilar, A. (2018). Stable Isotope Analysis of Fecal Material Provides Insight Into the Diet of Fin Whales. *Marine Mammal Sci.* 34, 1059–1069. doi: 10.1111/mms.12504

Baylis, A. M. M., Page, B., and Goldsworthy, S. D. (2008). Effect of Seasonal Changes in Upwelling Activity on the Foraging Locations of a Wide-Ranging Central-Place Forager, the New Zealand Fur Seal. *Can. J. Zool.* 86, 774–789. doi: 10.1139/Z08-055

Bearhop, S., Waldron, S., Thompson, D., and Furness, R. (2000). Bioamplification of Mercury in Great Skua *Catharacta Skua* Chicks: The Influence of Trophic Status as Determined by Stable Isotope Signatures of Blood and Feathers. *Marine Pollution Bull.* 40, 181–185. doi: 10.1016/S0025-326X(99)00205-2

Bethge, P., Nicol, S., Culik, B., and Wilson, R. (1997). Diving Behaviour and Energetics in Breeding Little Penguins (Eudyptula Minor). *J. Zool.* 242, 483–502. doi: 10.1111/j.1469-7998.1997.tb03851.x

Campana, S. E. (1999). Chemistry and Composition of Fish Otoliths: Pathways, Mechanisms and Applications. *Marine Ecol. Prog. Ser.* 188, 263–297. doi: 10.3354/meps188263

Cherel, Y., and Hobson, K. (2007). Geographical Variation in Carbon Stable Isotope Signatures of Marine Predators: A Tool to Investigate Their Foraging Areas in the Southern Ocean. *Marine Ecol. Prog. Ser.* 329, 281–287. doi: 10.3354/meps329281

Cherel, Y., Jaquemet, S., Maglio, A., and Jaeger, A. (2014). Differences in Δ^{13}c and Δ^{15}n Values Between Feathers and Blood of Seabird Chicks: Implications for Non-Invasive Isotopic Investigations. *Marine Biol.* 161, 229–237. doi: 10.1007/s00227-013-2314-5

Chiaradia, A. K. (1999). Daily Nest Attendance and Breeding Performance in the Little Penguin *Eudyptula minor* at Phillip Island, Australia. *Marine Ornithol.* 27, 13–20.

Chiaradia, A., Forero, M. G., Hobson, K. A., Swearer, S. E., Hume, F., Renwick, L., et al. (2012). Diet Segregation Between Two Colonies of Little Penguins *Eudyptula minor* in Southeast Australia. *Austral Ecol.* 37, 610–619. doi: 10.1111/j.1442-9993.2011.02323.x

Collins, M., Cullen, J., and Dann, P. (1999). Seasonal and Annual Foraging Movements of Little Penguins From Phillip Island, Victoria. *Wildlife Res.* 26, 705–721. doi: 10.1071/WR98003

Coplen, T. B., Brand, W. A., Gehre, M., Gröning, M., Meijer, H. A., Toman, B., et al. (2006). New Guidelines for Δ 13C Measurements. *Analytical Chem.* 78, 2439–2441. doi: 10.1021/ac052027c

Croxall, J. P., Butchart, S. H. M., Lascelles, B. E. N., Stattersfield, A. J., Sullivan, B. E. N., Symes, A., et al. (2012). Seabird Conservation Status, Threats and Priority Actions: A Global Assessment. *Bird Conserv. Int.* 22, 1–34. doi: 10.1017/S0959270912000020

Dammshäuser, A., Wagener, T., and Croot, P. L. (2011). Surface Water Dissolved Aluminum and Titanium: Tracers for Specific Time Scales of Dust Deposition to the Atlantic? *Geophysical Res. Lett.* 38, 24–30. doi: 10.1029/2011gl049847

Dann, P., Cullen, J., Thoday, R., and Jessop, R. (1992). Movements and Patterns of Mortality at Sea of Little Penguins *Eudyptula Minor* From Phillip Island, Victoria. *Emu-Austral Ornithol.* 91, 278–286. doi: 10.1071/MU9910278

Derbridge, J. J., Krausman, P. R., and Darimont, C. T. (2012). Using Bayesian Stable Isotope Mixing Models to Estimate Wolf Diet in a Multi-Prey Ecosystem. *J. Wildlife Manage.* 76, 1277–1289. doi: 10.1002/jwmg.359

Dias, M. P., Martin, R., Pearmain, E. J., Burfield, I. J., Small, C., Phillips, R. A., et al. (2019). Threats to Seabirds: A Global Assessment. *Biol. Conserv.* 237, 525–537. doi: 10.1016/j.biocon.2019.06.033

Du Toit, M., Bartlett, P., Bester, M., and Roux, J. (2004). Seabird Predation by Individual Seals at Ichaboe Island, Namibia. *South Afr. J. Wildlife Res.* 34, 45–54. doi: 10.10520/EJC117184

Fea, N., and Harcourt, R. (1997). Assessing the Use of Faecal and Regurgitate Analysis as a Means of Determining the Diet of New Zealand Fur Seals, in *Marine Mammal Research of the Southern Hemisphere*, Eds. M Hindell and C Kemper. (Norton, NSW: Surrey Beatty & Sons Chipping). 143–150.

Finger, A., Lavers, J. L., Dann, P., Nugegoda, D., Orbell, J. D., Robertson, B., et al. (2015). The Little Penguin (*Eudyptula Minor*) as an Indicator of Coastal Trace Metal Pollution. *Environ. Pollution* 205, 365–377. doi: 10.1016/j.envpol.2015.06.022

Foo, D., Mcmahon, C., Hindell, M., Goldsworthy, S., and Bailleul, F. (2019). Influence of Shelf Oceanographic Variability on Alternate Foraging Strategies in Long-Nosed Fur Seals. *Marine Ecol. Prog. Ser.* 615, 189–204. doi: 10.3354/meps12922

Force, E. R. (1991). Geology of Titanium-Mineral Deposits Geol. *Soc. Am. Bull.* 259, 3–6. doi: 10.1130/SPE259-p1

Fromant, A., Schumann, N., Dann, P., Cherel, Y., and Arnould, J. P. (2020). Trophic Niches of a Seabird Assemblage in Bass Strait, South-Eastern Australia. *PeerJ* 8, e8700. doi: 10.7717/peerj.8700

Furness, R., Muirhead, S., and Woodburn, M. (1986). Using Bird Feathers to Measure Mercury in the Environment: Relationships Between Mercury Content and Moult. *Marine Pollution Bull.* 17, 27–30. doi: 10.1016/0025-326X(86)90801-5

Gales, R., Green, B., and Stahel, C. (1988). The Energetics of Free-Living Little Penguins *Eudyptula Minor* (Spheniscidae), During Molt. *Aust. J. Zool.* 36, 159–167. doi: 10.1071/ZO9880159

Gibbs, C., Arnott, G., Longmore, A., and Marchant, J. (1991). Nutrient and Plankton Distribution Near a Shelf Break Front in the Region of the Bass Strait Cascade. *Marine Freshwater Res.* 42, 201–217. doi: 10.1071/MF9910201

Gibbs, C., Tomczak, M.Jr., and Longmore, A. (1986). The Nutrient Regime of Bass Strait. *Marine Freshwater Res.* 37, 451–466. doi: 10.1071/MF9860451

Goldsworthy, S. D., Bailleul, F., Nursey-Bray, M., Mackay, A., Oxley, A., Reinhold, S.-L., et al. (2019a). *Assessment of the Impacts of Seal Populations on the Seafood Industry in South Australia* (Adelaide: South Australian Research and Development Institute (Aquatic Sciences).

Goldsworthy, S. D. S., Smart, J., Mackay, A., Bailleul, F., Reinhold, S.-L., Stonnill, M., et al. (2019b). "Monitoring of Seal Bay and Other Pinniped Populations on Kangaroo Island: 2017/2018," in *Report to the Department for Environment and Water* (Adelaide: South Australian Research and Development Institute Aquatic Sciences). SARDI Publication No. F2014/000322-5. SARDI Research Report Series No. 1018 59pp.

Hauser-Davis, R. A., Monteiro, F., Da Rocha, R. C. C., Lemos, L., Cardoso, M. D., and Siciliano, S. (2020). Titanium as a Contaminant of Emerging Concern in the Aquatic Environment and the Current Knowledge Gap Regarding Seabird Contamination. *Ornithologia* 11, 7–15.

Hobson, K. A., and Clark, R. G. (1992). Assessing Avian Diets Using Stable Isotopes I: Turnover of 13C in Tissues. *Condor* 94, 181–188. doi: 10.2307/1368807

Hobson, K. A., Piatt, J. F., and Pitocchelli, J. (1994). Using Stable Isotopes to Determine Seabird Trophic Relationships. *J. Anim. Ecol.* 63, 786–798. doi: 10.2307/5256

Hoskins, A. J., Schumann, N., and Costa, D. P. (2017). Foraging Niche Separation in Sympatric Temperate-Latitude Fur Seal Species. *Marine Ecol. Prog. Ser.* 566, 229–241. doi: 10.3354/meps12024

Hunter, M. D., and Price, P. W. (1992). Playing Chutes and Ladders: Heterogeneity and the Relative Roles of Bottom-Up and Top-Down Forces in Natural Communities. *Ecology* 73, 724–732. doi: 10.2307/1940152

Hunt, G. L.Jr., Stabeno, P., Walters, G., Sinclair, E., Brodeur, R. D., Napp, J. M., et al. (2002). Climate Change and Control of the Southeastern Bering Sea Pelagic Ecosystem. *Deep Sea Res. Part II: Topical Stud. Oceanography* 49, 5821–5853. doi: 10.1016/S0967-0645(02)00321-1

Kämpf, J. (2015). Phytoplankton Blooms on the Western Shelf of Tasmania: Evidence of a Highly Productive Ecosystem. *Ocean Sci.* 11, 1–11. doi: 10.5194/os-11-1-2015

Kirkwood, R., and Goldsworthy, S. (2013). *Fur Seals and Sea Lions*. (Collingwood Victoria: CSIRO Publishing). doi: 10.1071/9780643109834

Kowalczyk, N. D., Chiaradia, A., Preston, T. J., and Reina, R. D. (2015). Fine-Scale Dietary Changes Between the Breeding and Non-Breeding Diet of a Resident Seabird. *R. Soc. Open Sci.* 2, 140–291. doi: 10.1098/rsos.140291

Ling, J. (1999). Exploitation of Fur Seals and Sea Lions From Australian, New Zealand and Adjacent Subantarctic Islands During the Eighteenth, Nineteenth and Twentieth Centuries. *Aust. Zoologist* 31, 323–350. doi: 10.7882/AZ.1999.036

Magera, A. M., Mills Flemming, J. E., Kaschner, K., Christensen, L. B., and Lotze, H. K. (2013). Recovery Trends in Marine Mammal Populations. *PloS One* 8, e77908. doi: 10.1371/journal.pone.0077908

Marchant, S., and Higgins, P. J. (1990). *Handbook of Australian, New Zealand & Antarctic Birds. Vol. 1, Ratites to Ducks, Part B: Australian Pelicans to Ducks* (Melbourne: Oxford University Press Australia and New Zealand).

Marshall, K. N., Stier, A. C., Samhouri, J. F., Kelly, R. P., and Ward, E. J. (2016). Conservation Challenges of Predator Recovery. *Conserv. Lett.* 9, 70–78. doi: 10.1111/conl.12186

Matson, P., and Hunter, M. (1992). Special Feature: Top-Down and Bottom-Up Forces in Population and Community Ecology. *Ecology* 73, 723–765. doi: 10.2307/1940151

Mccutcheon, C., Dann, P., Salton, M., Renwick, L., Hoskins, A., Gormley, A., et al. (2011). The Foraging Range of Little Penguins (*Eudyptula Minor*) During Winter. *Emu* 111, 321–329. doi: 10.1071/MU10078

Middleton, J. F., Arthur, C., Van Ruth, P., Ward, T. M., Mcclean, J. L., Maltrud, M. E., et al. (2007). El Nino Effects and Upwelling Off South Australia. *J. Phys. Oceanography* 37, 2458–2477. doi: 10.1175/JPO3119.1

Middleton, J. F., and Bye, J. A. (2007). A Review of the Shelf-Slope Circulation Along Australia's Southern Shelves: Cape Leeuwin to Portland. *Prog. Oceanography* 75, 1–41. doi: 10.1016/j.pocean.2007.07.001

Miller, R. J., Bennett, S., Keller, A. A., Pease, S., and Lenihan, H. S. (2012). Tio_2 Nanoparticles are Phototoxic to Marine Phytoplankton. *PloS One* 7, e30321. doi: 10.1371/journal.pone.0030321

Morrison, K. W., Armstrong, D. P., Battley, P. F., Jamieson, S. E., and Thompson, D. R. (2016). Predation by New Zealand Sea Lions and Brown Skuas is Causing the Continued Decline of an Eastern Rockhopper Penguin Colony on Campbell Island. *Polar Biol.* 40, 735–751. doi: 10.1007/s00300-016-1996-9

Norman, F., Dann, P., Du Guesclin, P., Drynan, D., and Sutherland, D. (2017). Recoveries of Little Penguins *Eudyptula Minor* Flipper-Banded at Colonies in Western Victoria. *Corella* 41, 20–26.

Norman, F., Dann, P., Unthank, S., and Montague, T. (2012). Movements of Little Penguins *Eudyptula Minor* Banded at Rabbit Island and the Seal Island Group, Wilsons Promontory, Victoria. *Corella* 3, 57–62.

Page, B., Mckenzie, J., and Goldsworthy, S. D. (2005). Dietary Resource Partitioning Among Sympatric New Zealand and Australian Fur Seals. *Marine Ecol. Prog. Ser.* 293, 283–302. doi: 10.3354/meps293283

Paleczny, M., Hammill, E., Karpouzi, V., and Pauly, D. (2015). Population Trend of the World's Monitored Seabirds. *PloS One* 10, 1950–2010. doi: 10.1371/journal.pone.0129342

Pelletier, L., Chiaradia, A., Kato, A., and Ropert-Coudert, Y. (2014). Fine-Scale Spatial Age Segregation in the Limited Foraging Area of an Inshore Seabird Species, the Little Penguin. *Oecologia* 176, 399–408. doi: 10.1007/s00442-014-3018-3

Preston, T. J., Ropert-Coudert, Y., Kato, A., Chiaradia, A., Kirkwood, R., Dann, P., et al. (2008). Foraging Behaviour of Little Penguins *Eudyptula Minor* in an Artificially Modified Environment. *Endangered Species Res.* 4, 95–103. doi: 10.3354/esr00069

Radhalakshmi, R., Sivakumar, V., and Ali, H. (2014). Analysis of Selected Species of Ascidians as Bioindicators of Metals in Marine Ecosystem. *Internation J. Curr. Microbiol. Appl. Sci.* 3, 755–764.

Reilly, P., and Cullen, J. (1981). The Little Penguin *Eudyptula Minor* in Victoria, II: Breeding. *Emu* 81, 1–19. doi: 10.1071/MU9810001

Reilly, P., and Cullen, J. (1982). The Little Penguin *Eudyptula Minor* in Victoria III. Dispersal of Chicks and Survival After Banding. *Emu-Austral Ornithol.* 82, 137–142. doi: 10.1071/MU9820137

Rey, A. R., Samaniego, R. S., and Petracci, P. F. (2012). New Records of South American Sea Lion *Otaria Flavescens* Predation on Southern Rockhopper Penguins *Eudyptes Chrysocome* at Staten Island, Argentina. *Polar Biol.* 35, 319–322. doi: 10.1007/s00300-011-1072-4

Ridgway, K. (1997). Seasonal Cycle of the East Australian Current. *J. Geophysical Res. Oceans* 102, 921–936. J. S. doi: 10.1029/97JC00227

Roman, J., Dunphy-Daly, M. M., Johnston, D. W., and Read, A. J. (2015). Lifting Baselines to Address the Consequences of Conservation Success. *Trends Ecol. Evol.* 30, 299–302. doi: 10.1016/j.tree.2015.04.003

Ross, G., Burbidge, A., Brothers, N., Canty, P., Dann, P., Fuller, P., et al. (1995). "The Status of Australia's Seabirds," in *The State of the Marine Environment Report for Australia: Technical Annex: 1*. Eds. L. P. Zann and P. Kailola (Townsville, Qld: Great Barrier Reef Marine Park Authority), 167–182.

Salton, M., Carr, M., Tarjan, L. M., Clarke, J., Kirkwood, R., Slip, D., et al. (2021). Protected Area Use by Two Sympatric Marine Predators Repopulating Their Historical Range. *Endangered Species Res.* 45, 181–194. doi: 10.3354/esr01129

Sandery, P. A., and Kämpf, J. (2007). Transport Timescales for Identifying Seasonal Variation in Bass Strait, South-Eastern Australia. *Estuarine Coastal Shelf Sci.* 74, 684–696. doi: 10.1016/j.ecss.2007.05.011

Scheuhammer, A. (1987). The Chronic Toxicity of Aluminium, Cadmium, Mercury, and Lead in Birds: A Review. *Environ. Pollution* 46, 263–295. doi: 10.1016/0269-7491(87)90173-4

Shaughnessy, P. D., Goldsworthy, S. D., and Mackay, A. I. (2015). The Long-Nosed Fur Seal (*Arctocephalus forsteri*) in South Australia in 2013–14: Abundance, Status and Trends. *Aust. J. Zool.* 63, 101–110. doi: 10.1071/ZO14103

Shi, H., Magaye, R., Castranova, V., and Zhao, J. (2013). Titanium Dioxide Nanoparticles: A Review of Current Toxicological Data. *Particle Fibre Toxicol.* 10, 1–33. doi: 10.1186/1743-8977-10-15

Sidhu, L. A., Dann, P., Chambers, L., and Catchpole, E. A. (2012). Seasonal Ocean Temperature and the Survival of First-Year Little Penguins *Eudyptula Minor* in South-Eastern Australia. *Marine Ecol. Prog. Ser.* 454, 263–272. doi: 10.3354/meps09709

Sun, T., Wu, H., Wang, X., Ji, C., Shan, X., and Li, F. (2020). Evaluation on the Biomagnification or Biodilution of Trace Metals in Global Marine Food Webs by Meta-Analysis. *Environ. Pollution* 264, 113856. doi: 10.1016/j.envpol.2019.113856

Vanderklift, M. A., and Ponsard, S. (2003). Sources of Variation in Consumer-Diet δ^{15}n Enrichment: A Meta-Analysis. *Oecologia* 136, 169–182. doi: 10.1007/s00442-003-1270-z

Visser, I. N., Drennan, M. P., White, R. W., Maclean, S. F., Lagerstrom, L. C., and Francis, J. M. (2008). Antarctic Fur Seals (*Arctocephalus Gazella*) Observed Predating Adélie (*Pygoscelis Adeliae*) and Chinstrap Penguins (*P. Antarctica*), Antarctic Peninsula. *Aquat. Mammals* 34, 193–199. doi: 10.1578/AM.34.2.2008.193

Walsh, P. (2018). "The Use of Seabirds as Monitors of Heavy Metals in the Marine Environment," in *Heavy Metals in the Marine Environment*, vol. 183-204 . Eds. R. W. Furness and P. S. Rainbow (Florida USA: CRC Press). doi: 10.1007/978-3-030-73613-2_1

Weir, A., Westerhoff, P., Fabricius, L., Hristovski, K., and Von Goetz, N. (2012). Titanium Dioxide Nanoparticles in Food and Personal Care Products. *Environ. Sci. Technol.* 46, 2242–2250. doi: 10.1021/es204168d

Xavier, J. C., and Trathan, P. N. (2020). "Penguins: Diversity, Threats, and Role in Marine Ecosystems," in *Life Below Water*. Eds. W. Leal Filho, A. M. Azul, L. Brandli, A. Lange Salvia and T. Wall. (Cham: Springer International Publishing), 1–10.

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Deciphering the Trophic Ecology of Three Marlin Species Using Stable Isotope Analysis in Temperate Waters Off Southeastern Australia

Tristan A. Guillemin[1]*, Julian G. Pepperell[2], Troy Gaston[3] and Jane E. Williamson[1,4]

[1] School of Natural Sciences, Macquarie University, Sydney, NSW, Australia, [2] Pepperell Research and Consulting Pty Ltd., Noosaville, QLD, Australia, [3] School of Environmental and Life Sciences, University of Newcastle, Ourimbah, NSW, Australia, [4] Sydney Institute of Marine Science, Mosman, NSW, Australia

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Nuno Queiroz,
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Sofia Ortega-Garcia,
Instituto Politécnico Nacional (IPN), Mexico
Tatiana Acosta-Pachon,
Universidad Autónoma de Baja California Sur, Mexico

***Correspondence:**
Tristan A. Guillemin
tristan.guillemin@students.mq.edu.au

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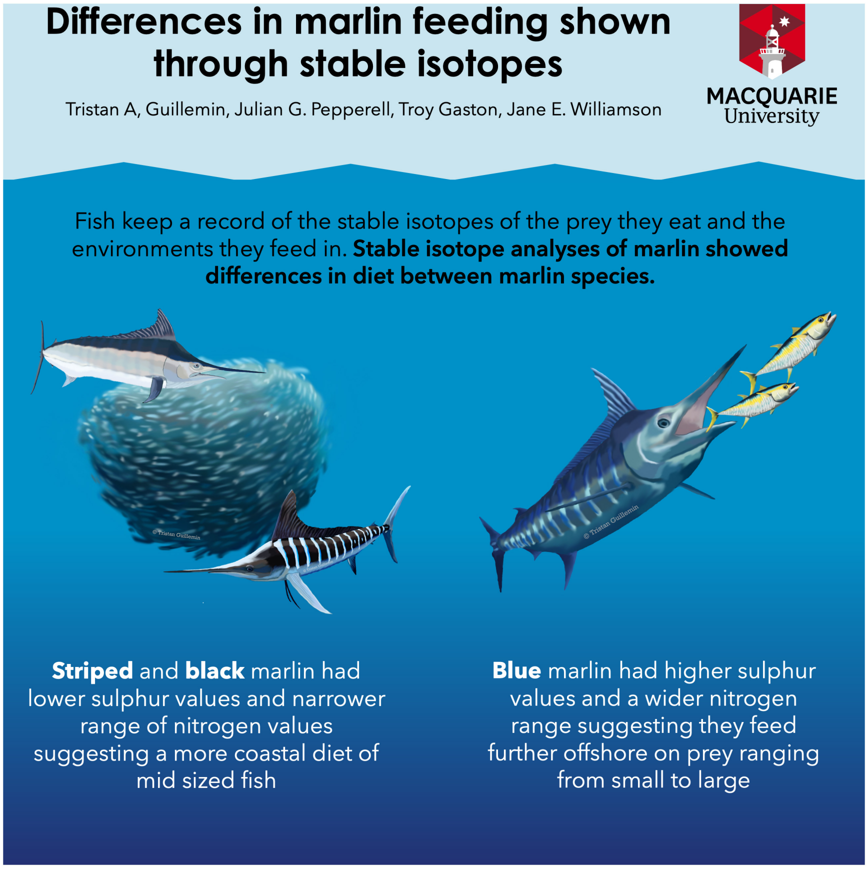
Understanding the unique feeding behaviours of oceanic fish, such as marlin, is key to their effective management. Marlin are notoriously difficult to study, however, and the limited research on marlin feeding shows that diet can vary greatly between species and geographic regions. One region where marlin feeding behaviours are particularly poorly understood are temperate eastern Australian waters. This study collected marlin tissue from game fishing tournaments between latitudes 32°43′06.5′′S/152°08′50.1′′E to 34°40′12.9′′S/150°51′34.3′′E between 2010 and 2021, and used stable isotope analysis (SIA) to assess the trophic ecology of the three species of marlin occurring in the region: black (*Istiompax indica*), blue (*Makaira nigricans*), and striped (*Kajikia audax*) marlin. All species had similar δ^{13}C values, but δ^{15}N differed between species, with higher variability observed in blue marlin than in the other two species. Sulphur isotopes were key in identifying the relative contribution of coastal or benthic influences on marlin diet, with δ^{34}S suggesting that blue marlin had less coastal/benthic dietary influence than black or striped marlin. Incorporation of δ^{34}S into SIA for marlin is thus recommended for future studies. Some differences in isotope values across locations and dates were found, however, the uneven sample sizes due to the opportunistic sampling limited the ability to understand spatial or seasonal differences. These findings show that marlin followed similar dietary trends to conspecifics in other regions despite temperate eastern Australian waters being one of the few with three marlin species commonly co-occuring. This suggests that interspecies resource competition is not a major force driving the demography of these species in eastern Australian waters. This research highlights a need for specific management strategies at a species level, particularly for blue marlin. Future research incorporating prey isoscapes and baselines assessed over a wider range of marlin sizes is suggested to further improve our knowledge and capacity to manage the marlin of eastern Australian waters.

Keywords: marlin, trophic ecology, stable isotope, feeding, gamefish, sulphur



Differences in marlin feeding shown through stable isotopes

Tristan A, Guillemin, Julian G. Pepperell, Troy Gaston, Jane E. Williamson

MACQUARIE University

Fish keep a record of the stable isotopes of the prey they eat and the environments they feed in. **Stable isotope analyses of marlin showed differences in diet between marlin species.**

Striped and **black** marlin had lower sulphur values and narrower range of nitrogen values suggesting a more coastal diet of mid sized fish

Blue marlin had higher sulphur values and a wider nitrogen range suggesting they feed further offshore on prey ranging from small to large

GRAPHICAL ABSTRACT | Summarizing some of the key differences revealed by stable isotope analysis of three marlin species (black, blue and striped marlin) in this study. Graphical abstract drawn by TGu, Macquarie University.

INTRODUCTION

The role that apex predators play in ecosystem dynamics has long been recognised as pivotal (Estes et al., 2011; Ripple et al., 2014). Due to this perceived importance, apex predators are often the target of conservation and management efforts (Sergio et al., 2008). In ecosystems where multiple predatory species are present, competition for food and trophic partitioning can influence diet and therefore the role that individual species play (Raoult et al., 2015; Curnick et al., 2019). In some instances, high diversity of predators can even lead to functional redundancy in which multiple species play similar trophic roles (Frisch et al., 2016). A lack of understanding of this overlap in trophic ecology can lead to mismanagement of already limited conservation resources (Sergio et al., 2008). Therefore, understanding these inter-predatory interactions is crucial to the efficient management of predatory function in ecosystems.

Marlin are large, oceanic fish considered keystone predators in their environment (Hinman, 1998; Kitchell et al., 2006; Chang et al., 2019). Marlin are also one of the most iconic and targetted fishes by recreational fishers (Ditton and Stoll, 2000; Ward et al., 2012) and are important to commercial fisheries, both as targetted species and bycatch (Restrepo et al., 2003; Langley et al., 2006). Our understanding of their biology and behaviours, however, is limited by the difficulties associated with researching these species and a lack of rigorous data collection on recreational or game fisheries (Holland, 2003; Griffiths, 2012). Managing marlin is particularly challenging as their geographic distributions are large and their often extensive oceanic movements mean that individuals regularly cross multiple jurisdictional boundaries (Hillary et al., 2015). Knowledge of marlin behaviours, including movement and species-specific and regionally specific prey choice are not well understood (Chang et al., 2019). Such information is important when identifying spatial "hotspots" and setting sustainable catch rates and management strategies for recreational and commercial target species such as marlin (Hillary et al., 2015; Lynch et al., 2019).

Marlin in waters off temperate eastern Australia specifically are difficult to manage due to our poor understanding of their behaviours and pressures they face (Findlay et al., 2003). Three species of marlin commonly occur in these waters: black (*Istiompax indica*), blue (*Makaira nigricans*), and striped (*Kajikia audax*). These marlin typically migrate down from the equator into eastern Australia to feed during the warmer months of the year, though the timings of these migrations vary annually and between species (Ghosn et al., 2015). The average size of each species caught and landed by recreational fishers in this region also varies, with striped marlin averaging 91 kg, black marlin averaging 104 kg, and blue marlin averaging 155 kg (Pepperell, 2018). Tag and release data reveals that the sizes of captured blue and striped marlin are roughly representative of the population. However, some years juvenile black marlin weighing 25–40 kg dominate the size distribution of fish tagged (Ghosn et al., 2015) but are not captured as they fall below the minimum tournament weight cut-off of 60 kg.

Research to date indicates that marlin diet varies between stocks and species and that these patterns are complex (Ortiz et al., 2003; Shimose et al., 2006; Torres Rojas et al., 2013; Chiang et al., 2020). Tagged marlin can display distinct geographical ranges and movement patterns, both within and between species (Ortiz et al., 2003; Domeier et al., 2019). Diets as indicated by stomach content analysis are highly variable both in terms of species consumed and prey size across regions (Ueyanagi and Wares, 1972; Shimose et al., 2006, 2008). Stomach content analyses undertaken in temperate eastern Australia have shown that teleosts were the primary, and squid the secondary prey items for striped marlin in this region (Young et al., 2010). The high variability in diet across regions and limited understanding of diet preferences at different life history stages of these animals constrains cohesive management strategies.

One method of studying the trophic ecology of marlin is through stable isotope analysis (SIA). SIA has been used to examine nutritional origin, trophic relationships, ontogeny and broad spatial movements in a wide range of marine animals (Hesslein et al., 1991; Kiljunen et al., 2006; Rodgers and Wing, 2008; Raoult et al., 2015, 2019; Park et al., 2017; Whitfield, 2017). Typically, this method uses varying isotopic turnover rates of nitrogen (δ^{15}N) and carbon (δ^{13}C) among tissues as tracers of diet source within an organism (Vander Zanden et al., 1997). These two isotopes are commonly used for their ability to discriminate between trophic levels (δ^{15}N) and between foraging location or prey types (δ^{13}C) as well as their low analysis cost (relative to other stable isotopes) (Raoult et al., 2019). Varying isotopic turnover rates of different tissue types allow them to provide different temporal insights into fish isotopes, with muscle tissue generally considered to have turnover rates of 6 months to a year (Madigan et al., 2012; Malpica-Cruz et al., 2012).

The few studies that have assessed SIA in marlin show great variation in δ^{15}N and δ^{13}C isotopic ratios within and between species in a manner similar to gut-content analyses. In blue marlin, for example, δ^{15}N is far more variable than δ^{13}C (Logan and Lutcavage, 2013; Torres Rojas et al., 2013; Chang et al., 2019; Chiang et al., 2020), suggesting this species consistently feeds within similar food webs but consumes prey occupying different trophic levels. Striped marlin show different δ^{13}C and δ^{15}N signatures to blue marlin (Torres Rojas et al., 2013; Acosta-Pachón et al., 2015), suggesting less predictability within this species and a high degree of variability in feeding that could be considered opportunistic. The only study to have evaluated black marlin SIA found high variability in δ^{13}C and δ^{15}N and reported higher δ^{15}N values than in other marlin species (Chiang et al., 2020). Moreover, the studies comparing SIA for two co-occurring marlin species have all documented niche segregation in marlin, occurring between blue and striped marlin off Mexico (Torres Rojas et al., 2013; Ordiano-Flores et al., 2021), and between black and blue marlin off eastern Taiwan (Chiang et al., 2020).

All marlin SIA studies to date have been limited to these two isotopic tracers, however, use of a greater number of tracers allows increased clarity in mixed model analyses of SIA and can result in different and more comprehensive interpretations of trophic ecology (Raoult et al., 2019). Analysis of sulphur (δ^{34}S) as a third natural tracer has been included in some isotope studies due to its' ability to contrast benthic and pelagic origins, and distinguish terrestrial from oceanic or even anthropogenic sources (Connolly et al., 2004; Croisetiere et al., 2009; Raoult et al., 2019). Black and striped marlin are more commonly caught and encountered inside the continental shelf break whereas blue marlin are caught wide of the shelf break, potentially due to differences in diet between the species (Ghosn et al., 2015). Including δ^{34}S in SIA in addition to the usual δ^{13}C and δ^{15}N would help tease apart trophic ecology for such enigmatic species. A similar research question was asked by Plumlee and Wells (2016), who used δ^{34}S to successfully discriminate between diets of three coastal shark species with perceived differing coastal and pelagic foraging. Other studies have similarly shown that adding δ^{34}S increases certainty when comparing dietary sources between teleost groups with varying degrees of coastal or pelagic influence in their diet (Thomas and Cahoon, 1993; Wells et al., 2008).

This study used nitrogen, carbon and sulphur SIA to assess commonalities and differences in the trophic ecology for three species of marlin occurring off eastern Australian waters. This is the first study to evaluate SIA for marlin in the South Pacific, filling crucial knowledge gaps for the region. This study is also the first to incorporate δ^{34}S in a three tracer approach to evaluate the trophic ecology of marlin species. Two key research questions were posed: (1) do different marlin species in temperate eastern Australian waters share similar isotopic niches, and (2) is the use of δ^{34}S as an environmental tracer in marlin useful for trophic assessments?

MATERIALS AND METHODS

Sample Collection

White muscle samples ($\sim$1,000 mm^3) from black, blue and striped marlin were opportunistically sourced from individuals captured across fourteen game fishing tournaments (a total of 34 tournaments). All tournaments were run by clubs affiliated with the New South Wales (NSW) Game Fishing Association in Australia and occurred between Port Stephens (32°43′06.5″S/152°08′50.1″E) and Kiama (34°40′12.9″S/150°51′34.3″E) between 2018 and 2021 (**Table 1**). The range of fishing boats from any port was within a 70 km arc. Additional marlin tissue preserved in the same manner as the current study (see below) but from earlier fishing competitions dating back to 2010 were also used. Tissue samples were removed from the ventral surface of each marlin near the anal fin and stored individually and immediately frozen to -30°C until processed. The whole weight of each fish (as weighed by the tournament weighmaster) and the "short length" (tip of the

TABLE 1 | Locations from which tissue was collected and the sample size (number of individuals) of tissue collected for three different marlin species: black marlin (*Istiompax indica*), blue marlin (*Makaira nigricans*), and striped marlin (*Kajikia audax*).

Sampling location	Lat	Long	Black marlin			Blue marlin			Striped marlin	
			♀	♂	NR	♀	♂	NR	♀	♂
Port Stephens (2016–2020)	32°43′06.5″S	152°08′50.1″E	1	8	0	21	4	16	6	17
Newcastle (2019)	32°55′11.4″S	151°45′40.5″E	0	0	0	1	0	2	0	0
Gosford (2012, 2019)	33°26′12.6″S	151°20′27.8″E	2	0	0	1	1	0	0	2
Broken Bay (2012)	33°39′07.1″S	151°18′09.2″E	0	0	0	1	0	0	0	0
Watsons Bay (2014, 2016–2017, 2019)	33°50′36.1″S	151°16′51.8″E	0	0	1	8	1	3	1	0
Botany Bay (2012, 2014, 2021)	33°59′57.9″S	151°07′19.5″E	0	2	0	1	0	1	1	0
Port Hacking (2011–2012, 2015–2017)	34°03′44.6″S	151°08′27.8″E	0	0	0	3	1	0	1	1
Kiama (2019)	34°40′12.9″S	150°51′34.3″E	0	0	0	3	1	0	1	0
Location NR (2016)			0	0	0	1	1	1	0	0

Samples were collected from several different fishing tournaments hosted by a variety of game fishing clubs and by the New South Wales Game Fishing Association (NR, Not Recorded).

lower jaw to caudal fork; the most commonly used measurement of length in Istiophorid research) were recorded. Sex was determined by making an incision in the underside of the fish and macroscopically inspecting the gonads.

Stable Isotope Analyses

Tissue samples were individually placed in a drying oven (Binder, ED115) and dried for 48 h at 60°C. Desiccated samples were ground into a fine powder using a mortar and pestle, which was rinsed thoroughly with deionised water and dried between each sample. Powdered tissue (∼1 g per sample) was placed into separate 5 mL plastic centrifuge tubes and sent to Griffith University Stable Isotope Laboratory in Queensland, Australia, for analysis. Nitrogen, carbon and sulphur stable isotopes were assessed using a Europa EA GSL element analyser (Europa Scientific Inc., Cincinnati, OH, United States) coupled to a Hydra 20–22 automated Isoprime isotope ratio mass spectrometer (Sercon Ltd., Crewe, Cheshire, United Kingdom). Ratios of ^{15}N:^{14}N ($\delta^{15}N$) were expressed as the relative difference between the sample and a standard of atmospheric nitrogen. Ratios of ^{13}C:^{12}C ($\delta^{13}C$) were expressed as the relative difference between the sample and the PDB (Pee Dee belemnite) standard. Ratios of ^{34}S:^{32}S ($\delta^{34}S$) were expressed as the relative difference between the sample and the Vienna-Canyon Diablo Troilite. Ten standards of bovine liver, glycine NBS127 and glycineLSU 1 delta were run with each tray. The standard deviation for measurements of standards was 0.2–0.4‰ for $\delta^{13}C$, 0.1–0.3‰ for $\delta^{15}N$, and 0.4‰ for $\delta^{34}S$.

Data Analyses

All statistical analyses were undertaken using R (R Development Core Team, 2021). As lipid extractions were not done on the samples, the $\delta^{13}C$ values were corrected in individuals with high C:N ratios as per Kiljunen et al. (2006). Linear mixed-effects models were constructed in R using the lme4 package (Bates et al., 2018) with the isotope type included as the response variables in three separate models. Linear models were used to test whether isotope values varied between years and locations or between different sexes and sizes of fish. Significance of each of these main effects were obtained with an ANOVA type III table using the anova function in the lmertest package (Kuznetsova et al., 2017). When comparing isotopic values between marlin species, sex, date (day, month, and year), and weight were included as fixed effects with location included as a random effect in all models. Weight was used as a proxy of size instead of length as length correlated closely with weight, and weight was recorded for a higher proportion of our samples. Residuals from the models met linearity and normality assumptions. Pairwise comparisons among main effects were obtained using the pairwise method and a *p*-value adjustment equivalent to the Tukey test in the emmeans package (Lenth et al., 2019). Trophic niches for the three marlin species were estimated and compared using the r package nicheROVER (Swanson et al., 2015). Within niche rover, trophic niches were generated using Bayesian analysis of $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values at 1,000 runs with a probability level of alpha = 0.95. A random 10 niche regions were plotted to create 2-dimensional niche projections, these were plotted alongside biplots and probability plots as part of the nicheROVER package. The size (as individual values and standard deviations) of the trophic niche was calculated based on the parameters μ and Σ in a Bayesian context. This allowed the probability of individual marlin from one species falling within the niche of another species to be calculated.

RESULTS

Tissue was sampled from a total of 13 black marlin (*Istiompax indica*), 73 blue marlin (*Makaira nigricans*), and 30 striped marlin (*Kajikia audax*) (**Table 2**) and $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ were analysed for each fish (**Table 3**). The majority of samples were obtained during the 2018–2021 seasons, with 1 black marlin, 27 blue marlin, and 6 striped marlin sampled in other seasons (2012–2017). Mixed effects models determined that find weight, sex, date, or sampling locations had no significant effect on any of the three isotopes for black marlin (**Supplementary Appendix 1**). For blue marlin, sampling location had a significant effect on $\delta^{34}S$ values (ANOVA: $F(7,36) = 3.7093$, $p = 0.0040$), no other

TABLE 2 | Mean size (±1SD) and size range of male and female marlin of each of the three species sampled: black marlin (*Istiompax indica*), blue marlin (*Makaira nigricans*), and striped marlin (*Kajikia audax*).

		Length (cm)				Weight (kg)			
	Sex	**Mean**	**St. Dev**	**Min**	**Max**	**Mean**	**St. Dev**	**Min**	**Max**
Black Marlin	F	210.3	19.5	196.0	239.0	87.0	25.9	68.5	125.4
	M	207.0	17.4	187.0	240.0	80.1	19.8	61.5	126.5
Blue Marlin	F	247.0	25.7	207.0	330.0	136.4	62.0	63.8	348.5
	M	232.1	17.3	206.0	260.0	120.8	26.0	77.0	171.5
Striped Marlin	F	237.4	10.4	214.0	253.0	87.7	13.2	70.0	120.2
	M	224.3	7.4	211.0	239.0	76.4	9.8	62.2	97.1

TABLE 3 | Mean (±1SD), minimum and maximum stable isotope (δ^{13}C, δ^{15}N, and δ^{34}S) values of each of the three species sampled: black marlin (*Istiompax indica*) blue marlin (*Makaira nigricans*), and striped marlin (*Kajikia audax*).

	δ^{13}C				δ^{15}N				δ^{34}S			
	Mean	*Standard Deviation*	*Min*	*Max*	*Mean*	*Standard Deviation*	*Min*	*Max*	*Mean*	*Standard Deviation*	*Min*	*Max*
Black Marlin	−15.5	0.5	−16.7	−14.9	13.1	0.5	12.1	13.7	18.9	0.6	17.5	19.6
Blue Marlin	−15.2	0.6	−16.5	−12.8	12.5	1.0	9.4	15.1	19.3	0.5	18.4	21.0
Striped Marlin	−15.7	0.5	−16.7	−14.2	12.9	0.7	11.5	14.3	18.7	0.7	17.5	20.2

significant effects of weight, sex, date, or sampling location were found (**Supplementary Appendix 1**). In striped marlin, capture date was found to have significant effects on both δ^{15}N (ANOVA: $F(1,21) = 12.6305$, $p = 0.0019$) and δ^{34}S (ANOVA: $F(1,21) = 9.1723$, $p = 0.0064$) values, no other significant effects of weight, sex, date, or sampling location were found (**Supplementary Appendix 1**).

Neither mean δ^{13}C or mean δ^{15}N values differed significantly between any marlin species (**Figure 1** and **Table 4**). Blue marlin had a wider range of both δ^{13}C and δ^{15}N values than black and striped marlin (**Figure 2**). δ^{34}S also differed significantly between species with blue marlin having significantly higher mean δ^{34}S than both black and striped marlin (**Figure 2** and **Table 4**).

Blue marlin had the largest isotopic niche (25.85 ± 1SD 4.25) followed by striped marlin (22.49 ± 1SD 3.74) and then black marlin (11.95 ± 1SD 3.29). Black marlin showed the highest probability to be found in niche regions of other marlin with an 85.98% probability for blue marlin and 89.60% striped marlin (**Figure 3**). Blue marlin had the lowest probability to be found in the niche region of other species with 50.95% chance to occur within the black marlin niche and 66.73% chance for the striped marlin niche (**Figure 3**). Lastly, the chances for striped marlin to fall within niche of black marlin and blue marlin were 63.68 and 70.61%, respectively (**Figure 3**).

DISCUSSION

Overall isotopic values and ranges were similar between marlin, but there were some differences which suggest some disparities in their diets and/or movements in temperate eastern Australian waters. In particular, the isotopic niche that blue marlin occupied differed to that occupied by black and striped marlin. The similar mean δ^{13}C and δ^{15}N values across marlin species suggest all three feed on similar types and sizes of prey sources and likely within similar environments. However, wider range of both δ^{13}C and δ^{15}N values in blue marlin than in the other two species suggests greater dietary variability in prey size/trophic level and prey type for this species. δ^{34}S was useful in differentiating between blue marlin and the other two species. Specifically, the significantly higher mean and narrower range of δ^{34}S values of blue marlin are indicative of a less benthic or coastal influence in their prey. These results suggest a slight disparity between the ecological roles played by different marlin species off eastern Australia. Statistical analyses showed blue marlin δ^{34}S differed significantly between locations and that striped marlin δ^{15}N and δ^{34}S differed significantly between sampling dates. The locations and dates in which marlin isotopes differed significantly had sample sizes of 4 or less. The effect of location and date was noted and included in our models, however, it is unclear whether these results are ecologically relevant or whether our opportunistic sampling limited the ability to build a robust dataset. Samples from a greater latitude and range of dates are needed to determine the ecological significance of these effects.

Stable isotope analysis of marlin in our study typically supported what is known from other isotope studies in other areas of the world for these species. The only other study to have analysed black marlin isotopes, undertaken in Taiwan, recorded remarkably similar means and ranges for both δ^{15}N and δ^{13}C (Chiang et al., 2020) possibly suggesting similarities in feeding ecology between the two regions for this species. While specific values differed, blue marlin in our study demonstrated similarly higher variability in δ^{15}N compared to δ^{13}C observed in other regions (Logan and Lutcavage, 2013; Torres Rojas et al., 2013; Chang et al., 2019; Chiang et al., 2020). The two studies that have

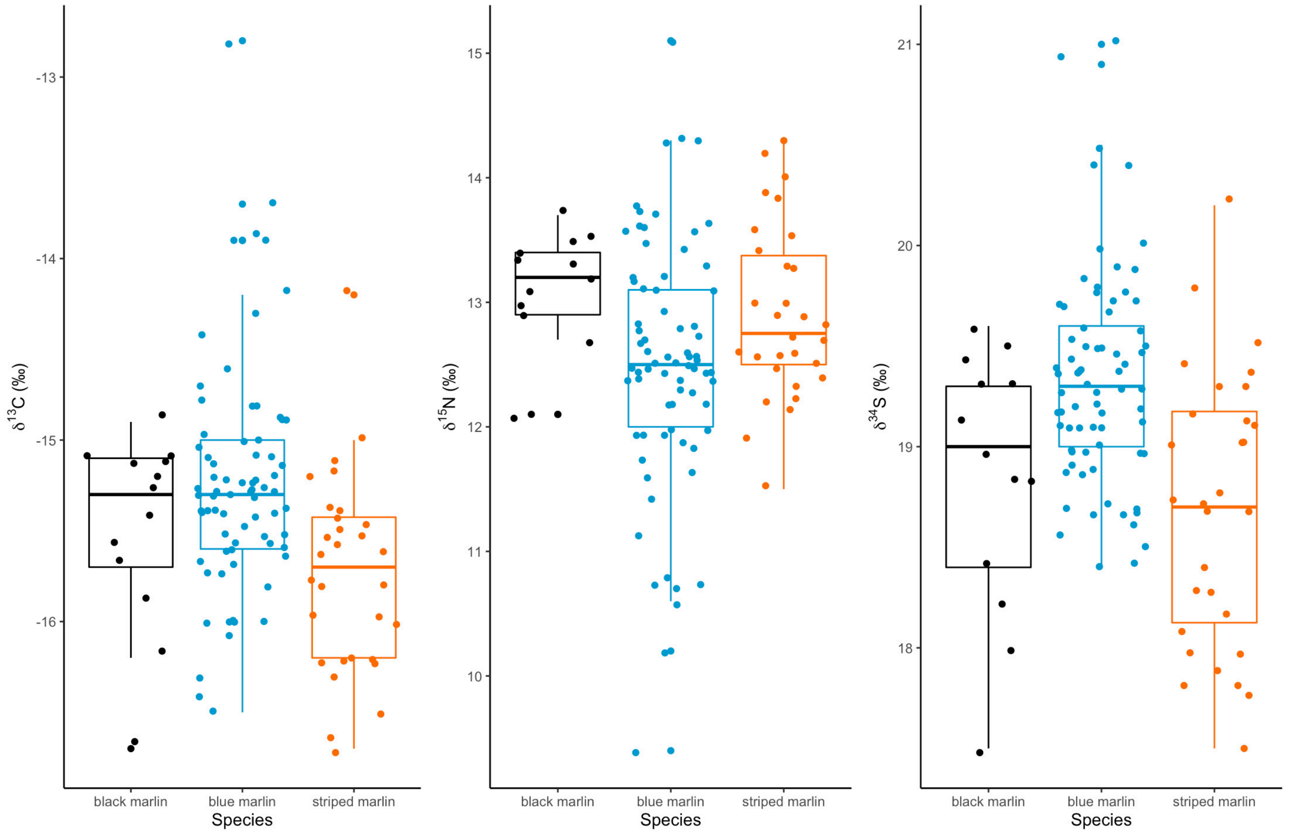


FIGURE 1 | Boxplots of mean isotope ($\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$) values for three marlin species: black marlin (*Istiompax indica*), blue marlin (*Makaira nigricans*), and striped marlin (*Kajikia audax*).

TABLE 4 | Results of ANOVA tests run on linear mixed effects models comparing isotope ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$) values between three marlin species: black marlin (*Istiompax indica*) blue marlin (*Makaira nigricans*), and striped marlin (*Kajikia audax*).

	$\delta^{13}C$	$\delta^{15}N$	$\delta^{34}S$
Black Marlin vs. Blue Marlin	*F*(84) = 2.0911 *p* = 0.9869	*F*(82) = 2.3688 *p* = 0.1557	*F*(83) = 8.6424 *p* = 0.0486*
Black Marlin vs. Striped Marlin	*F*(83) = 2.0911 *p* = 0.3531	*F*(84) = 2.3688 *p* = 0.8604	*F*(84) = 8.6424 *p* = 0.6836
Blue Marlin vs. Striped Marlin	*F*(82) = 2.0911 *p* = 0.1712	*F*(84) = 2.3688 *p* = 0.1738	*F*(83) = 8.6424 *p* = 0.0003*

** Indicates significance.*

analysed striped marlin isotopes (both undertaken in the Gulf of California) report higher variability in $\delta^{15}N$ and $\delta^{13}C$ values than found here (Torres Rojas et al., 2013; Acosta-Pachón et al., 2015). Every region has its own isotopic baselines and behaviors limiting cross regional comparison (Cherel and Hobson, 2007), however, there were similarities between regions which may help uncover big-picture marlin isotope ecology with future isoscape information.

Mean $\delta^{13}C$ values suggested little overall difference between the prey sources or food webs utilised by all three species of marlin on the east coast of Australia, except for potentially higher prey variability in blue marlin. However, stomach content analyses undertaken on marlin in other regions consistently show both inter- and intra- specific differences and variability in prey species (Ueyanagi and Wares, 1972; Abitia-Cardenas et al., 1999; Shimose et al., 2006, 2008). While the similarities we observed in $\delta^{13}C$ values may reflect similar prey use in Australian marlin, they may also reflect the limitations of using $\delta^{13}C$ in discriminating diets in oceanic fish. Specifically, oceanic $\delta^{13}C$ variability is largely driven by latitudinal gradients in phytoplankton carbon (Raoult et al., 2020), $\delta^{13}C$ may therefore not be as effective in discriminating between prey sources within a relatively narrow latitude of open ocean. Future studies using $\delta^{13}C$ isotopes in oceanic predators may benefit from collecting prey isoscapes or from using additional trophic ecology methods such as stomach content or fatty acid analysis (Young et al., 2018).

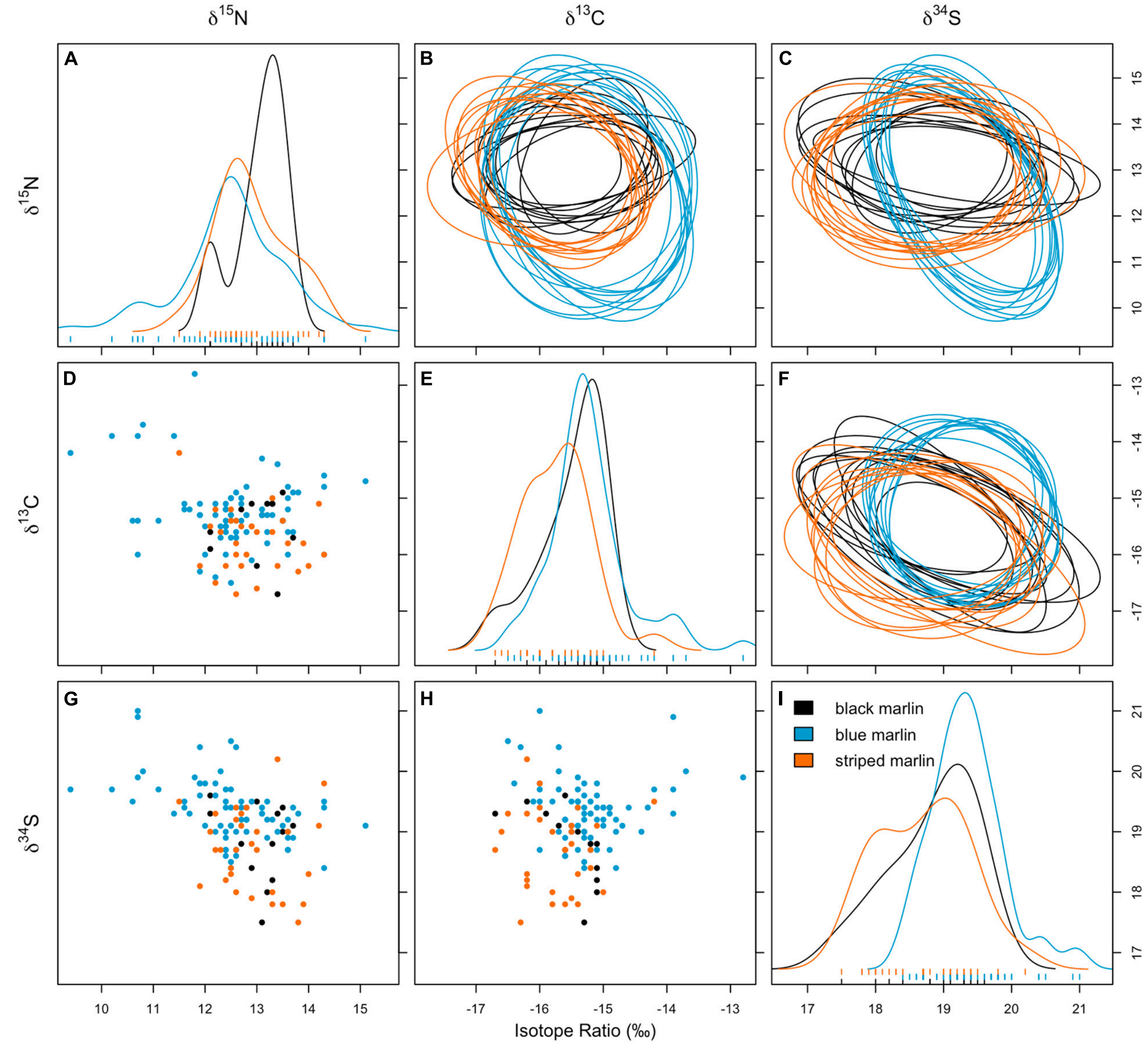


FIGURE 2 | Biplots for δ^{13}C vs. δ^{15}N **(D)**, δ^{15}N vs. δ^{34}S **(G)**, and δ^{13}C vs. δ^{34}S **(H)**; density plots showing distribution of isotope values of δ^{15}N **(A)**, δ^{13}C **(E)**, and δ^{34}S **(I)**; and bayesian ellipse areas (10 runs plotted) using posterior estimates of ellipses for δ^{13}C vs. δ^{15}N **(B)**, δ^{15}N vs. δ^{34}S **(C)**, and δ^{13}C vs. δ^{34}S **(F)** for three marlin species: black marlin (*Istiompax indica*), blue marlin (*Makaira nigricans*), and striped marlin (*Kajikia audax*).

The δ^{15}N results in our research largely aligned with what is known about marlin feeding through dietary studies. The similar δ^{15}N range between black and striped marlin suggested a wider trophic niche or they fed on comparable trophic levels, while the wider range of blue marlin suggested far more variability in prey size. Black and striped marlin are known to feed largely on mid-sized schooling teleosts, though black marlin can also feed on larger pelagic and mesopelagic prey (Ueyanagi and Wares, 1972; Shimose et al., 2008; Young et al., 2010; Chiang et al., 2020; Ordiano-Flores et al., 2021). Blue marlin are known to preferentially feed on scombrids and squid of highly varying size (Shimose et al., 2006, 2007; Rudershausen et al., 2010). Again, the SIA of prey species or a multi-method approach (Young et al., 2018) would allow a more specific identification of the trophic levels at which marlin species feed and is recommended for future studies.

Use of δ^{34}S as an environmental tracer proved constructive in assessment of marlin trophic ecology and differentiating between species. It is known that bacteria in sediments discriminating against specific sulphur isotopes leads to differences in isotope ratios between the coast/benthos and the pelagic environment (Jorgensen, 1979; Connolly et al., 2004). There is a need for more evidence of δ^{34}S differences in oceanic species to establish its use and limits in trophic assessments. As is known through local recreational fisher catches, black and striped marlin typically occur far closer to coast than blue marlin in eastern Australian waters (Ghosn et al., 2015). This created the perfect scenario for testing the effectiveness of δ^{34}S in discriminating

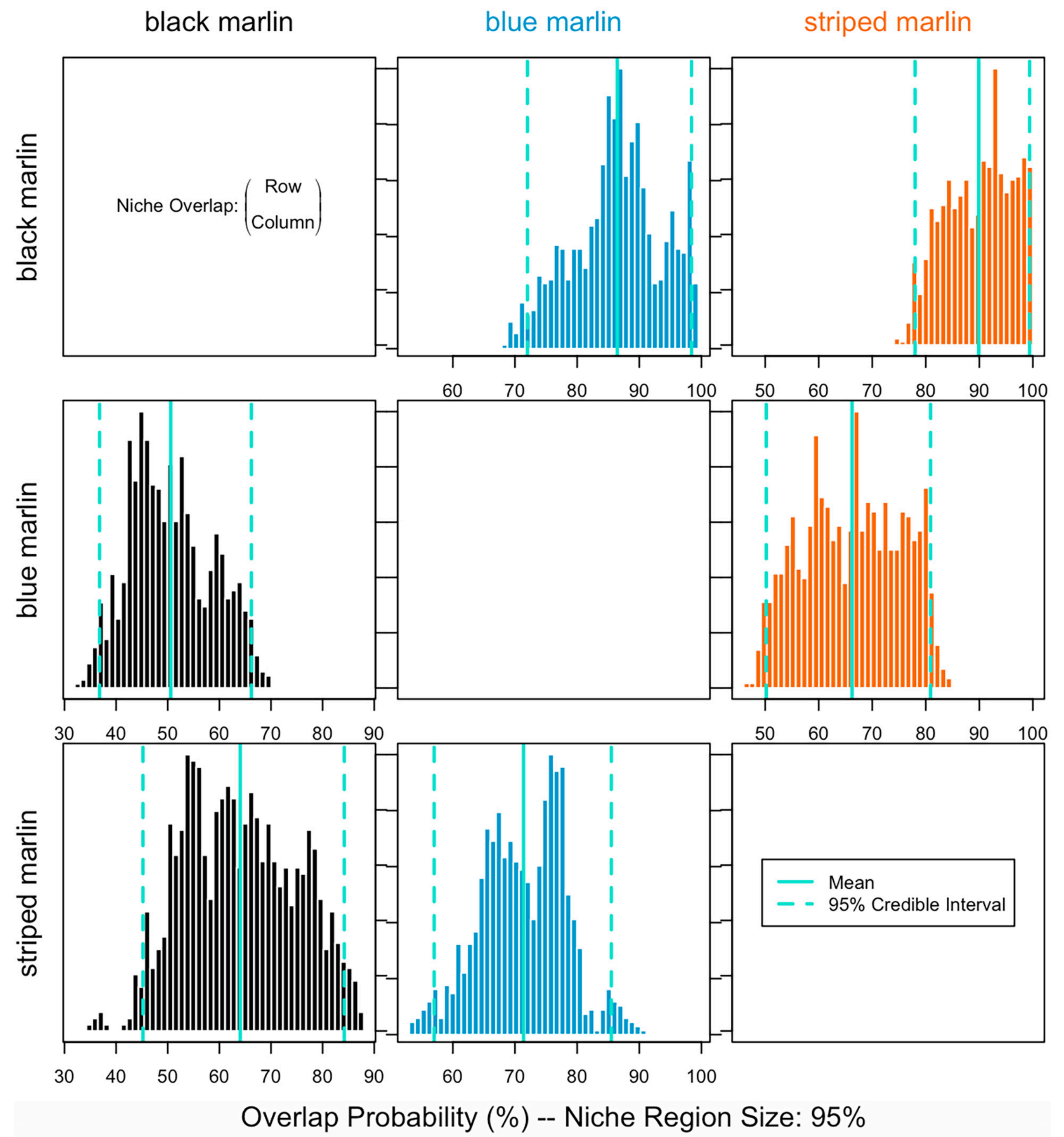


FIGURE 3 | Probability of individual marlin isotope values of placing it within the isotopic niche of another marlin species (1,000 runs with probability level of alpha = 95%) for three marlin species: black marlin (*Istiompax indica*), blue marlin (*Makaira nigricans*), and striped marlin (*Kajikia audax*).

coastal dietary influences in large oceanic predators. Consistent with the local knowledge, we found lower $\delta^{34}S$ in black and striped marlin and higher $\delta^{34}S$ in blue. While more research using $\delta^{34}S$ is needed to truly understand the sensitivity of sulphur to benthic influences in diet of mostly pelagic fish, this study provides one of the first examples of $\delta^{34}S$ pathways in apex pelagic predatory fish. Interestingly, other studies have recorded diving behaviours in marlin that have been attributed to feeding on more benthic prey (Domeier, 2006; Shimose et al., 2006). As $\delta^{34}S$ is typically lower in benthic fish than in pelagic fish (Connolly et al., 2004), the high $\delta^{34}S$ values observed in our study were not indicative of any such diving behaviours in marlin. Such differences in results, however, may just reflect limits in our ability to conclude whether this diving behaviour is present or not off eastern Australia due to the small number of studies assessing δ^{34}S and the lack of any prey isoscapes.

The distinct feeding behaviours found in eastern Australian marlin have key implications for effective management strategies. Prey stock management is necessary to maintain populations of predatory fish (Barnett et al., 2010). In having different prey preferences, anthropogenic or natural changes to prey abundance may affect blue marlin differently to black or striped marlin (Layman et al., 2007). This supports the need for species-specific management for marlin off eastern Australia (Hillary et al., 2015). In being the first to use δ^{34}S in marlin research, our findings also have key implications for δ^{34}S use in oceanic environments. This study adds to the growing amount of research showing the effectiveness of δ^{34}S in differentiating feeding patterns in marine species and supports the use of more than two isotopic tracers in stable isotope research.

The opportunistic sampling undertaken and the lack of ability to collect any prey or baseline items greatly limited our capacity to comprehensively understand isotope variation in marlin in this region. While useful in its lack of invasiveness on marlin stocks (i.e., no marlin were collected specifically for this research), a lack of size ranges and sexes for each species makes comprehensive evaluation difficult. Fish smaller than 60 kg, predominantly black marlin, are often caught during tournaments, however, as these fall below the minimum weight allowed at tournaments, our study lacked representation of these smaller marlin. Our samples predominantly came from a single location (Port Stephens) and a narrow range of dates, as such, it limited our ability to determine whether the differences observed in location and date were ecologically relevant. While the size and sex of marlin had no significant effects on the isotope ratios of all three species in our research, this may be an artefact of our sample range. Other studies found mixed results regarding the significance of size, sex and date of capture on marlin isotope ratios (Wells et al., 2010; Logan and Lutcavage, 2013; Torres Rojas et al., 2013; Acosta-Pachón et al., 2015; Chang et al., 2019). Similarly, research from dietary studies directly assessing gut contents found that juvenile blue marlin consumed smaller and more diverse prey than their larger counterparts, and that juvenile blue marlin consume a higher quantity of benthic fishes than adults (Ueyanagi and Wares, 1972; Shimose et al., 2006). SIA of prey samples can be key in not only identifying the most likely prey species consumed, but also in interpreting consumer isotope ratios (Raoult et al., 2019). The lack of prey or baselines largely limited the ability to identify the causes of the observed variability for all three isotopes in marlin. While we are confident in our results for adults in this area, caution should be taken before extrapolating our research beyond the parameters sampled in our study.

This study documented some similarities and some differences in the stable isotope ratios between marlin species and found δ^{34}S to be a key isotope in understanding marlin feeding ecology. Our findings suggest black and striped marlin feed on similar trophic levels relatively near to the coast while blue marlin have higher variability in their trophic level and feed further from the coast. Prey isoscapes and baselines would further our understanding of their trophic ecology and explain some of the differences observed in this study. Nonetheless, our findings are the first to show isotopic values of marlin in the South Pacific and contribute to the global understanding of how marlin feed across oceans and how they may adapt their trophic niches regionally. Further research is needed on the movement, ontogeny and seasonality of marlin in eastern Australian waters. While our findings have revealed trophic differences that have important implications for the conservation and management of these species, more research is needed to effectively manage and protect these keystone predators.

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

Ethical review and approval was not required for the animal study because samples were opportunistically collected from animals already captured and deceased at fishing tournaments. No live animals were handled or killed for the purpose of this study.

AUTHOR CONTRIBUTIONS

TGu, JW, and JP designed the study. TGu undertook field and laboratory work, analyzed the data and wrote up the research. TGa assisted with analysis of isotope results and write up. JP advised on the research and assisted in sourcing marlin samples. JW led the project and assisted with sample collection, experimental design, analyses and wrote up. 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.2022.795436/full#supplementary-material

REFERENCES

Abitia-Cardenas, L. A., Galvan-Magaña, F., Gutierrez-Sanchez, F. J., Rodriguez-Romero, J., Aguilar-Palomino, B., and Moehl-Hitz, A. (1999). Diet of blue marlin Makaira mazara off the coast of Cabo San Lucas, Baja California Sur, Mexico. *Fish. Res.* 44, 95–100. doi: 10.1016/s0165-7836(99)00053-3

Acosta-Pachón, T. A., Ortega-García, S., and Graham, B. (2015). Stable carbon and nitrogen isotope values of dorsal spine age rings indicate temporal variation in the diet of striped marlin (*Kajikia audax*) in waters around Cabo San Lucas, Mexico. *Rapid Commun. Mass Spectrom.* 29, 1676–1686. doi: 10.1002/rcm.7271

Barnett, A., Abrantes, K., Stevens, J. D., Yick, J. L., Frusher, S. D., and Semmens, J. M. (2010). Predator–prey relationships and foraging ecology of a marine apex predator with a wide temperate distribution. *Mar. Ecol. Prog. Ser.* 416, 189–200.

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., et al. (2018). *Package 'lme4'. Version 1, 437*.

Chang, C. T., Chiang, W. C., Chang, Y. C., Musyl, M. K., Sun, C. L., Madigan, D. J., et al. (2019). Stable isotope analysis reveals ontogenetic feeding shifts in Pacific blue marlin (*Makaira nigricans*) off eastern Taiwan. *J. Fish Biol.* 94, 958–965. doi: 10.1111/jfb.13902

Cherel, Y and Hobson, K (2007). Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. Mar Ecol Prog Ser 329: 281–287

Chiang, W.-C., Chang, C.-T., Madigan, D. J., Carlisle, A. B., Musyl, M. K., Chang, Y.-C., et al. (2020). Stable isotope analysis reveals feeding ecology and trophic position of black marlin off eastern Taiwan. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 175:104821.

Connolly, R. M., Guest, M. A., Melville, A. J., and Oakes, J. M. (2004). Sulfur stable isotopes separate producers in marine food-web analysis. *Oecologia* 138, 161–167. doi: 10.1007/s00442-003-1415-0

Croisetiere, L., Hare, L., Tessier, A., and Cabana, G. (2009). Sulphur stable isotopes can distinguish trophic dependence on sediments and plankton in boreal lakes. *Freshw. Biol.* 54, 1006–1015.

Curnick, D. J., Carlisle, A. B., Gollock, M. J., Schallert, R. J., and Hussey, N. E. (2019). Evidence for dynamic resource partitioning between two sympatric reef shark species within the British Indian Ocean Territory. *J. Fish Biol.* 94, 680–685. doi: 10.1111/jfb.13938

Ditton, R. B., and Stoll, J. R. (2000). A socio-economic review of recreational billfish fisheries. *Mar. Freshw. Res.* 54, 545–554. doi: 10.1071/mf01279

Domeier, M. L. (2006). An analysis of Pacific striped marlin (*Tetrapturus audax*) horizontal movement patterns using pop-up satellite archival tags. *Bull. Mar. Sci.* 79, 811–825.

Domeier, M. L., Ortega-Garcia, S., Nasby-Lucas, N., and Offield, P. (2019). First marlin archival tagging study suggests new direction for research. *Mar. Freshw. Res.* 70, 603–608. doi: 10.1071/mf18160

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., et al. (2011). Trophic downgrading of planet Earth. *Science* 333, 301–306. doi: 10.1126/science.1205106

Findlay, J. D., Cross, C. M., and Bodsworth, A. G. (2003). Marlin fisheries management in Australia. *Mar. Freshw. Res.* 54, 535–543.

Frisch, A. J., Ireland, M., Rizzari, J. R., Lönnstedt, O. M., Magnenat, K. A., Mirbach, C. E., et al. (2016). Reassessing the trophic role of reef sharks as apex predators on coral reefs. *Coral Reefs* 35, 459–472. doi: 10.1111/cobi.12385

Ghosn, D. L., Collins, D. P., and Gould, A. P. (2015). *The NSW Game Fish Tournament Monitoring Program 1994–2013: data summary and assessment of program role and design*. Nelson Bay, NSW: NSW Department of Primary Industries

Griffiths, S. P. (2012). Recreational catch composition, catch rates, effort and expenditure in a specialised land-based pelagic game fish fishery. *Fish. Res.* 127, 40–44.

Hesslein, R., Capel, M., Fox, D., and Hallard, K. (1991). Stable isotopes of sulfur, carbon, and nitrogen as indicators of trophic level and fish migration in the lower Mackenzie River basin, Canada. *Can. J. Fish. Aquat. Sci.* 48, 2258–2265. doi: 10.1139/f91-265

Hillary, R., Preece, A., Kolody, D., Evans, K., and Davies, C. (2015). Development of an approach to harvest strategy management of internationally managed multi-species fisheries. *Fish. Res. Dev. Corporation* 203, 1–161.

Hinman, K. (1998). *Ocean roulette: conserving swordfish, sharks and other threatened pelagic fish in longline-infested waters*. Southeast Leesburg: National Coalition for Marine Conservation

Holland, K. N. (2003). A perspective on billfish biological research and recommendations for the future. *Mar. Freshw. Res.* 54, 343–347.

Jorgensen, B. B. (1979). A theoretical model of the stable sulfur isotope distribution in marine sediments. *Geochim. Cosmochim. Acta* 43, 363–374. doi: 10.1016/j.scitotenv.2004.01.011

Kiljunen, M., Grey, J., Sinisalo, T., Harrod, C., Immonen, H., and Jones, R. I. (2006). A revised model for lipid-normalizing δ13C values from aquatic organisms, with implications for isotope mixing models. *J. Appl. Ecol.* 43, 1213–1222.

Kitchell, J. F., Martell, S. J., Walters, C. J., Jensen, O. P., Kaplan, I. C., Watters, J., et al. (2006). Billfishes in an ecosystem context. *Bull. Mar. Sci.* 79, 669–682.

Kuznetsova, A., Brockhoff, P. B., and Christensen, R. H. (2017). lmerTest package: tests in linear mixed effects models. *J. Stat. Softw.* 82, 1–26.

Langley, A., Molony, B., Bromhead, D., Yokawa, K., and Wise, B. (2006). *Stock assessment of striped marlin (Tetrapturus audax) in the southwest Pacific Ocean. WCPFC SC2 SA WP-6*. Manila, Philippines: Western and Central Pacific Fisheries Commission Scientific Committee, 7–18.

Layman, C. A., Quattrochi, J. P., Peyer, C. M., and Allgeier, J. E. (2007). Niche width collapse in a resilient top predator following ecosystem fragmentation. *Ecol. Lett.* 10, 937–944. doi: 10.1111/j.1461-0248.2007.01087.x

Lenth, R., Singmann, H., Love, J., Buerkner, P., and Herve, M. (2019). *Package 'emmeans': Estimated Marginal Means, aka Least-Squares Means*. Available online at: https://github.com/rvlenth/emmeans

Logan, J. M., and Lutcavage, M. E. (2013). Assessment of trophic dynamics of cephalopods and large pelagic fishes in the central North Atlantic Ocean using stable isotope analysis. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 95, 63–73. doi: 10.1016/j.dsr2.2012.07.013

Lynch, T., Smallwood, C., Ochwada-Doyle, F., Lyle, J., Williams, J., Ryan, K., et al. (2019). A cross continental scale comparison of Australian offshore recreational fisheries research and its applications to Marine Park and fisheries management. *ICES J. Mar. Sci.* 78, 1190–1205. doi: 10.1093/icesjms/fsz092

Madigan, D. J., Litvin, S. Y., Popp, B. N., Carlisle, A. B., Farwell, C. J., and Block, B. A. (2012). Tissue turnover rates and isotopic trophic discrimination factors in the endothermic teleost, Pacific bluefin tuna (Thunnus orientalis). *PLoS One* 7:e49220. doi: 10.1371/journal.pone.0049220

Malpica-Cruz, L., Herzka, S. Z., Sosa-Nishizaki, O., and Lazo, J. P. (2012). Tissue-specific isotope trophic discrimination factors and turnover rates in a marine elasmobranch: empirical and modeling results. *Can. J. Fish. Aquat. Sci.* 69, 551–564.

Ordiano-Flores, A., Galván-Magaña, F., Sánchez-González, A., Soto-Jiménez, M. F., and Páez-Osuna, F. (2021). Mercury, selenium, and stable carbon and nitrogen isotopes in the striped marlin *Kajikia audax* and blue marlin *Makaira nigricans* food web from the Gulf of California. *Mar. Pollut. Bull.* 170:112657. doi: 10.1016/j.marpolbul.2021.112657

Ortiz, M., Prince, E. D., Serafy, J. E., Holts, D. B., Davy, K. B., Pepperell, J. G., et al. (2003). Global overview of the major constituent-based billfish tagging programs and their results since 1954. *Mar. Freshw. Res.* 54, 489–507. doi: 10.1071/mf02028

Park, J. M., Gaston, T. F., and Williamson, J. E. (2017). Resource partitioning in gurnard species using trophic analyses: the importance of temporal resolution. *Fish. Res.* 186, 301–310. doi: 10.1016/j.fishres.2016.10.005

Pepperell, J. (2018). *NSW DPI Game Fish Tagging Program Report 2017-2018*. New South Wales, Australia: Pepperell Research, 29.

Plumlee, J. D., and Wells, R. D. (2016). Feeding ecology of three coastal shark species in the northwest Gulf of Mexico. *Mar. Ecol. Prog. Ser*. 550, 163–174.

R Development Core Team (2021). *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Raoult, V., Broadhurst, M. K., Peddemors, V. M., Williamson, J. E., and Gaston, T. F. (2019). Resource use of great hammerhead sharks *Sphyrna mokarran* off eastern Australia. *J. Fish Biol.* 95, 1430–1440. doi: 10.1111/jfb.14160

Raoult, V., Gaston, T. F., and Williamson, J. E. (2015). Not all sawsharks are equal: species of co-existing sawsharks show plasticity in trophic consumption both within and between species. *Can. J. Fish. Aquat. Sci.* 72, 1769–1775. doi: 10.1139/cjfas-2015-0307

Raoult, V., Trueman, C. N., Kingsbury, K. M., Gillanders, B. M., Broadhurst, M. K., Williamson, J. E., et al. (2020). Predicting geographic ranges of marine animal populations using stable isotopes: a case study of great hammerhead sharks in eastern Australia. *Front. Mar. Sci.* 7:594636. doi: 10.3389/fmars.2020.594636

Restrepo, V., Prince, E. D., Scott, G. P., and Uozumi, Y. (2003). ICCAT stock assessments of Atlantic billfish. *Mar. Freshw. Res.* 54, 361–367.

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., et al. (2014). Status and ecological effects of the world's largest carnivores. *Science* 343:1241484. doi: 10.1126/science.1241484

Rodgers, K. L., and Wing, S. R. (2008). Spatial structure and movement of blue cod *Parapercis colias* in Doubtful Sound, New Zealand, inferred from δ13C and δ15N. *Mar. Ecol. Prog. Ser.* 359, 239–248.

Rudershausen, P. J., Buckel, J. A., Edwards, J., Gannon, D. P., Butler, C. M., and Averett, T. W. (2010). Feeding ecology of blue marlins, dolphinfish, yellowfin tuna, and wahoos from the North Atlantic Ocean and comparisons with other oceans. *Trans. Am. Fish. Soc.* 139, 1335–1359. doi: 10.1577/t09-105.1

Sergio, F., Caro, T., Brown, D., Clucas, B., Hunter, J., Ketchum, J., et al. (2008). Top predators as conservation tools: ecological rationale, assumptions, and efficacy. *Annu. Rev. Ecol. Evol. Syst.* 39, 1–19. doi: 10.1146/annurev.ecolsys.39.110707.173545

Shimose, T., Shono, H., Yokawa, K., Saito, H., and Tachihara, K. (2006). Food and feeding habits of blue marlin, *Makaira nigricans*, around Yonaguni Island, southwestern Japan. *Bull. Mar. Sci.* 79, 761–775.

Shimose, T., Yokawa, K., Saito, H., and Tachihara, K. (2007). Evidence for use of the bill by blue marlin, *Makaira nigricans*, during feeding. *Ichthyol. Res.* 54, 420–422.

Shimose, T., Yokawa, K., Saito, H., and Tachihara, K. (2008). Seasonal occurrence and feeding habits of black marlin, *Istiompax indica*, around Yonaguni Island, southwestern Japan. *Ichthyol. Res.* 55, 90–94. doi: 10.1007/s10228-007-0004-3

Swanson, H. K., Lysy, M., Power, M., Stasko, A. D., Johnson, J. D., and Reist, J. D. (2015). A new probabilistic method for quantifying n-dimensional ecological niches and niche overlap. *Ecology* 96, 318–324. doi: 10.1890/14-0235.1

Thomas, C. J., and Cahoon, L. B. (1993). Stable isotope analyses differentiate between different trophic pathways supporting rocky-reef fishes. *Mar. Ecol. Prog. Ser.* 95, 19–19.

Torres Rojas, Y., Hernandez Herrera, A., Ortega-Garcia, S., and Domeier, M. (2013). Stable isotope differences between blue marlin (*Makaira nigricans*) and striped marlin (*Kajikia audax*) in the southern Gulf of California, Mexico. *Bull. Mar. Sci.* 89, 421–436.

Ueyanagi, S., and Wares, P. (1972). "Synopsis of biological data on striped marlin, *Tetrapturus audax* (Philippi), 1887," in *Proceedings of the International Billfish Symposium, Kailua–Kona, Hawaii,* eds R. S. Shomura and F. Williams (Washington, DC: United States Government Printing Office), 9–12.

Vander Zanden, M. J., Cabana, G., and Rasmussen, J. B. (1997). Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios (δ15N) and literature dietary data. *Can. J. Fish. Aquat. Sci.* 54, 1142–1158.

Ward, P., Mazur, K., Stenekes, N., Kancans, R., Curtotti, R., Summerson, R., et al. (2012). *A socioeconomic evaluation of three eastern Australian game-fishing regions. ABARES report to client prepared for the Fisheries Research and Development Corporation*. Canberra: Australian Bureau of Agricultural and Resource Economics and Sciences.

Wells, R. D., Cowan, J. H. Jr., and Fry, B. (2008). Feeding ecology of red snapper Lutjanus campechanus in the northern Gulf of Mexico. *Mar. Ecol. Prog. Ser.* 361, 213–225. doi: 10.1371/journal.pone.0144051

Wells, R. D., Rooker, J. R., and Prince, E. D. (2010). Regional variation in the otolith chemistry of blue marlin (*Makaira nigricans*) and white marlin (*Tetrapturus albidus*) from the western North Atlantic Ocean. *Fish. Res.* 106, 430–435. doi: 10.1016/j.fishres.2010.09.017

Whitfield, A. K. (2017). The role of seagrass meadows, mangrove forests, salt marshes and reed beds as nursery areas and food sources for fishes in estuaries. *Rev. Fish Biol. Fish.* 27, 75–110.

Young, J. W., Lansdell, M. J., Campbell, R. A., Cooper, S. P., Juanes, F., and Guest, M. A. (2010). Feeding ecology and niche segregation in oceanic top predators off eastern Australia. *Mar. Biol.* 157, 2347–2368. doi: 10.1007/s00227-010-1500-y

Young, T., Pincin, J., Neubauer, P., Ortega-García, S., and Jensen, O. P. (2018). Investigating diet patterns of highly mobile marine predators using stomach contents, stable isotope, and fatty acid analyses. *ICES J. Mar. Sci.* 75, 1583–1590. doi: 10.1093/icesjms/fsy025

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The Multi-Annual Residency of Juvenile Smooth Hammerhead Shark in an Oceanic Island Nursery

Pedro Afonso[1,2*], Miguel Gandra[3], Gonçalo Graça[1], Bruno Macena[1,2], Frederic Vandeperre[1] and Jorge Fontes[1*]

[1] Ocean Sciences Institute (Okeanos), University of the Azores, Horta, Portugal, [2] Institute of Marine Research (IMAR), Horta, Portugal, [3] Centre of Marine Sciences (CCMAR), Universidade do Algarve, Campus de Gambelas, Faro, Portugal

Edited by:
Nuno Queiroz,
Centro de Investigacao em Biodiversidade e Recursos Geneticos (CIBIO-InBIO), Portugal

Reviewed by:
Píndaro Díaz-Jaimes,
National Autonomous University of Mexico, Mexico
Carlos Polo,
Universidad de Bogotá Jorge Tadeo Lozano,
Colombia
James T. Ketchum,
Pelagios Kakunjá, Mexico

***Correspondence:**
Pedro Afonso
pafonsopim@gmail.com
Jorge Fontes
jorge.mr.fontes@uac.pt

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The increased risk of local extinction becomes critical for sharks depending on the narrow and isolated coastal habitats of oceanic islands. This includes large pelagic oceanic sharks that use such habitats as nurseries, as previously hypothesized for the smooth hammerhead *Sphyrna zygaena*, the least known of cosmopolitan large hammerhead sharks. We used a combination of acoustic and satellite telemetry in a juvenile population of Faial and Pico islands, Azores, mid-north Atlantic, to confirm if this isolated archipelago holds nurseries, and to answer questions related to their function and spatial–temporal stability. Our long-term acoustic tracking data showed a cluster of individual core home ranges in specific areas of north shore Faial, and surface positions from five Argos-linked tagged individuals also showed a clustering overlap in those areas for up to 1 year. These patterns seem to reveal a true habitat preference within the Faial-Pico island (sub) population of juvenile smooth hammerhead shark, and thus constitute strong evidence for this area to be considered a nursery. Some individuals remained in this nursery for up to 4 years, especially during summers. Sharks also showed a strong diel behavior, typically using the inshore nurseries during the day and moving further offshore during the night, during which they increased activity and dove deeper, most possibly to feed. We speculate that a combination of increased feeding opportunities, expanded trophic niche, and reduced predatory pressure may be a key evolutionary driver for the existence, prolonged use, and even preference of coastal nurseries at oceanic islands by juvenile smooth hammerhead shark. Given that these nurseries may constitute essential fish habitat for this species, they should be explicitly included in spatial management measures at the local and regional scales, as they may also play a role of greater importance to the north Atlantic population of this oceanic species.

Keywords: *Sphyrna zygaena*, essential fish habitat, shark nursery, acoustic telemetry, satellite telemetry

INTRODUCTION

Sharks are key top predators in the marine food web. They are globally threatened by fisheries given the high numbers taken driving over one-third of all elasmobranchs towards extinction (Dulvy et al., 2021) and because their K-selected life-history traits (slow growth, late maturity, and low fecundity) bring very slow recovery rates in heavily impacted populations (Stevens et al., 2000). Due to this vulnerability and their importance in balancing marine ecosystems, there is an emerging consensus on the urgent need to improve shark management strategies.

International agencies [e.g., Food and Agriculture Organization (FAO) and European Commission (EC)] and regional fisheries management organizations [e.g., International Commission for the Conservation of Atlantic Tunas (ICCAT)] now propose the use of Ecosystem-Based Management (EBM) for the sustainable management of sharks and to reduce conflicts between sharks and humans. However, this approach relies on the science-based knowledge of their spatial distribution and its relationships with ecosystem components. At present, such efforts are critically impaired by the lack of data on shark spatial ecology, especially with regard to their essential fish habitats (EFHs) such as nursery grounds and mating aggregations (Heupel et al., 2007; Kinney and Simpfendorfer, 2009; Meyer et al., 2009). Because sharks play a key role as moderators of trophic food webs and ecosystem functioning, protection of their EFHs should bring major benefits to many other species that make use of these habitats (Heupel et al., 2007; Kinney and Simpfendorfer, 2009; Meyer et al., 2009). As a result, those agencies emphasize that threats to shark populations must be assessed and their EFH must be identified and protected.

Coastal sharks face increased risks of local extinction due to fishing as well as through habitat degradation or severe climate change, as they frequently show high site fidelity or philopatry (they return to natal grounds to lay eggs or to pup) (Hueter et al., 2005; Field et al., 2009; Meyer et al., 2009). These threats may become critical for sharks depending on the narrow, isolated coastal habitats of oceanic islands, such as the Macaronesian archipelagos in the north Atlantic, including some oceanic migratory species. For example, adult pregnant female smooth hammerhead shark (*Sphyrna zygaena* Linnaeus, 1758) are thought to migrate and pup in coastal nurseries in the Azores, where juveniles grow until they are large enough to become oceanic (Afonso et al., 2014; Das and Afonso, 2017). This species is cosmopolitan, migratory, and Red-listed as Vulnerable to extinction by the International Union for Conservation of Nature (IUCN). It is frequently by-caught in the industrial longline and purse seine oceanic fisheries in sub-tropical regions (Rigby et al., 2019). This indicates that the island EFHs may be important to support populations that move throughout the Atlantic basin.

Yet, there is a great deal of uncertainty regarding the spatial and temporal location of the putative EFHs of smooth hammerhead shark (or most other pelagic sharks), or the present and future conditions of these areas under continued human disturbance. Commitments to conservation policies [e.g., the EU Marine Strategy Framework Directive (MSFD), the Oslo-Paris Convention (OSPAR), and the Convention on Biological Diversity (CBD)], coastal development, conflicting marine uses, and the emergence of local ecotourism industry all pose new challenges to the management of these island shark populations. Understanding the role of EFH for island shark ecology and conservation thus emerges as an urgent and difficult mission, given the ubiquitous lack of baseline ecological information and the challenge of studying their populations in the remote habitats across their distribution range, including oceanic seamounts and the open ocean.

The two central research questions addressed in this study were as follows: (i) Do juvenile smooth hammerhead sharks segregate from adults in space and time, i.e., are there juvenile EFH nursery areas non-overlapping with the usual adult grounds? (ii) Are these nurseries discrete in space and temporally stable at the individual and (sub)population levels? We used a combination of acoustic and satellite telemetry to address these questions. As this was the first multi-electronic tagging study on juvenile smooth hammerhead shark known at the time it started, testing and refining tagging and detection methodologies was also an objective in view of future, larger-scale studies.

METHODS

Study Area

This study was conducted between 2010 and 2020 in the Azores, the most remote oceanic archipelago in the north Atlantic. Located right on the Mid-Atlantic Ridge (MAR), it comprises nine islands roughly spanning 600 km and hundreds of seamounts surrounded by depths regularly exceeding 1,500 m within the region's (sub) Exclusive Economic Zone (EEZ) of 1 million km^2. We focused on the putative nurseries along the north coast of Faial Island, but the adopted multi-scale approach spans the neighboring island of Pico (the two islands being separated only by a shallow 9-km-wide channel), the chain of seamounts close to the two islands, and, eventually, the whole archipelago. The islands' coastal habitats are greatly influenced by the region's ecotone position and dominant oceanographic regime whereby the southern branch of the warm Gulf Current, which passes south of the islands, and its eddies and filaments promote a dynamic sub-tropical influence on its warm-temperate general character (Santos et al., 1995; Afonso et al., 2020). The shelves of the islands are very narrow, typically dropping from the shore to the break (at ca. 200 m) in less than 3 km on average. Around Faial and Pico, this shelf is less than 1 km wide on average, with the north shore of Faial being the widest (**Figure 1B**). The substrate is a mix of sandy bottom and rocky basaltic reef resulting from the volcanic eruptions and the dismantling of the steep shores, and the tidal regime largely determines the local scale circulation pattern. The west/north shores are typically subjected to higher swells along the year and especially during autumn–winter.

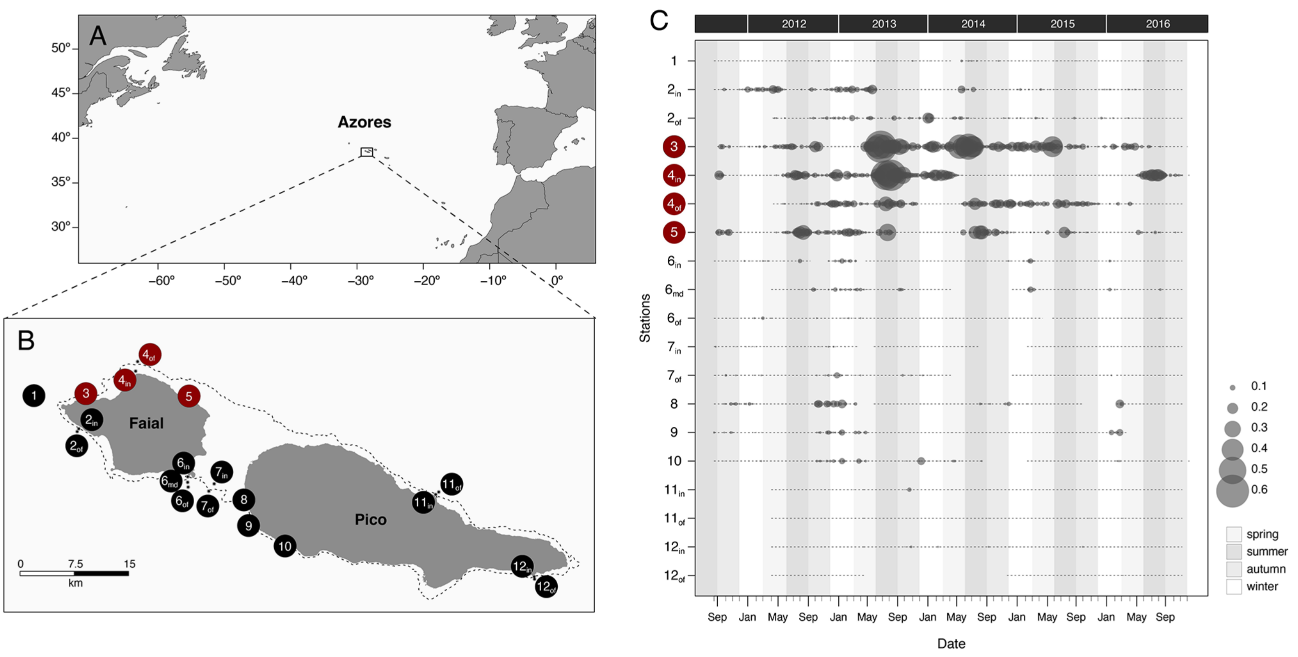

FIGURE 1 | **(A)** The Azores in the north Atlantic. **(B)** Locations of the acoustic receivers around Faial and Pico islands with the nursery sites highlighted in red, the dashed line marking the edge of the island shelf. **(C)** Inter-annual pattern of weekly presence of acoustically tagged juvenile smooth hammerhead shark (*Sphyrna zygaena*) at receivers around Faial and Pico; gray circles represent the total detections averaged per shark at each station, vertical shaded bars represent seasons, and interruptions in the horizontal dotted lines mark the inactivity periods of a receiver.

Tagging

The sharks were caught during the summer aggregation period (July–September) along the north shore of Faial. These aggregations are well known by local fishers and by the authors to occur during summer, and we therefore used the surface aggregations (anywhere from 2 to over 20 sharks swimming at the surface with i.e., <50 m of each other) as a proxy for the presence of the putative nurseries. We used a modified bottom-fixed mini-longline (ca. 20 circle hooks size 9/0 baited with sardine or squid) set in midwater. Prior to setting the line, we searched the coastline for the presence of aggregations of hammerheads at the surface and to select the fishing site. We always found these aggregations in the north shore of Faial either at the Salao, Cedros Point, or Praia do Norte areas and over bottoms of ca. 40 m depth at the transition from predominantly rocky to sandy substrate. The gear was set at sunset and left to soak for 1 h maximum before hauling.

Upon retrieval of the gear, sharks were restrained alongside the boat, kept in tonic immobility, and, if considered in good general condition, tagged at the surface with one or more of the three various types of electronic tags: single-position-only-transmitting satellite tag (Wildlife Computers SPOT5), archival pop-up satellite tag (Wildlife Computers MiniPAT), and passive acoustic tag (Innovasea/Vemco V16-4H or V13AP-1H) (**Table 1**). Each tag was used for a specific purpose reflecting the spatial and temporal scales offered/limited by each technology: Argos-linked SPOT tags, which make use of the sharks' occasional surfacing behavior, allowed the study of horizontal shark movements for up to 1 year at the local to broad spatial scales depending on the error in the obtained ARGOS positions (from a few hundred meters to tens of kilometers); PAT tags allowed the study of the shark's vertical behavior and its surrounding environment (temperature) for up to 1 year, its geolocation position estimates only allowing to detect eventual large-scale movements (i.e., oceanic migrations) of the sharks given their large error in latitudinal estimates (up to hundreds of kilometers); acoustic tags were used to monitor the long-term (up to 4 years) horizontal movements and habitat use at the local scale (i.e., nurseries) as determined by the positions (see below) and detection range of the fixed underwater acoustic receivers. A small subset of shorter-term acoustic tags is equipped with accelerometer and pressure (depth) sensors to complement the information regarding these two variables in the shark movements. Argos-linked SPOT tags were fin-mounted on the first dorsal fin through four nylon threaded rods across the fin fixed with stainless steel washers and nuts while miniPAT tags were fixed through inserting the stainless steel anchor into the musculature and through the pterygiophores (see details in Vandeperre et al., 2014). Acoustic tags were surgically inserted into the body cavity through a 3-cm ventral incision closed with catgut absorbable suture (see details in Afonso et al., 2016).

A total of 18 juvenile smooth hammerhead sharks ranging in size from 90 to 149 cm total length were electronically tagged in various tag combinations: 15 sharks were tagged with acoustic tags between 2010 and 2013, 3 of which were double-tagged with a SPOT tag and another 5 were double-tagged with a miniPAT

TABLE 1 | Summary data for tagged smooth hammerhead shark *Sphyrna zygaena*.

ID	Sex	Tl	Tagged	Site	Acoustic tag	No. of detections	No. of receivers	T_P	D_D	I_T	Sat. tag	DAL
*1	Female	138	08/26/2010	Cedros	53733	101,023	1	1,407	341	0.24	SPOT 70790	72
*2	Male	138	08/19/2011	Salao	55989	0	0	–	–	–	SPOT 70787	–
3	Female	144	08/19/2011	Salao	55991	877	10	97	43	0.44	SPOT 91066	103
4	Male	130	08/21/2011	P Norte	53738	7,950	17	1,093	540	0.49	miniPAT 98170	303
5	Female	140	08/21/2011	P Norte	55990	9,172	16	774	527	0.68	miniPAT 98753	40
*6	Female	147	08/21/2011	P Norte	55988	0	0	–	–	–	miniPAT 98752	nr
7	Male	90	07/30/2012	Salao	59471	9,253	18	1,594	633	0.40		
*8	Male	105	09/09/2012	Salao	59478	463	2	169	27	0.16		
*9	Female	136	09/09/2012	Salao	59479	2,825	1	–	–	–	miniPAT 70803	–
10	Male	131	09/28/2012	Salao	59480	15,841	19	1,421	793	0.56	miniPAT 70805	nr
11	Female	105	09/30/2012	Salao	59475	9,540	14	1,123	592	0.53		
12	Female	125	09/30/2012	Salao	59476	11,184	15	1,098	630	0.57		
13	Male	108	10/02/2012	Salao	59477	4,932	14	781	267	0.34		
14	Male	143	09/03/2013	Cedros	8950/51	726	4	53	33	0.62		
*15	Male	130	08/07/2013	Salao	8952/53	0	0	–	–	–		
16	Male	136	01/14/2019	Salao							SPOT 61494	498
17	Female	126	11/08/2019	P Norte							SPOT 61562	291
18	Male	147	11/08/2019	P Norte							SPOT 61649	180
Median		134				11,586	9	874	402	0.46		180

*Tl—total length (cm); T_P—total period of acoustic detection (days between 1st and last detection); D_D—days with acoustic detections; I_T—total residency index; DAL—days at liberty/transmitting of satellite tag; nr—non-reporting satellite tag. * denotes sharks excluded from analysis due to possible post release mortality or predation.*

tag; an additional 3 sharks were single-tagged in 2019 with a SPOT tag. Thus, we double-tagged 8 sharks, single-tagged 7 sharks with an acoustic tag only, and single-tagged 3 sharks with a satellite tag only, resulting in 15 acoustic tag datasets, 5 miniPAT datasets, and 6 SPOT datasets (**Table 1**). These 3 sharks were brought onboard the tagging vessel and maintained in a large tank (2,000 L) with hyper-saturated (ca. 120% O_2) running seawater during the procedure. All animals were released at the site of capture after ensuring they had recovered swimming behavior in the upright position.

Acoustic Array

To quantify the long-term movements of the 15 acoustically tagged sharks, we deployed an array of underwater acoustic receivers (hereafter referred to as the *array*) fixed above the seafloor. The array was primarily designed to study the habitat use of the juvenile sharks in the putative nurseries in the north shore of Faial (the three fishing areas), as well as the movements across the contiguous Faial-Pico island shelf, but also to detect potential migrations to or between this coastal habitat and the neighboring seamount habitats. Therefore, the array included (i) 20 receivers at specific locations ("stations") along the Faial-Pico shelf (**Figure 1**), mostly deployed in a "listening gate" fashion with 2 to 3 receivers from inshore (*in*) to middle (*mid*) to offshore (*of*) at each location to minimize the chance of a tagged shark swimming across it without being detected; (ii) 22 receivers on the summits and flanks of the nearby (ca. 18–80 km) Princess Alice seamount complex, including the Condor, S. Mateus, Açores, and Princess Alice banks; and (iii) 10 receivers at more distant and isolated seamounts (Gigante bank, 130 km; Formigas bank, 370 km) and islands (Santa Maria, 400 km) (**Figure S1**). The array was kept active for the whole study period (2010–2017), but a few stations were temporarily disabled due to malfunction or decommissioned after 2015 (in the more distant seamounts and islands).

We used Innovasea/Vemco VR2/VR2W acoustic receivers. Receivers at shallow stations (<40 m bottom depth) were rigged on a 3-m rope mooring suspended with small buoys and retrieved by SCUBA diving. Receivers at deeper stations (100–500 m) were rigged similarly except for the use of an acoustic release (AR50/60 SubSeaSonics, San Diego USA or ORE EdgeTech, USA) for retrieval from the surface. Stations were serviced every 6 to 12 months to download stored information. Range tests revealed a 50% detection probability of acoustic transmissions to be logged by receivers at approximately 450 m and 800 m radius for V13 and V16 transmitters of similar power output and in comparable environments to those in this study, respectively (Afonso et al., 2011; Afonso et al., 2012).

Data Analysis—Acoustic Telemetry

Data processing and analysis were conducted in R (R Core Team, 2014). Detections were first screened for false detections by excluding any detection that would occur isolated within the whole acoustic array in over 24 h. Data patterns were initially examined visually by plotting detections independently per fish and receiver across the study duration. This allowed verifying site fidelity of individuals to the putative nursery sites (or to any other site) by assessing whether they would return annually to these sites after long periods of absence (Chapman et al., 2015). To evaluate overall residency in the islands shelf, a residency index (I_R) was then calculated for each shark, dividing the number of days with actual detections (D_D) by the number of days between release and the last detection (i.e., detection span; T_P). I_R ranges between 0 for non-resident fish and 1 for full-time residents and was calculated for the whole acoustic array.

To estimate habitat use and movement metrics, detections were pooled into 60-min bins and used to calculate the center of activity positions (COAs) following Simpfendorfer et al. (2002). Movement trajectories of each shark were then projected based on the shortest path between each two consecutive positions

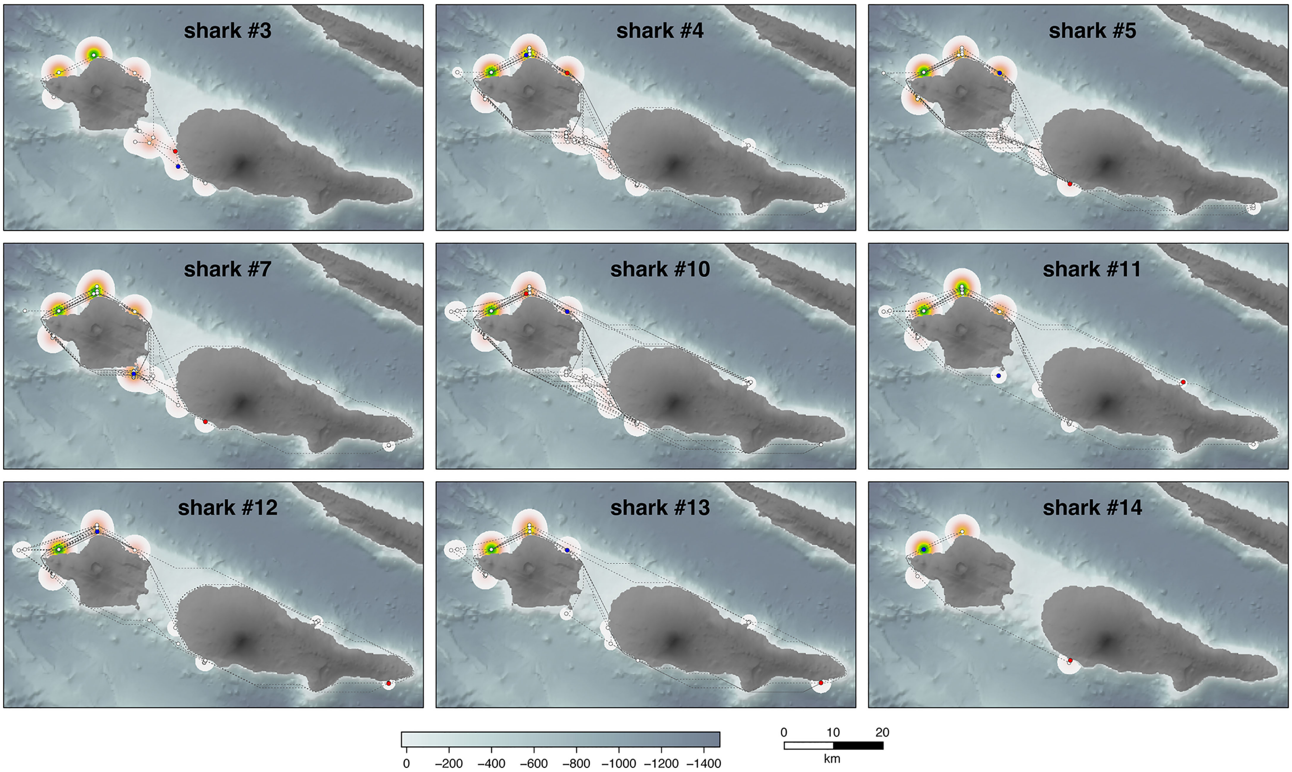

FIGURE 2 | Individual trajectory paths (dotted lines) and home ranges (kernel utilization distributions) of nine acoustically tagged juvenile smooth hammerhead shark (*Sphyrna zygaena*). Trajectories were calculated based on the shortest path between each two consecutive COAs (centre of activity positions) taking into account land surfaces; white dots mark the COA, and blue and red dots signal the first and last positions, respectively, for each individual.

using a least-cost distance approach (Dijkstra's algorithm, "gdistance" package; van Etten, 2017) to avoid intersection with land surfaces. Therefore, these tracks correspond to an approximation of the minimum possible distance travelled. The rate of movement (ROM) of each shark was estimated by interpolating travelled distances over each hour (i.e., splitting the distance between each two successive detections in different stations by the number of time bins in between). Additionally, a linearity index (L_I) was calculated for each individual dividing the distance between the first and last registered positions by the total distance travelled. This parameter ranges between 0 and 1, with higher values indicating strong directional movement and lower values indicating site attachment and high reuse of the same activity space (Villegas-Ríos et al., 2013).

To assess habitat use, COAs were used to estimate bivariate kernel utilization distributions (KUDs; Worton, 1989) for each shark using the "adehabitatHR" package (Calenge, 2006). These KUDs were then translated into core activity and home-range areas by calculating the area lying within a 50% and 95% occurrence probability threshold, respectively (Afonso et al., 2008). All distributions were calculated using a 1,000 fixed kernel bandwidth (h), selected after taking into consideration both the species ecology and the array characteristics, and corrected by excluding areas overlapping with land surfaces.

The potential occurrence of aggregative behavior ("aggregations") was investigated by calculating a spatiotemporal overlap index between each possible pair of tagged individuals (see Gandra et al., 2020 for details). This parameter is analogous to the "simple-ratio" association index (Cairns and Schwager, 1987; Ginsberg and Young, 1992), ranging from 0% (no overlap) to 100% (complete overlap). This metric was also used to test size-mediated differences in joint space usage, that is, the effect of both individual size and size similarity in the extent of overlaps registered. With this aim, we fitted both linear and quadratic regressions and computed Pearson's correlation coefficients between the modeled equations and the observed data.

Temporal patterns in movements and habitat use were investigated by calculating the aforementioned metrics separately for each diel period and season. Diel periods were assigned based on sunrise and sunset times (UTC −1), while boreal seasonal phases were defined on a monthly basis, with spring ranging from March to May, summer from June to August, autumn from September to November, and winter from December to February. Differences were first visually investigated through boxplots and contour plots, and then statistically tested for diel (day vs. night) and seasonal differences through pairwise Wilcoxon signed-rank tests using

Bonferroni correction to adjust *p*-values and correct for Type I errors, given that most data were non-normally distributed. Finer-scale rhythmic patterns were also assessed using Fast Fourier Transform (FFT) on the hourly number of detections of each tagged shark across the entire array. This analysis decomposes data series into the frequency domain enabling the identification of spectral peaks that may reveal, for example, tidal (6–12 h) or diel (24 h) cyclic patterns in habitat use (Afonso et al., 2009).

Data Analysis—Satellite Telemetry

Geographical positions of the SPOT tag transmissions and the popup locations of the miniPAT tags were obtained through the CLS-Argos satellite system.

Most probable geolocations from the miniPAT tags were reconstructed from archived light intensity curves transmitted by the tags after popup or retrieved after physical recovery of the tag. Light geolocations were estimated using a discretized hidden Markov model (HMM) provided by the tag manufacturer (WC-GPE3 software). The WC-GPE3 algorithm uses observations of light level, sea surface temperature, maximum depths, and any known locations from different sources, and incorporates a movement model based on a speed parameter chosen by the user (Pedersen et al., 2011). The output was provided on a 0.25° by 0.25° grid with an associated probability that the animal was in each grid cell at each time step.

The SPOT tags geolocation estimates and associated errors were inspected for any arbitrary position fixes. The LC-Z class locations were discarded and the unlikely swimming speeds (>2 m s^{-1}) between two consecutive locations were filtered using the R package argosfilter (Freitas, 2012). The Argos tracks, together with the locations of acoustic detections for double-tagged sharks (#1 and #3), were subsequently corrected in a state-space model framework using a continuous-time correlated random walk taking location errors into account (Johnson et al., 2008). KUDs using the SPOT tags were then calculated as above.

RESULTS

Survival and Data Throughput

Thirteen out of 15 acoustic transmitters implanted in juvenile smooth hammerhead sharks were detected in the array of acoustic receivers for periods ranging from 49 to 1,555 days (4.26 years), totalling 173,000 detections across the 20 coastal stations located on the Faial-Pico shelf (**Table 1**, **Figure 1C**). There were no detections on any of the remaining receivers of the Azorean acoustic telemetry network, such as the nearby seamounts. Two very contrasting patterns of individual acoustic detection emerged: either sharks were detected at a large number of stations (stations 10 to 19) over medium to long periods (94 to 1,555 days), or they were undetected or detected only at one single station (**Table 1**; **Figure S2**).

Three out of five miniPAT and eight out of nine SPOT tags reported data (**Table 1**). Three double-tagged (i.e., satellite and acoustic) individuals most probably died upon release: sharks #2 and #6 never reported from either tag, and shark #9 stayed in a vertical stationary position at 50 m depth (i.e., on the bottom) for 48 h upon release, after which the PAT tag (i.e., the shark's carcass) was apparently ingested by a deepwater shark for 4 months while doing reversed diel vertical migrations between 140 and 650 m, until it finally popped offshore. This shark's acoustic tag was occasionally detected at Salao (station 7) for about 1 year, but its pattern is very unexpected for a shark and also indicates that the acoustic tag was lying in the bottom at a detectable distance from the receiver (**Figure S2**). Shark #1 stopped transmitting its SPOT tag after 72 days of regular movements around Faial's north and west shores (**Figure 3**), a period during which there were yet no acoustic stations deployed in Faial's north shore. Although it was consistently detected at the Cedros deep station (station 6) over 2 years later, these are also in great contrast with the detections of most other sharks and point out the possibility that this animal was potentially predated by large top predators that frequently visit the islands' shelf such as bluntnose sixgill shark (*Hexanchus griseus*) or shortfin mako shark (*Isurus oxyrhinchus*). Shark #8 was only first detected nearly 3 months upon release at Salao (1 detection) and Cedros Point, and it is unclear whether this was just a different behavioral pattern, or if it was predated or even dead upon release. Shark #15 was also never detected, but this tag was only set for 75 days battery life, thus making it impossible to properly evaluate the animal's fate. Finally, all three single-SPOT-tagged sharks in 2019 survived and successfully transmitted positions.

Taken together, these results indicate that at least 13 out of 18 (72%) tagged juvenile smooth hammerhead sharks survived and behaved consistently for long periods. Therefore, for the purpose of this paper, and specifically for the spatial analysis based on acoustic telemetry, we used only data for which we could be reasonably certain about the natural behavior of the animal in the longer term, i.e., the nine individuals (hereafter referred to as the "multiple detection group"; **Table 1**).

Long-Term Habitat Use

The nine sharks in the multiple detection group exhibited a markedly vagile coastal behavior. They moved widely over the contiguous island shelf of Faial-Pico (**Figure 2**), being detected at anywhere from 10 to 20 stations over a median 929-day period (for the eight long-lasting transmitters) and eventually roaming around the shelf (**Figure S2**). Shark #14 also moved around the north and southwest shores of Faial Island during its short-term (75 days) acoustic tag lifetime. This behavior is reflected in their relatively low residency (R_I median = 0.49, 0.34 to 0.68), the long total distance covered (average 3,338 km), and the large home range (KUD 77.6 km^2) and even core activity (11.0 km^2) area that these individuals used during the whole study period (**Table 2**). The three satellite SPOT tags deployed in 2019 showed similar movement patterns. All five transmitting SPOT-tagged individuals revealed a constant moving pattern over the island shelf for months even when away from the acoustic receiver detection range: sharks #1, 16, 17, and 18 roamed Faial's north shore back and forth while #3 was detected all around the two neighbor islands before going silent (**Figure 3**). In spite of this mobility, all acoustically tagged sharks showed greater site fidelity and resulting home ranges centered at the sites located in

TABLE 2 | Habitat use and movement statistics estimated for nine acoustically tagged smooth hammerhead shark *Sphyrna zygaena* (ID), including total distance travelled (km), mean (ROM) and maximum (Max ROM) rates of movement (m h^{-1}), linearity index (L_I), core activity (KUD 50%, km^2), and home range (KUD 95%, km^2) areas.

ID	Total distance (km)	ROM (m h^{-1})	Max ROM (m h^{-1})	L_I	KUD 50% (km^2)	KUD 95% (km^2)
3	156.5	68.8	2,664.5	0.02	11.7	91.3
4	3,592.6	138.6	4,275.7	0.00	13.2	93.9
5	3,975.9	217.5	6,002.2	0.01	13.6	77.6
7	3,577.2	93.7	4,279.4	0.00	15.6	88.2
10	4,628.4	135.9	4,275.7	0.00	10.5	90.0
11	2,702.9	100.5	2,853.3	0.01	11.0	52.5
12	3,334.1	126.7	8,059.8	0.02	8.1	55.7
13	1,435.0	76.6	2,131.2	0.04	8.2	54.1
14	105.8	90.5	1,590.6	0.39	6.4	36.2
Median	2,612.0	116.5	4,014.8	0.01	10.9	71.1

the north shore of Faial, especially at stations 3 and 4 (**Figures 1** and **2**).

Tagged individuals were co-detected at a given station (i.e., within the receiver listening range) and time (i.e., within 1-h bin) in numerous occasions (1,398 co-occurrences). These co-occurrences were predominantly at nursery stations, and consisted largely of two co-occurring tagged sharks (78.8%) and decreasing co-occurrence of three (14.8%), four (4.9%),

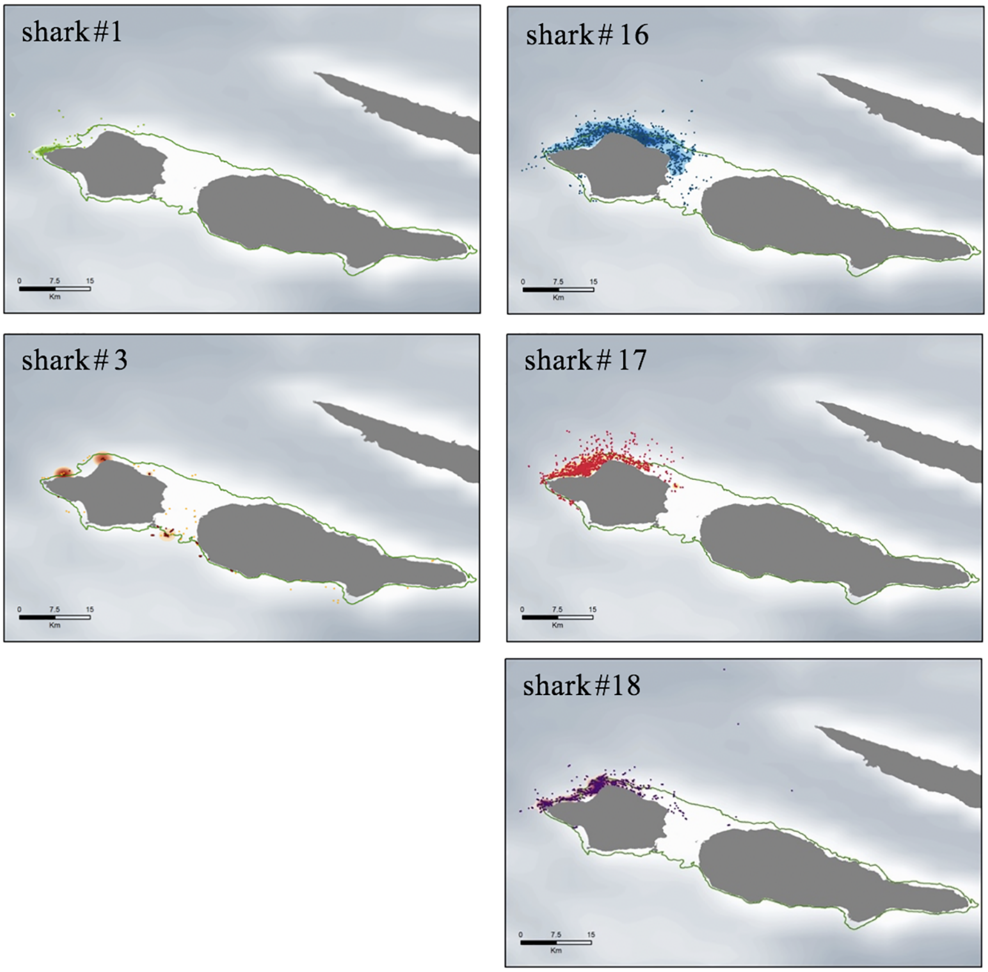

FIGURE 3 | The most probable positions estimated for five SPOT satellite-tagged smooth hammerhead sharks (*Sphyrna zygaena*) around Faial and Pico islands; acoustic detections of double tagged individuals (#1 and #3) were used in improving the ARGOS estimates; shaded areas denote the kernel utilization distribution (KUD) home ranges.

and five (1.4%) tagged sharks. Six tagged sharks eventually co-occurred in two occasions. Certain individual pairs had a much higher probability of co-occurrence than others (e.g., #5 and #14, #4 and #12; **Figure 4**). This overlap network was related to individual length: the probability of co-occurrence between given pairs was higher at mid-range sizes (ca. 110–130 cm FL, **Figure 4A**) than in the lower and upper size limits. There was also a size-assortative effect in these co-occurrences; i.e., the probability of co-occurrence was higher the smaller was the size difference between two given individuals (**Figure 4B**).

Seasonal Patterns

Seasonal patterns were clearly discernible in the acoustic detection data of juvenile smooth hammerhead sharks. There was an increase in both the number of detections and number of co-occurring sharks during the warm season months (**Figures 5A, B**, **Table S1**), which resulted in a statistically significant difference between summer and the remaining seasons (**Figures 5A, B**, **Table S2**). There was also a seasonal trend in habitat use, with a peak in HR and COA areas in winter followed by a decrease through spring and summer and then an increase again in autumn (**Figure S3**). This pattern resulted in a significant contraction of HR and COAs during the spring and summer periods, largely due to a significant increase in detections at the receivers along the north shore of Faial during summer (**Figures 6A, D, E**; **Table S3**, as well as co-detections (**Figure 6D**). This pattern was consistent during consecutive years for most individuals, albeit small differences within seasons as to the specific sites along the north shore (sharks #4, #5, #10, #11, #12, #13, **Figure S2**). ROM was also significantly higher during these months (**Figure 5C**).

Fine-Scale Behavior

A diel, fine-scale temporal rhythm was also quite evident in both the acoustic and satellite data. In general, sharks were much more often detected during daytime when at the three inshore stations of north shore Faial vs. at nighttime in all other stations (**Figures 7**, **8A, B**). The most visited deeper offshore stations had almost no daytime detections (stations 3 and 6; **Figure 1**). As a result, sharks significantly moved offshore (**Figures 5D**, **8C**) and increased their ROM at night (**Figures 5C**, **8D**). The summer increase in detections was also essentially the result of daytime presence close to receivers (**Figure 5A**), as was the concomitant increase in daytime vs. nighttime co-occurrences (**Figure 5B**). This behavior resulted in a clear 24-h periodicity in detection patterns, as all individuals showed a clear peak at ca. 24 h based on the FFT analysis (**Figure S4**).

The sharks' vertical behavior closely matched the diel rhythm described above. The two sharks tagged with PAT tags that provided useful data (#4 and #5) showed a reversed diel vertical migration pattern (RDVM), staying within the shallow (<20 m) mixed layer during daytime but frequently descending down to 60 m and beyond at nighttime (**Figure 9**). This pattern was remarkable in matching the times of dawn and dusk for the initiation of each diel phase behavior. Nocturnal descents showed a "yo-yo" dive pattern whereby individuals intersperse dives to deeper and cooler (22–17°C, depending on the season) water with frequent, rapid ascents to superficial warmer waters (25–17°C). Occasionally, the two sharks dove below the thermocline (180 m and 130 m, respectively) down to 15°C ambient temperature in the warm season. Both sharks stayed in shallower waters (<20 m) during the first week after tagging.

DISCUSSION

This is the fourth study worldwide to evaluate the movements and habitat use of the globally distributed and vulnerable smooth hammerhead shark using electronic tagging, but the second only to address its juvenile phase, and the first ever to offer any long-term movement data for this species—up to 4 years of individual tracking. It is also one of a few studies on nurseries of a pelagic/semi-pelagic shark species in a warm temperate region, and the most complete and multi-scale movement study of any hammerhead shark species to date, adding significant fine-scale data to the two previous satellite tagging studies of smooth hammerhead shark *via* eight successful archival/position tag

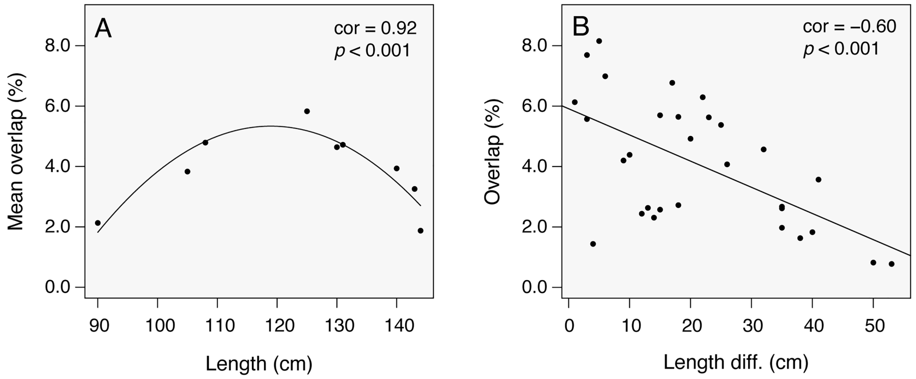

FIGURE 4 | The influence of individual size in the probability of co-occurrence (overlap) of nine acoustically tagged smooth hammerhead shark (*Sphyrna zygaena*): **(A)** body length vs. overlap (nonlinear regression using a quadratic equation); **(B)** body length vs. overlap scores (linear regression).

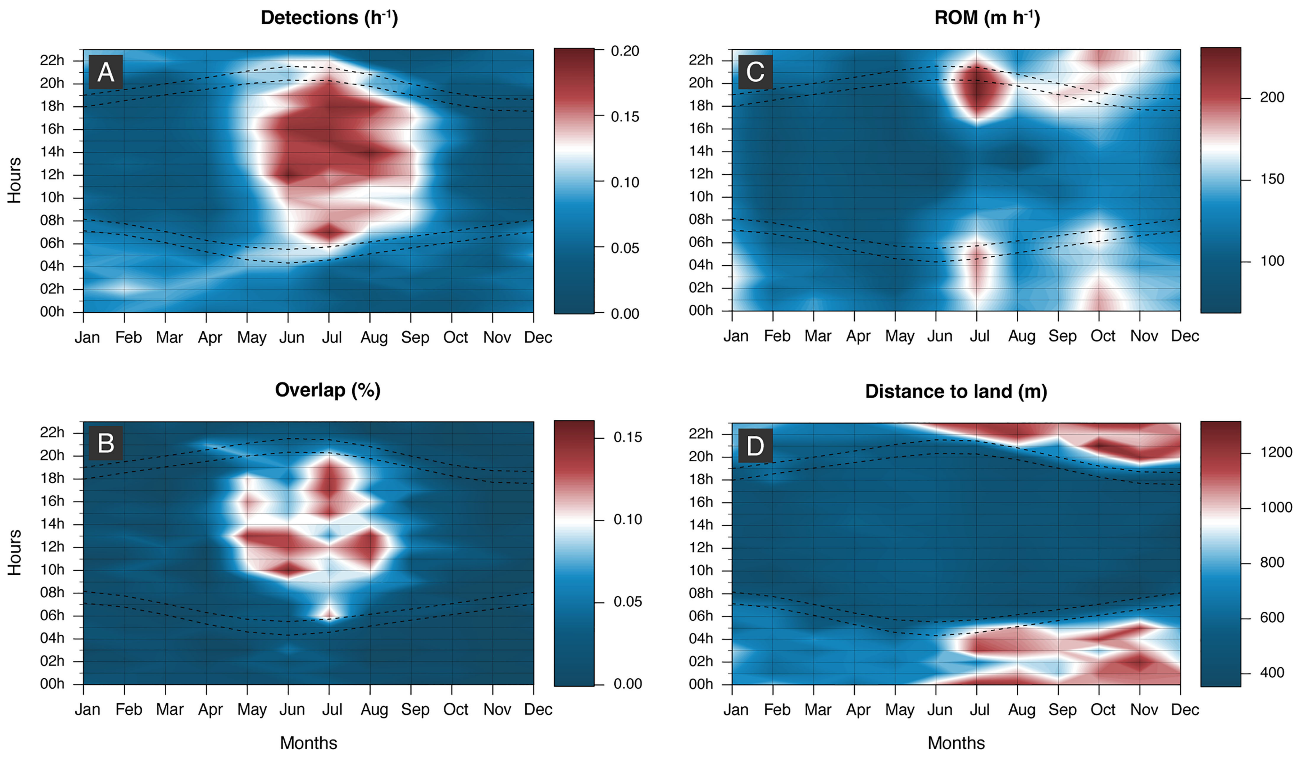

FIGURE 5 | Contour plots representing the overall **(A)** acoustic detection frequencies, **(B)** overlap, **(C)** rate of movement (ROM), and **(D)** distance to nearest coast averaged per hour and month of nine acoustically tagged smooth hammerhead shark (*Sphyrna zygaena*). Dashed lines mark the times of dawn and dusk estimated for the study site illustrating the annual variation in daylight period.

deployments. Taken collectively, these results substantially increase our limited knowledge of the movement ecology of this species at relevant scales, especially with regard to the critical conservation aspect of their nurseries.

Shark Survival and Data Quality

The smooth hammerhead shark is particularly vulnerable to hooking mortality in pelagic longline fisheries, with up to 71% of caught individuals being already dead upon gear retrieval (Coelho et al., 2012). Scalloped (*S. lewini*) and greater (*S. mokarran*) hammerhead sharks have also shown high sensitivity to capture and handling, substantially increasing their potential mortality upon release (Gallagher et al., 2014; Gulak et al., 2015). Although there are no direct studies on post-release mortality of smooth hammerhead shark, our results seem to indicate that this species is also vulnerable to increased potential mortality.

In total, we cannot exclude potential mortality upon release in five out of 18 (28%) tagged sharks. There is strong evidence from the patterns in our acoustic detection and satellite transmission data (see the *Survival and Data Throughput* section for details) that this was indeed the case in three out of eight double-tagged individuals versus two out of seven single-tagged individuals of undetermined fate (i.e., they might not have died) during the 2010–2013 tagging experiences. This difference indicates heavier physiological stress induced by the extended handling time (20 vs. 10 min max) and the more invasive manipulation of the double tagging, especially during the SPOT tag fixation. Our results match those of Francis (2016) in New Zealand and Santos and Coelho (2018) in the northeast tropical Atlantic, with three out of four and three out of eight SPOT-tagged smooth hammerhead sharks that did not transmit or did so for less than a week, respectively. There was no indication of size-related potential mortality in our study, as all surviving individuals provided very long acoustic tracking data and abundant high-quality satellite fixes, with no apparent behavioral change indicating long-term degradation of their condition.

In addition, all three single SPOT-tagged individuals in 2019 survived, even after being brought onboard and kept in a large oxygen-enriched saltwater tank. In spite of our initial tagging procedure with the sharks partially submersed in saltwater reducing their physiological stress in comparison to a classic handling procedure on deck, the combination of an oxygen-rich environment on the tank and reduced handling time (6 min maximum) proved efficient in reducing potential post release mortality and the animals were very active upon release. We therefore advise the use of this refined methodology when studying particularly sensitive individuals such as juvenile smooth hammerhead shark. These results highlight both the usefulness of multi-electronic tagging to study their multi-scale spatial ecology and the need to use refined tagging

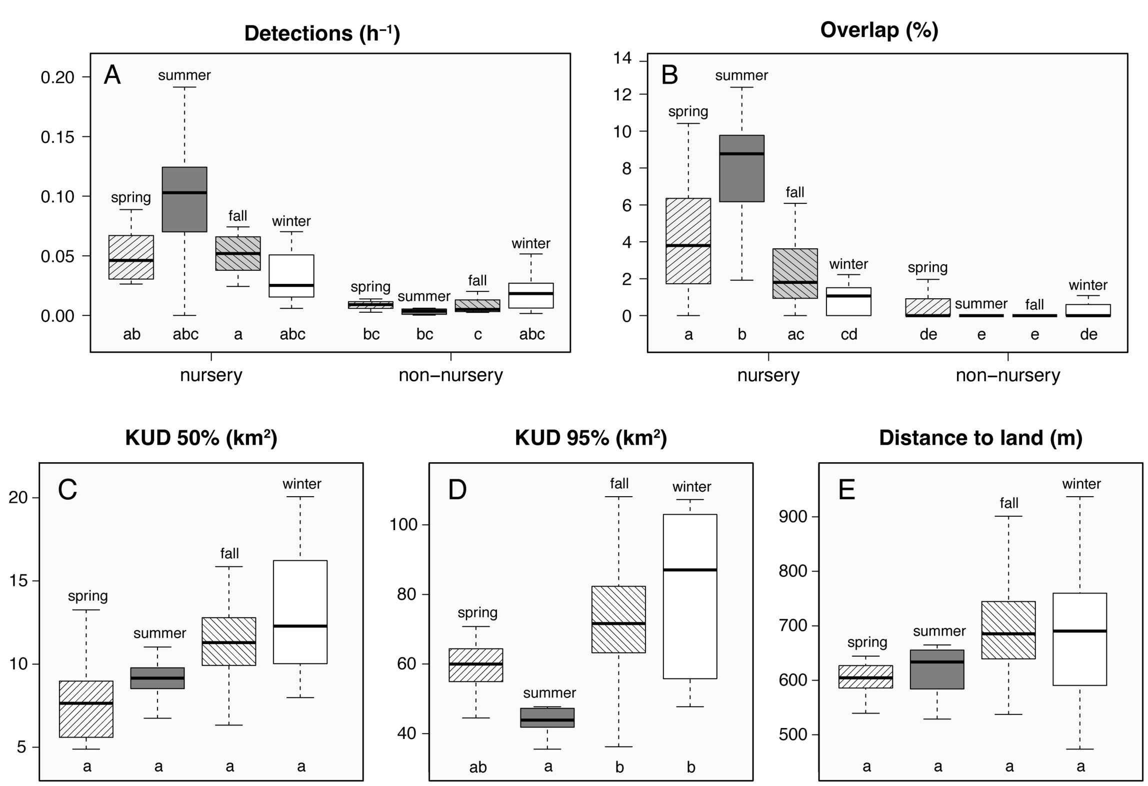

FIGURE 6 | Detection frequency of smooth hammerhead shark (*Sphyrna zygaena*) (detections h-1; **A**), overlap (%; **B**), distance to nearest land surface (m; **C**), core activity areas (km^2; **D**), and home range areas (km^2; **E**) estimated per season. Boxes' upper and lower limits represent the 75th and 25th quartiles, horizontal lines represent medians, and whiskers represent values within 1.5 interquartile ranges; outliers were removed in order to simplify visual interpretation; lowercase letters below the boxes represent significance groupings after a pairwise comparison (using Bonferroni correction) where groups sharing the same letter are not significantly different at $p < 0.05$.

methodologies to reduce the handling time and physiological stress of this rather sensitive shark.

Nurseries in Space and Time

The 18 sharks tagged in this study ranged in size from 90 to 147 cm total length (avg. 128 cm). During the 2010–2013 fishing sets, we caught only one slightly larger (T_l = 162 cm) and one smaller young-of-the-year (62 cm T_l) individual (total n = 28, avg. 123.4 cm). According to previous age-and-growth studies for the northeast Atlantic population (Rosa et al., 2017) and elsewhere (e.g., López-Martínez et al., 2020), all tagged individuals were immature juveniles between their second and fourth years of age. We argue that these juveniles typify the smooth hammerhead shark population in the Azores, and that the island shelves host nursery (growth) and, most probably, also pupping (parturition) juvenile

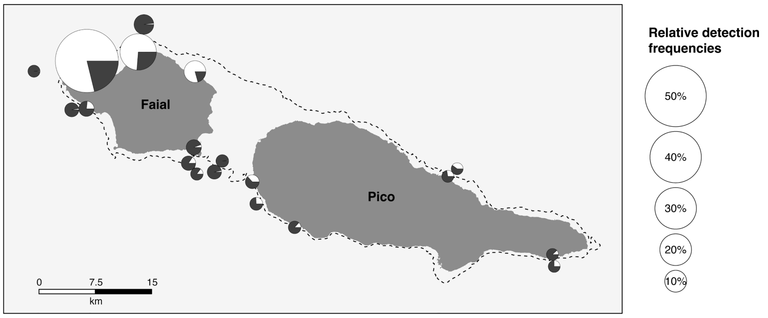

FIGURE 7 | Proportion of detection frequencies per diel phase (white for daytime, black for nighttime) and receiver for nine acoustically tagged smooth hammerhead sharks (*Sphyrna zygaena*). Node size is proportional to the average of relative detection frequencies; the dashed line marks the edge of the island shelf.

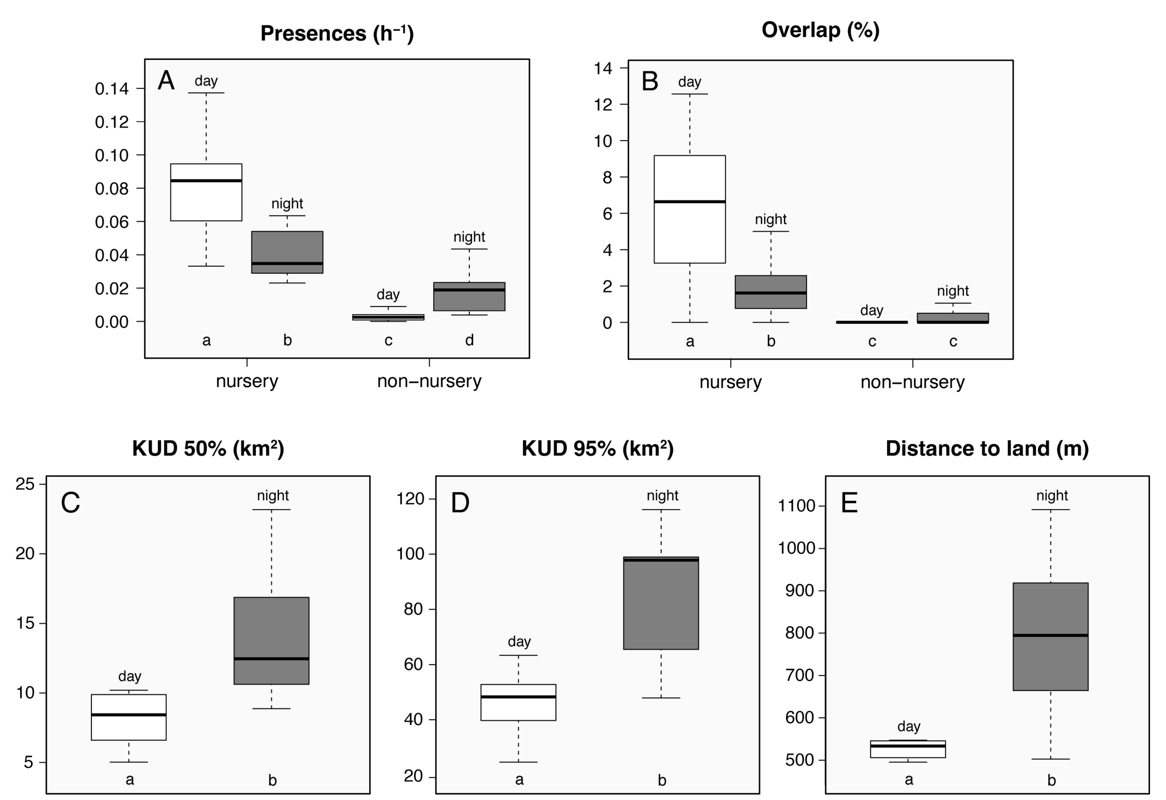

FIGURE 8 | Acoustic detection frequency of smooth hammerhead shark (*Sphyrna zygaena*) (detections h-1; **A**), overlap (%; **B**), distance to nearest land surface (m; **C**), core activity (km^2; **D**), and home range areas (km^2; **E**) estimated for each diel phase. Boxes' upper and lower limits represent the 75th and 25th quartiles, horizontal lines represent medians, and whiskers represent values within 1.5 interquartile ranges; outliers were removed in order to simplify visual interpretation; lowercase letters below the boxes represent significance groupings after a pairwise comparison (using Bonferroni correction) where groups sharing the same letter are not significantly different at $p < 0.05$.

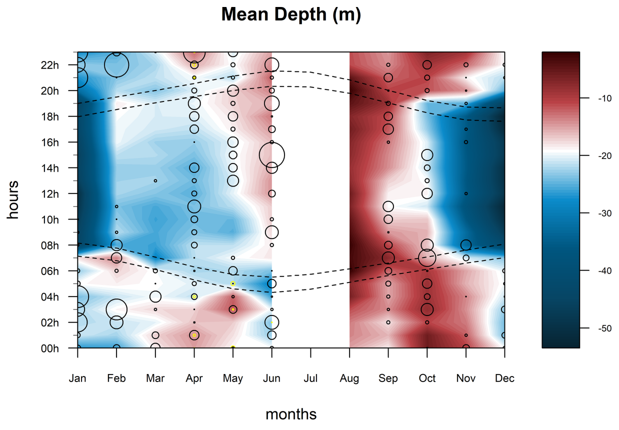

FIGURE 9 | Abacus plot of the average depth across a 300-day deployment period for #4 smooth hammerhead shark (*Sphyrna zygaena*) double-tagged (acoustic and PAT) in the Azores. Dashed lines indicate the times of dawn and dusk across the year; circles represent the detections of this individual in acoustic receivers with the size being proportional to the number of detections; yellow dots signal receivers moored at deep (200 m) acoustic stations on the shelf edge, and hollow circles signal those at shallow (ca. 30 m) stations.

habitats for this species within their broader life history context in the north Atlantic.

Our acoustic tracking data showed an agglomeration of detections and resulting cluster of individual core home ranges in the sites along the north shore of Faial. The five SPOT tags also showed that their estimated surface positions clustered in this coastal area even if the sharks occasionally moved offshore and out of the receivers' detection ranges. Importantly, they also showed that juvenile sharks stayed within or just next to the continuous Faial-Pico island shelf, a behavioral pattern broadly concurred by the miniPAT geolocation position estimates, which included this shelf in all the position error radius estimates, and even by their vertical behavior, as those sharks never dove into mesopelagic or deep-sea depths. Thus, these juveniles seem to adopt an essentially coastal lifestyle and reside (Chapman et al., 2015) in the shelf during their first years of life, during which they use the north shore of Faial as their preferred habitat.

According to Heupel et al. (2007), three criteria should be met to define a shark nursery: "(1) sharks are more commonly encountered in the area than other areas; (2) sharks have a tendency to remain or return for extended periods; and (3) the area or habitat is repeatedly used across years". Traditional surveys (e.g., fishing or underwater censuses) in combination with acoustic tracking inside and outside assumed nursery habitats can be used to address the three criteria (Heupel et al., 2019). Although we did not perform long-term traditional surveys, the acoustic telemetry clearly showed higher presence and residency inside the putative nursery areas along the north shore of Faial Island than in the remaining stations year-round (**Figures 8A, B**) and seasonally (**Figures 6A, B**). Also, overlapped detections of 2 to 6 out of 9 successfully tagged individuals at these stations (**Figure 4**) confirm that juveniles are more commonly encountered and have a tendency to aggregate in these areas (Criterion 1). The persistence of use (Criterion 2) and residency (*sensu* Chapman et al., 2015) (Criterion 3) of juveniles in the nursery habitat along 4 years (**Table 1**) were confirmed by the long-term acoustic telemetry.

Although the listening range of the acoustic receiver array used in this study was far from fully covering the Faial-Pico shelf, it was designed (1) to broadly distribute receivers along the two contiguous islands, and (2) to reduce the chances of a shark moving along the shelf without being detected by using an "acoustic gate" approach with receivers closely placed perpendicular from the shoreline to the shelf break (**Figure 1B**). As in virtually all other tracking studies, we are not sure if sharks tagged elsewhere (e.g., in east Pico or along the south shores) would reveal a different use of the nursery areas. However, these sites were initially selected for tagging because they are well known by local fishers to hold larger quantities of juvenile hammerhead sharks, and subsequently proven to be so after our catch trials, which also included areas in south shore Faial. In addition, the temporal patterns in detections showed that the increased use of Faial north shore areas varies along the year and that sharks eventually move all around the two contiguous islands with no apparent habitat barriers to this behavior. Thus, the high use of Faial's north shore seems to be, to a large extent, a true habitat preference within the local shark (sub) population.

The few studies that have addressed the movements of juvenile smooth hammerhead shark concluded that there are higher residency areas in coastal habitats, both for neonates and for larger, older juveniles, and that was considered to provide direct evidence for pupping and nursery areas, respectively (Diemer et al., 2011; Francis, 2016). Apparently, our results also indicate that the juvenile residency of smooth hammerhead shark may be higher than in other continental shelf areas, where there seem to be stronger seasonal migrations linked to seasonal changes in sea surface temperature and primary productivity (Diemer et al., 2011; Francis, 2016; Logan et al., 2020). This is not surprising given the fragmented nature of the coastal nursery habitat in oceanic islands such as the Azores, which apparently constrains the juvenile sharks to stay within coastal (shelf) habitat by preventing them from crossing the open ocean even between relatively close islands with a distance of only tens of kilometers from each other. However, those studies also found high potential residency within a given season, most notably during local summer. Thus, both our results and those of other studies show a clear seasonal trend in the strength of the spatial behavior during the nursery habitat use phase.

Finally, although we did not directly assess pregnancy or studied the pups in this study, we have only observed sharks the size of those tagged in this study at the surface-oriented aggregations in multiple years of observations, and never larger adult sharks (>200 cm). These adults are only occasionally seen in nearshore habitats by fishers, divers, and researchers (personal observation), always isolated, and in the summer. One adult pregnant female was reportedly caught inshore in Faial by a fixed gillnet in August 1997 (personal observation). Also, we caught some individuals in their first and second years of age, and filmed pups in Faial shores using underwater baited cameras as part of another study (unpublished results). These findings broadly support the hypothesis that pregnant females come in the Azorean summer to give birth (Afonso et al., 2014), as in other hammerhead shark populations (e.g., Guttridge et al., 2017; Félix-López et al., 2019), and that these pups reside and grow in the island where the pupping ground is located, spending most of its time in the nursery areas for up to 4 years. More research on the adult female and pup behavior is needed to confirm this hypothesis.

Fine-Scale Behavior and Use of the Nurseries

Juvenile smooth hammerhead shark seems to inhabit the shelves and upper slope of the islands in the Azores until they reach a certain age (this study), upon which they supposedly leave the coastal habitat and switch to an oceanic lifestyle (Afonso et al., 2014). Yet, their spatial behavior and nursery habitat use during the juvenile (post-pup) coastal phase is both typified by certain traits and variable across individuals and size.

The most striking movement characteristic of all tracked sharks was the clear and ubiquitous long-term preference for the nurseries located in the monitored coastal habitats located along the north shore of Faial. However, there were individual differences in the use of the remaining coastal areas around Faial and Pico, from individuals residing in the nursery sites to others that were occasionally detected all around the two islands. As there was no clear relationship between these patterns and either individual size or sex, they seem to reflect a true individual variability in space use and range of movements. This finding adds to the large body of evidence that individual variability is a widespread characteristic in the movement ecology of reef fishes (e.g., Afonso et al., 2008; Afonso et al., 2009; Villegas-Ríos et al., 2013; Afonso et al., 2016) and sharks (e.g., Matich and Heithaus, 2015; Munroe et al., 2016), including this species (Francis, 2016; Santos and Coelho, 2018; Logan et al., 2020).

We also saw a general diel trend in their use of the coastal nursery habitat; that is, they used the inshore sites of the nursery areas typically during the day and moved further offshore around the island shelf break during the night. This diel pendular movement was accompanied by an increase in activity, as indicated by the horizontal movements and by the frequent and deeper diving behavior at nighttime revealed in the vertical miniPAT data. Pre-adult smooth hammerhead shark also displays this behavior when in the open ocean, but not the adults (Santos and Coelho, 2018). Noticeably, we did not see this pattern when sharks were close to stations located away from the nursery, as the presence in the other coastal areas was always more frequent at nighttime than at daytime regardless of their shallower or deeper location. However, these detections were typically isolated and in areas where the island shelf is much narrower than in the north shore Faial. Diel movement patterns recorded from tracking studies have generally found that sharks increase their activity and home range at night, which has been attributed to increased foraging activity (Speed et al., 2010), but the 24-h periodicity of the use of nurseries, at least in the shorter term, is a relatively undescribed behavior in sharks.

Although based on few observations, the report of a narrow and shallow vertical habitat envelope used by smooth hammerhead shark, restricted to the first 50–60 m of water except for sporadic deeper dives, is remarkably consistent across regions (Azores, tropical eastern Atlantic, and New Zealand), habitats (oceanic island shelf, continental shelf, and open ocean), and even life stages (juvenile, pre-adult, and adult) (this study, Francis, 2016; Santos and Coelho, 2018). In the juvenile coastal phase, this behavior is most probably associated to a bentho-pelagic feeding behavior. Immature smooth hammerheads feed primarily on cephalopods and teleost fishes within the pelagic and bento-pelagic zone of shallow coastal habitats in the South-African continental shelf (Smale, 1991; Dicken et al., 2018). There is no information published on the diet of juvenile smooth hammerhead shark in the Azores or in any other oceanic island, but a recent study revealed that the Azorean juvenile population shows stable isotope values highly consistent with a coastal-associated diet (Priester, 2020). Thus, their diel forays may well reflect a nighttime foraging behavior. Future studies should investigate the dependency of the juveniles on coastal prey and their nighttime, more offshore predatory behavior, as both aspects have an implication for their conservation.

Function of the Nurseries and Management Implications

Our results provide compelling evidence that juvenile smooth hammerhead sharks are full-time residents in the coastal shelf habitat around Azorean islands. They also show that individuals aggregate seasonally in discrete areas during their first years of life, and that they consistently show seasonal high residency and annual site fidelity to these areas, configuring what is usually termed as nursery areas (Heupel et al., 2007). These findings pose questions about the function of these nurseries, their connectivity with other coastal and oceanic habitats in the north Atlantic, and the implications for the conservation and management of the north Atlantic population of smooth hammerhead shark.

As in many shark studies (e.g., Heupel et al., 2007; Heupel et al., 2019), it was postulated that nurseries of smooth hammerhead shark are located in areas of abundant food, either permanently (Smale, 1991) or seasonally (Logan et al., 2020), and reduce chances of cannibalism from the adults (Smale, 1991). One should therefore ask whether these assumptions are still valid and remain the main evolutionary drivers for the existence of coastal nurseries in highly constrained and fragmented coastal habitats around oceanic islands, such as the Azores.

The combination of an increased productivity due to local to regional oceanographic phenomena with the very existence of a shallow seabed habitat around oceanic islands and nearby shallow seamounts is thought to create favorable conditions for higher local food resources when compared with the oligotrophic open ocean, including in the Azores region (Santos et al., 1995; Morato et al., 2010; Caldeira and Reis, 2017). For a coastal species of bentho-pelagic feeding habits such as juvenile smooth hammerhead shark, this could include small coastal pelagic fishes, squid, and even other smaller elasmobranchs such as stingrays and skates, all of which occur in abundance and support local fisheries (Torres et al., 2022). and constitute their main staple elsewhere (Smale, 1991; Bornatowski et al., 2007). The little information available about the trophic ecology of the species in the Azores seems to support this theory (Priester, 2020). Juveniles may also benefit from increased opportunities to feed on the vast mesopelagic resources that occur in the region and frequently invade the coastal pelagic habitat during their nighttime diel vertical migrations (DVMs). This combination would offer an expanded trophic niche during their juvenile phase as well as a more heterogeneous diet as juveniles grow and approach their adult oceanic lifestyle, after which they will essentially depend on mesopelagic resources, especially squid (Galván-Magaña et al., 2013; Estupiñán-Montaño et al., 2019).

The risk of cannibalistic predation should also be much lower in these nursery areas given that the occurrence of adults is rare and probably limited to pregnant females (Afonso et al., 2014). This advantage may, however, be offset by the potential increased predation from other large predators, namely, sharks. However, the only other coastal shark species occurring abundantly in the region and broadly sharing the same habitat is the tope shark *Galeorhinus galeus* (Das and Afonso, 2017). In contrast to other apex predator reef sharks typical of tropical regions but absent in the Azores, such as carcharhinids and tiger sharks, tope shark predates small fishes and squid rather than other elasmobranchs (Morato et al., 2003). Additionally, the one deepwater shark potentially predating these juveniles, the locally abundant bluntnose sixgill shark, occurs in shallower habitats but typically at depths greater than 100 m (unpublished data). Thus, it is very likely that juvenile hammerhead sharks also benefit from reduced predation at these coastal oceanic nurseries. Interestingly, individuals tended to co-occur (aggregate) at the nurseries with other similarly sized individuals and less so among the larger juveniles, which may indicate a release of predatory pressure by local predators as they grow and, possibly, a dilution effect against predation for smaller individuals. It would be useful to validate this assumption by investigating if pups aggregate in higher numbers than larger juveniles.

In conclusion, the combination of increased feeding opportunities and expanded trophic niche with reduced predatory pressure may be a key evolutionary driver for the existence, prolonged use, and even preference of coastal nurseries at oceanic islands by juvenile smooth hammerhead shark. Aggregations at coastal nurseries could additionally increase survival of juveniles through socialization benefits, such as cooperative learning in hunting and predator avoidance, as previously hypothesized for juvenile lemon shark (Guttridge et al., 2009; Jacoby et al., 2012; Heupel et al., 2019).

At the local scale, it is also worth considering why the areas in north shore Faial are selected as nurseries. This area is the widest, with more sandy habitat around the two islands combined, with the exception of the channel between them. This may implicate that those habitats offer more feeding opportunities upon sandy associated prey and/or less predation opportunities from vertically migrating deepwater sharks or other ambushing reef predators such as dusky grouper (*Mycteroperca marginatus*), although we have no means of validating these assumptions. It is thus vital to assess if other nurseries exist across the islands in the archipelago and if they are located in the same type of coastal habitat. This would allow translating the knowledge gathered in this study to support the species conservation *via* protection of its coastal EFH, the nurseries. It follows that the threats to such EFH should also be objectively assessed. Although there is no indication of appreciable directed catch or by-catch of this species in the Azores (Fauconnet et al., 2019), it is possible that the bycatch of juveniles and even pupping females from the hook-and-line and especially gillnet coastal fisheries impacts the population, especially if they are carried out in the nurseries. A potential precautionary measure could be the inclusion of these nurseries in areas closed to fishing.

Finally, these putative EFHs may also play a role of greater importance to the north Atlantic smooth hammerhead population(s) the juveniles (and pupping females) belong to. For example, it is very possible that the oceanic adults and pre-adults in the tropical north-east Atlantic were born at nurseries located in the Azores and other oceanic islands (Afonso et al., 2020), and that females return to these nurseries to pup later in life *via* philopatric behavior, as seems to be the case in the Northern Mexican Pacific (Félix-López et al., 2019). In this case, oceanic island nurseries/EFH should explicitly be put in context with other (adult) EFH, including the pupping migrating corridors, in current international fisheries management approaches as implemented by the international bodies (e.g., ICAAT, CBD, and OSPAR).

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article may be made available by the authors upon request.

ETHICS STATEMENT

This study was performed according to national Portuguese laws for the use of vertebrates in research, and the animal handling and tagging protocols approved by the Azorean Directorate of Sea Affairs of the Azores Autonomous region (permits DRAM/SRRN ref. 24/2010), which oversees and issues permits for scientific activities. All procedures followed the guidelines for the use of fishes in research of the American Fisheries Society. No animals were sacrificed, and procedures for reduction, replacement and refinement were thoroughly adopted.

AUTHOR CONTRIBUTIONS

PA and JF designed the study. PA, GG, FV, BM, and JF conducted the study. PA drafted the manuscript, and all other authors improved the draft and critically reviewed the manuscript. MG performed the acoustic telemetry analyses. BM and FV performed the satellite telemetry analyses. PA secured funding for fieldwork. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

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REFERENCES

Afonso, P., Abecasis, D., Santos, R. S., and Fontes, J. (2016). Contrasting Movements and Residency of Two Serranids in a Small Macaronesian MPA. *Fisheries Res.* 177. doi: 10.1016/j.fishres.2015.12.014

Afonso, P., Fontes, J., Giacomello, E., Magalhães, M. C., Martins, H. R., Morato, T., et al. (2020). The Azores: A Mid-Atlantic Hotspot for Marine Megafauna Research and Conservation. *Front. Mar Sci.* 6. doi: 10.3389/fmars.2019.00826

Afonso, P., Fontes, J., Holland, K. N., and Santos, R. S. (2008). Social Status Determines Behaviour and Habitat Usage in a Temperate Parrotfish: Implications for Marine Reserve Design. *Marine Ecol. Prog. Ser.* 359. doi: 10.3354/meps07272

Afonso, P., Fontes, J., Holland, K. N., and Santos, R. S. (2009). Multi-Scale Patterns of Habitat Use in a Highly Mobile Reef Fish, the White Trevally Pseudocaranx Dentex, and Their Implications for Marine Reserve Design. *Marine Ecol. Prog. Ser.* 381. doi: 10.3354/meps07946

Afonso, P., Fontes, J., and Santos, R. S. (2011). Small Marine Reserves can Offer Long Term Protection to an Endangered Fish. *Biol. Conserv.* 144. doi: 10.1016/j.biocon.2011.07.028

Afonso, P., Fontes, J., Vandeperre, F., and Porteiro, F. (2014). Conservation of Pelagic Elasmobranchs in the Azores. *Arquipélago. Life Marine Sci.*, 25–30.

Afonso, P., Graça, G., Berke, G., and Fontes, J. (2012). First Observations on Seamount Habitat Use of Blackspot Seabream (Pagellus Bogaraveo) Using Acoustic Telemetry. *J. Exp. Marine Biol. Ecol.* 436–437. doi: 10.1016/j.jembe.2012.08.003

Bornatowski, H., Costa, L., Robert, M., and Pina, J. (2007). Feeding Habits of Young Smooth Hammerhead Sharks, Sphyrna Zygaena (Carcharhiniformes: Sphyrnidae), in the Southern Coast of Brazil. *Biota Neotropica* 7. doi: 10.1590/S1676-06032007000100025

Cairns, S. J., and Schwager, S. J. (1987). A Comparison of Association Indices. *Anim. Behav.* 35. doi: 10.1016/S0003-3472(87)80018-0

Caldeira, R. M. A., and Reis, J. C. (2017). The Azores Confluence Zone. *Front. Mar Sci.* 4. doi: 10.3389/fmars.2017.00037

Calenge, C. (2006). The Package "Adehabitat" for the R Software: A Tool for the Analysis of Space and Habitat Use by Animals. *Ecol. Modelling* 197. doi: 10.1016/j.ecolmodel.2006.03.017

Chapman, D. D., Feldheim, K. A., Papastamatiou, Y. P., and Hueter, R. E. (2015). There and Back Again: A Review of Residency and Return Migrations in Sharks, With Implications for Population Structure and Management. *Annu. Rev. Marine Sci.* 7. doi: 10.1146/annurev-marine-010814-015730

Coelho, R., Fernandez-Carvalho, J., Lino, P. G., and Santos, M. N. (2012). An Overview of the Hooking Mortality of Elasmobranchs Caught in a Swordfish Pelagic Longline Fishery in the Atlantic Ocean. *Aquat. Living Resour.* 25. doi: 10.1051/alr/2012030

Das, D., and Afonso, P. (2017). Review of the Diversity, Ecology, and Conservation of Elasmobranchs in the Azores Region, Mid-North Atlantic. *Front. Mar Sci.* 4. doi: 10.3389/fmars.2017.00354

Dicken, M. L., Winker, H., Smale, M. J., and Cliff, G. (2018). Sharks Caught in the KwaZulu-Natal Bather Protection Programme, South Africa. 14. The Smooth Hammerhead Shark Sphyrna Zygaena (Linnaeus). *Afr. J. Marine Sci.* 40. doi: 10.2989/1814232X.2018.1470031

Diemer, K. M., Mann, B. Q., and Hussey, N. E. (2011). Distribution and Movement of Scalloped Hammerhead Sphryna Lewini and Smooth Hammerhead Sphyrna Zygaena Sharks Along the East Coast of Southern Africa. *Afr. J. Marine Sci.* 33. doi: 10.2989/1814232X.2011.600291

Dulvy, N. K., Pacoureau, N., Rigby, C. L., Pollom, R. A., Jabado, R. W., Ebert, D. A., et al. (2021). Overfishing Drives Over One-Third of All Sharks and Rays Toward a Global Extinction Crisis. *Curr. Biol.* doi: 10.1016/j.cub.2021.08.062

Estupiñán-Montaño, C., Cedeño-Figueroa, L., Estupiñán-Ortiz, J. F., Galván-Magaña, F., Sandoval-Londoño, A., Castañeda-Suarez, D., et al. (2019). Feeding Habits and Trophic Level of the Smooth Hammerhead Shark, Sphyrna Zygaena (Carcharhiniformes: Sphyrnidae), Off Ecuador. *J. Marine Biol. Assoc. United Kingdom* 99. doi: 10.1017/S0025315418000474

Fauconnet, L., Pham, C. K., Canha, A., Afonso, P., Diogo, H., Machete, M., et al. (2019). An Overview of Fisheries Discards in the Azores. *Fisheries Res.* 209. doi: 10.1016/j.fishres.2018.10.001

Félix-López, D. G., Bolaño-Martinez, N., Díaz-Jaimes, P., Oñate-González, E. C., Ramírez-Pérez, J. S., García-Rodríguez, E., et al. (2019). Possible Female Philopatry of the Smooth Hammerhead Shark Sphyrna Zygaena Revealed by Genetic Structure Patterns. *J. Fish Biol.* 94, 671–679. doi: 10.1111/jfb.13949

Field, I. C., Meekan, M. G., Buckworth, R. C., and Bradshaw, C. J. A. (2009). Susceptibility of Sharks, Rays and Chimaeras to Global Extinction. *Adv. Marine Biol.* 56. doi: 10.1016/S0065-2881(09)56004-X

Francis, M. P. (2016). Distribution, Habitat and Movement of Juvenile Smooth Hammerhead Sharks (Sphyrna Zygaena) in Northern New Zealand. *New Z. J. Marine Freshwater Res.* 50. doi: 10.1080/00288330.2016.1171244

Freitas, C. (2012). *Argosfilter: Argos Locations Filter* (R package).

Gallagher, A. J., Serafy, J. E., Cooke, S. J., and Hammerschlag, N. (2014). Physiological Stress Response, Reflex Impairment, and Survival of Five Sympatric Shark Species Following Experimental Capture and Release. *Marine Ecol. Prog. Ser.* 496. doi: 10.3354/meps10490

Galván-Magaña, F., Polo-Silva, C., Berenice Hernández-Aguilar, S., Sandoval-Londoño, A., Ruth Ochoa-Díaz, M., Aguilar-Castro, N., et al. (2013). Shark Predation on Cephalopods in the Mexican and Ecuadorian Pacific Ocean. *Deep-Sea Res. Part II: Topical Stud. Oceanography* 95. doi: 10.1016/j.dsr2.2013.04.002

Gandra, M., Afonso, P., and Fontes, J. (2020). Intra- And Interspecific Associations in Two Predatory Reef Fishes at a Shallow Seamount. *Marine Ecol. Prog. Ser.* 654. doi: 10.3354/meps13501

Ginsberg, J. R., and Young, T. P. (1992). Measuring Association Between Individuals or Groups in Behavioural Studies. *Anim. Behav.* 44. doi: 10.1016/0003-3472(92)90042-8

Gulak, S. J. B., de Ron Santiago, A. J., and Carlson, J. K. (2015). Hooking Mortality of Scalloped Hammerhead Sphyrna Lewini and Great Hammerhead Sphyrna Mokarran Sharks Caught on Bottom Longlines. *Afr. J. Marine Sci.* 37. doi: 10.2989/1814232X.2015.1026842

Guttridge, T. L., Gruber, S. H, Gledhill, K. S, Croft, D. P, Sims, , D. W, and Krause, J. (2009). Social Preferences of Juvenile Lemon Sharks, Negaprion brevirostris.. *Anim. Behav* 78(2), 543–548. doi: 10.1016/j.anbehav.2009.06.009

Guttridge, T. L., van Zinnicq Bergmann, M. P. M., Bolte, C., Howey, L. A., Finger, J. S., Kessel, S. T., et al. (2017). Philopatry and Regional Connectivity of the Great Hammerhead Shark, Sphyrna Mokarran in the U.S. And Bahamas. *Front. Mar Sci.* 4. doi: 10.3389/fmars.2017.00003

Heupel, M. R., Carlson, J. K., and Simpfendorfer, C. A. (2007). Shark Nursery Areas: Concepts, Definition, Characterization and Assumptions. *Marine Ecol. Prog. Ser.* 337, 287–297. doi: 10.3354/meps337287

Heupel, M. R., Kanno, S., Martins, A. P. B., and Simpfendorfer, C. A. (2019). Advances in Understanding the Roles and Benefits of Nursery Areas for Elasmobranch Populations. *Marine Freshwater Res.* 70. doi: 10.1071/MF18081

Hueter, R. E., Heupel, M. R., Heist, E. J., and Keeney, D. B. (2005). Evidence of Philopatry in Sharks and Implications for the Management of Shark Fisheries. *J. Northwest Atlantic Fishery Sci.* 35, 239–247. doi: 10.2960/j.v35.m493

Jacoby, D. M. P., Croft, D. P., and Sims, D. W. (2012). Social Behaviour in Sharks and Rays: Analysis, Patterns and Implications for Conservation. *Fish Fisheries* 13, 399–417. doi: 10.1111/j.1467-2979.2011.00436.x

Johnson, D. S., London, J. M., Lea, M.-A., and Durban, J. W. (2008) *CONTINUOUS-TIME CORRELATED RANDOM WALK MODEL FOR ANIMAL TELEMETRY DATA*. Available at: https://www.argos-system.org/manual/i.

Kinney, M. J., and Simpfendorfer, C. A. (2009). Reassessing the Value of Nursery Areas to Shark Conservation and Management. *Conserv. Lett.* 2, 53–60. doi: 10.1111/j.1755-263x.2008.00046.x

Logan, R. K., Vaudo, J. J., Sousa, L. L., Sampson, M., Wetherbee, B. M., and Shivji, M. S. (2020). Seasonal Movements and Habitat Use of Juvenile Smooth Hammerhead Sharks in the Western North Atlantic Ocean and Significance for Management. *Front. Mar Sci.* 7. doi: 10.3389/fmars.2020.566364

López-Martínez, J., Cabanilla-Carpio, C., Ruiz Choez, W., and Arzola-Sotelo, E. A. (2020). Interannual Variability of Distribution, Abundance and Population Dynamics of the Smooth Hammerhead Sphyrna Zygaena (Linnaeus, 1758) in the Central-Southeast Pacific Ocean. *J. Fish Biol.* 97. doi: 10.1111/jfb.14360

Matich, P., and Heithaus, M. R. (2015). Individual Variation in Ontogenetic Niche Shifts in Habitat Use and Movement Patterns of a Large Estuarine Predator (Carcharhinus Leucas). *Oecologia* 178. doi: 10.1007/s00442-015-3253-2

Meyer, C. G., Clark, T. B., Papastamatiou, Y. P., Whitney, N. M., and Holland, K. N. (2009). Long-Term Movement Patterns of Tiger Sharks Galeocerdo Cuvier in Hawaii. *Marine Ecol. Prog. Ser.* 381. doi: 10.3354/meps07951

Morato, T., Hoyle, S. D., Allain, V., and Nicol, S. J. (2010). Seamounts are Hotspots of Pelagic Biodiversity in the Open Ocean. *Proc. Natl. Acad. Sci. U.S.A.* 107. doi: 10.1073/pnas.0910290107

Morato, T., Solà, E., Grós, M. P., and Menezes, G. (2003). Diets of Thornback Ray (Raja Clavata) and Tope Shark (Galeorhinus Galeus) in the Bottom Longline Fishery of the Azores, Northeastern Atlantic. *Fishery Bull.* 101.

Munroe, S. E. M., Simpfendorfer, C. A., and Heupel, M. R. (2016). Variation in Blacktip Shark Movement Patterns in a Tropical Coastal Bay. *Environ. Biol. Fishes* 99. doi: 10.1007/s10641-016-0480-2

Pedersen, M. W., Patterson, T. A., Thygesen, U. H., and Madsen, H. (2011). Estimating Animal Behavior and Residency From Movement Data. *Oikos* 120, 1281–1290. doi: 10.1111/j.1600-0706.2011.19044.x

Priester, C. R. (2020). *Trophic Ecology and Coastal Habitat Use of Two Sympatric Shark Species in the Azores Using CNS Stable Isotope Analysis*.

R Core Team (2014). *R: A Language and Environment for Statistical Computing* (Vienna, Austria: R Foundation for Statistical Computing). Available at: http://www.R-project.org/.

Rigby, C. L., Barreto, R., Carlson, J., Fernando, D., Fordham, S., Herman, K., et al. (2019). Sphyrna Zygaena. *IUCN Red List Threatened Species*. doi: 10.2305/IUCN.UK.2019-3Affilia

Rosa, D., Coelho, R., Fernandez-Carvalho, J., and Santos, M. N. (2017). Age and Growth of the Smooth Hammerhead, Sphyrna Zygaena, in the Atlantic Ocean: Comparison With Other Hammerhead Species. *Marine Biol. Res.* 13. doi: 10.1080/17451000.2016.1267366

Santos, C. C., and Coelho, R. (2018). Migrations and Habitat Use of the Smooth Hammerhead Shark (Sphyrna Zygaena) in the Atlantic Ocean. *PloS One* 13. doi: 10.1371/journal.pone.0198664

Santos, R. S., Hawkins, S., Monteiro, L. R., Alves, M., and Isidro, E. J. (1995). Marine Research, Resources and Conservation in the Azores. *Aquat. Conservation: Marine Freshwater Ecosystems* 5. doi: 10.1002/aqc.3270050406

Simpfendorfer, C. A., Heupel, M. R., and Hueter, R. E. (2002). Estimation of Short-Term Centers of Activity From an Array of Omnidirectional Hydrophones and its Use in Studying Animal Movements. *Can. J. Fisheries Aquat. Sci.* 59. doi: 10.1139/f01-191

Smale, M. J. (1991). Occurrence and Feeding of Three Shark Species, Carcharhinus Brachyurus, C. Obscurus and Sphyrna Zygaena, on the Eastern Cape Coast of South Africa. *South Afr. J. Marine Sci.* 11. doi: 10.2989/025776191784287808

Speed, C. W., Field, I. C., Meekan, M. G., and Bradshaw, C. J. A. (2010). Complexities of Coastal Shark Movements and Their Implications for Management. *Marine Ecol. Prog. Ser.* 408. doi: 10.3354/meps08581

Stevens, J. D., Bonfil, R., Dulvy, N. K., and Walker, P. A. (2000). The Effects of Fishing on Sharks, Rays, and Chimaeras (Chondrichthyans), and the Implications for Marine Ecosystems. *ICES J. Marine Sci*. doi: 10.1006/jmsc.2000.0724

Torres, P., Milla i Figueras, D., Diogo, H., and Afonso, P. (2022). Risk Assessment of Coastal Fisheries in the Azores (North-Eastern Atlantic). *Fisheries Res.* 246. doi: 10.1016/j.fishres.2021.106156

Vandeperre, F., Aires-da-Silva, A., Fontes, J., Santos, M., Serrão Santos, R., and Afonso, P. (2014). Movements of Blue Sharks (Prionace Glauca) Across Their Life History. *PloS One* 9. doi: 10.1371/journal.pone.0103538

van Etten, J. (2017). R Package Gdistance: Distances and Routes on Geographical Grids. *J. Stat. Software* 76. doi: 10.18637/jss.v076.i13

Villegas-Ríos, D., Alós, J., March, D., Palmer, M., Mucientes, G., and Saborido-Rey, F. (2013). Home Range and Diel Behavior of the Ballan Wrasse, Labrus Bergylta, Determined by Acoustic Telemetry. *J. Sea Res.* 80. doi: 10.1016/j.seares.2013.02.009

Worton, B. J. (1989). Kernel Methods for Estimating the Utilization Distribution in Home- Range Studies. *Ecology* 70. doi: 10.2307/1938423

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Long-Term Monitoring of In-Water Abundance of Juvenile Pelagic Loggerhead Sea Turtles (*Caretta caretta*): Population Trends in Relation to North Atlantic Oscillation and Nesting

Thomas Dellinger[1,2,3], Vladimir Zekovic[4,5] and Marko Radeta[4,6,7]*

[1] CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Universidade do Porto, Vairão, Portugal, [2] Estação de Biologia Marinha do Funchal, Universidade da Madeira, Funchal, Portugal, [3] BIOPOLIS Program in Genomics, Biodiversity and Land Planning, Centro de Investigação em Biodiversidade e Recursos Genético (CIBIO), Vairão, Portugal, [4] Department of Astronomy, Faculty of Mathematics, University of Belgrade, Belgrade, Serbia, [5] Department of Astrophysical Sciences, Princeton University, New Jersey, NJ, United States, [6] MARE - Marine and Environmental Sciences Centre / ARNET - Aquatic Research Network, Agência Regional para o Desenvolvimento da Investigação Tecnologia e Inovação (ARDITI) Funchal, Madeira, Portugal, [7] Wave Labs, Faculty of Exact Sciences and Engineering, University of Madeira, Funchal, Portugal

Edited by:
Nuno Queiroz,
Centro de Investigacao em Biodiversidade e Recursos Geneticos (CIBIO-InBIO), Portugal

Reviewed by:
Gail Schofield,
Queen Mary University of London, United Kingdom
Nathan Freeman Putman,
LGL, United States

***Correspondence:**
Thomas Dellinger
thomas.dellinger@cibio.up.pt

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Sea turtles have various life-stages, typically being oceanic foragers as juveniles while shifting to more coastal habitats as they mature. The present study focuses on the least studied and well known of these, the juvenile oceanic life stage for the loggerhead sea turtle, *Caretta caretta*. Loggerhead sea turtles remain threatened by fisheries and their distribution and habitat change in the North Atlantic remains poorly understood. After hatching and swimming out to sea, turtles spend 7 or more years in the pelagic life stage. Madeira Island has an advantage of being situated in the middle of the North Atlantic developmental habitat for loggerheads originating both from the US, as well as, from Cape Verde and other mixed source rookeries. Understanding the demographics of this oceanic life stage has been described as a research priority. We here present a population trendline and the abundance variation of oceanic stage loggerheads, measured at a single geographic spot in Madeiran waters, over the period of 15 years. We find that the observed loggerhead distribution results from combined effects of physical and biological processes within the North Atlantic. We explore physical phenomena that influence abundance variability, and find that oscillations in climate affect the turtle migrations, as does the population recruitment from the nesting rookeries. For this, we use novel cost-effective census methods that take advantage of platforms of opportunity from the blue ecotourism industry. To study the time series and their correlations we use spectral analysis, a method not commonly used in traditional population assessments, including Wavelet and Fourier Transformations (WT and FFT), and Digital Signal Processing (DSP) techniques. A strong anti-correlation between sea turtle sightings and North Atlantic Oscillation seasonal components was found, which implies that loggerhead sea turtles are less abundant during positive NAO phases. We also detected long period trends in the sighting data which we relate to La Niña and El Niño oscillations. Source rookeries also influenced the sighting data with a time-lag of ~ 7 *years*, which coincides with the average time that turtles spend as oceanic juveniles.

Keywords: sea turtles, wavelet transformation, El Niño, NAO, in-water abundance, oceanic life stage, digital signal processing (DSP), marine monitoring

1 INTRODUCTION

Marine megavertebrates are a vulnerable and threatened group of organisms (Peltier and Ridoux, 2015). Widely migrating megavertebrates deserve special attention (Furey et al., 2018) because of their longevity, the inaccessibility and international character of their habitat. This makes it more difficult to take coordinated protective actions (Lascelles et al., 2014). Understanding their demographics is essential for the population assessments and the implementation of protective actions. Reliable long-term indicators of their abundances are needed, measured throughout their distributional and habitat range, allowing to assess the possible causes that may affect such abundances.

Sea turtles have complex life histories that involve ontogenetic habitat shifts and large scale migrations (Hays and Scott, 2013), the usage of terrestrial, coastal and oceanic habitats and the passage through territorial waters of different countries. All species are classified as endangered. After emerging from their terrestrial nests, loggerhead sea turtles (*Caretta caretta*) typically move offshore as juvenile oceanic foragers and then shift to more coastal habitats as they mature (Bolten, 2003a; Bolten, 2003b). They are found in all tropical and temperate seas worldwide with 10 subpopulations recognized by the IUCN (Wallace et al., 2010; Wallace et al., 2011; Casale and Tucker, 2017). The North Eastern (NE) Atlantic where Madeira Island is situated is used exclusively by what is called the *juvenile developmental oceanic life stage* (Dellinger, 1998; Bolten, 2003a; Saavedra et al., 2018). Around Madeira at least 3 different subpopulations are found: Western Atlantic (45%), Cape Verde (5%) and mixed origins (48%) that may include Mediterranean turtles (Monzón-Argüello et al., 2009; Pipa et al., 2019). These proportions may vary seasonally in Madeiran waters (Freitas et al., 2018).

Sea turtle population assessments are based on numbers of nesting females and their nests (National Research Council, 2010; Casale and Tucker, 2017). Other life stages are used to estimate partial mortalities, though important knowledge gaps exist regarding the recruitment to the oceanic stage and the mortality during this stage. Although sea turtles can be monitored by in-water and remote sensing studies (Kobayashi et al., 2008), most of these studies do not address long-term population abundances.

Juvenile mortality is thought to be high for small juveniles that recruit into the oceanic stage (Bjorndal et al., 2003b; Sasso and Epperly, 2007; Salmon and Scholl, 2014) but rather low for animals during this life stage (Bjorndal et al., 2003b). Survival during the oceanic stage is deemed critical for population maintenance and growth (Crouse et al., 1987), however the oceanic stage is the least known and understood (Bolten, 2003b). Previous studies in Madeira Island indicated that turtles remain in this stage on average for 7 *years* (Bjorndal et al., 2003a). Individuals are thought to make the transition from the pelagic to the neritic life-stage at a minimum of 40 *cm* curved-carapace-length (CCL) (Witherington et al., 2006) which would correspond to an estimated age of around 6 *years* (Bjorndal et al., 2003a), although having the variable size and age (McClellan and Read, 2007; Casale et al., 2008; Avens et al., 2013). Since the mean age at sexual maturity for the Western Atlantic sub-population was estimated as 36 – 42 *years* (Avens et al., 2015), any variation in abundance during the oceanic stage will strongly affect the recruitment into the following life stages. Ideally, demographic parameters should be monitored across all life stages, but most importantly for the oceanic stage, as this would allow for a timely identification of potential threats. (Turtle Expert Working Group, 2009; Bjorndal et al., 2011).

Study objective. Obtaining data for spatio-temporal distribution during oceanic stage remains notoriously challenging (Carr, 1987; Putman et al., 2020). Oceanic stage turtles distribute widely on a basin-wide scale (Bolten et al., 1998; Dellinger, 1998; McCarthy et al., 2010; Putman et al., 2020). Reasons for local abundance changes can be due to spatial shifts or actual abundance changes. To address these questions we monitored loggerhead turtles on a single location within their distribution range for the period of 15 *years*. We used these data to test various variables that could influence both abundance as well as spatial shifts. Madeira Archipelago is situated within the NE Atlantic oceanic developmental area that includes the Azores, Madeira and the Canary Islands. We used the growing local touristic whale watching activities (IFAW, 2009; Sequeira et al., 2009; Krasovskaya, 2018; Radeta et al., 2018; Nunes et al., 2020) as platforms of opportunity to monitor the pelagic loggerhead sea turtles since year 2007 for the period of 15 years. Using spectral analysis we found climatic factors that correlate with abundance variations and indicate area shifts of turtle distribution, while the correlation with nesting data hint at abundance variations. These results contribute to a better understanding of the oceanic stage ecology, highlight the importance of hemisphere-wide influences on ocean life, and point to cost-effective methods capable of monitoring widely dispersed low-density species such as sea turtles.

2 METHODS

2.1 Study Location

The study was carried out in Madeira Island, Portugal (32°45'N, 17°00'W) located in the NE deep Atlantic Ocean. Since the conditions on the leeward marine area south of Madeira Island are more protected and warmer (Caldeira et al., 2002; Caldeira and Sangra, 2012; Alves et al., 2020), large traction of touristic activities focus on these areas (Sambolino et al., 2022). The insular platform of Madeira is rather steep (Geldmacher et al., 2000), such that whale-watching activities are mostly conducted over deep water and trenches reaching depths of up to 2000 *m*. Waters are oligotrophic with some localized small-scale upwelling cells at the island's flanks. They also include enriched mesoscale eddies of oceanic origin that interact with the islands (Caldeira, 2019; Narciso et al., 2019). Turtles mostly use the calmer and warmer southern waters to bask at the surface and are thus more easily spotted (Dellinger et al., 1997; Dellinger, 1998).

2.2 In-Water Monitoring

The crews from commercial whale watching boats were asked to record sea turtle sightings (STS) during each of their trips, primarily conducted once daily. Observers were instructed verbally by the authors of the study, while given a small booklet with all relevant information including a sea turtle identification key and the observation forms. Emphasis was placed on the request to record every trip, even if no turtles were seen.

In a separate dataset of the Madeira Turtle Project (MTP 1994-ongoing), turtles are sampled regularly by trained researchers (using methods as those described in Dellinger et al. (1997) and Delgado et al. (2010), where the frequencies of other species except loggerheads are negligible (99.83% of 1800 sightings and captures). Thus all turtle sightings were considered loggerheads, and the boat crew abilities were not rigorously validated as in other studies (Houghton et al., 2003). For instance, Leatherback-turtles (*Dermochelys coriacea*), Hawksbills (*Eretmochelys coriacea*) and Kemp's Ridleys (*Lepidochelys kempii*) are easily distinguished as different, however their frequencies, as recorded by an experienced researcher (TD), are in Madeira Island below 0.06%. Conversely, Greens (*Chelonia mydas*) are rare (~ 5 residents), only appeared regularly at Madeira since 2018, tend to stay close to the shore, and thus do not frequent the same areas as the boats. Most crew members were very experienced local seafarers and would register any turtle as different if they spotted it, since the observation form included specific areas for "other species".

We used 3 different whale watching companies, two based at Funchal marina (32°38.7'N, 16°54.6'W), and one at Calheta marina (32°43.1'N, 17°10.3'W) further westward (**Figure 1**). On average, single trip duration was generally between 2.5 - 3 hours. Crews consisted of 2 - 3 persons, with the one completing the observation forms typically being a marine biologist. Used sea vessels varied and included: rigid inflatable boats (RIB 9*m*), a wooden former fishing boat (12*m*), and large catamarans (20 – 24*m*). The distributed observation forms were printed on paper and were kept succinct, not to overload crew-members with data registration. Crew members performing the data entries were asked to write down the number of sighted turtles during the trip. Additional data registered included weather, the Beaufort scale (0-12, byWorld Meterological Organization, 2012), including the estimates of maximum distance to shore and average distance to the shore during the trip, but were not used in this study. Furthermore, crews were asked to record other important species for turtles such as jellyfish (as food species). In the remainder of the paper, to all of the observed loggerhead turtles by the boat crew, we will refer to as sea-turtle sightings (STS).

The observation form was improved through time. Until 2009, we solely recorded trip starting time since the average duration of whale-watching trips had a little variation. In 2009, we started recording return times and were thus able to compute the actual time-at-sea for each trip. We furthermore subdivided the island into 7 radial sectors based on conspicuous shoreline features (**Figure 1**). All crews were asked to register their visited sectors during each single trip. Starting in 2011, the observers were asked to record the data based on times spent in each sector for each trip. The last version was integrated into the local law on marine vertebrate observation (Regional da Madeira, 2013). In summary, turtle abundance is available in the collected database as "sightings per trip" (complete set), "sightings per hour at sea" (available since 2009), or "sightings per hour and sector" (available since 2011). Though all sectors were sampled, sampling of sectors 4 - 6 was negligible, as most sampling occurred in sectors 1 - 3 and to a lesser extent in sector 7.

2.3 Data Pre-Processing

We use the spectral decomposition by wavelets (Torrence and Compo, 1998) and Fast Fourier Transform (Brigham and Morrow, 1967) – WT and FFT, as well as DSP techniques to isolate, analyze, and correlate the most dominant periods in the time series of observed STS against Hurrell North Atlantic Oscillation (NAO) index (Hurrell and Deser, 2010) and Florida Index Nesting Beach Survey of loggerhead sea turtles nesting (NEST) by the Fish and Wildlife Research Institute's (FWRI). All three signals (**Figure 2**) were matched to the same period of the complete STS set (from 2007 - 01 to 2021 - 07).

STS Dataset. During 15 *years* of sampling, a total of 20032 *records* were obtained, representing 5300 *days*. Out of these, 1554 *days* had no surveying trips, 691 *days* had only a single record, while all remainder days had more than 1 record up to 28 records per day. Raw data were summarized by month and 10-day blocks by adding all turtles sighted in the period. The last block of a month can vary between 8-11 days. A maximum of 523 data points (i.e. 5230 *days*, **Figure 2A**) were formed. STS further contained 15 missing records which were linearly interpolated from nearby points.

NAO Dataset. NAO signal was obtained from its online repository.[1] Since the NAO signal points were given as a monthly average, we boosted the signal time resolution by applying a

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[1] NAO dataset: http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/norm.nao.monthly.b5001.current.ascii.

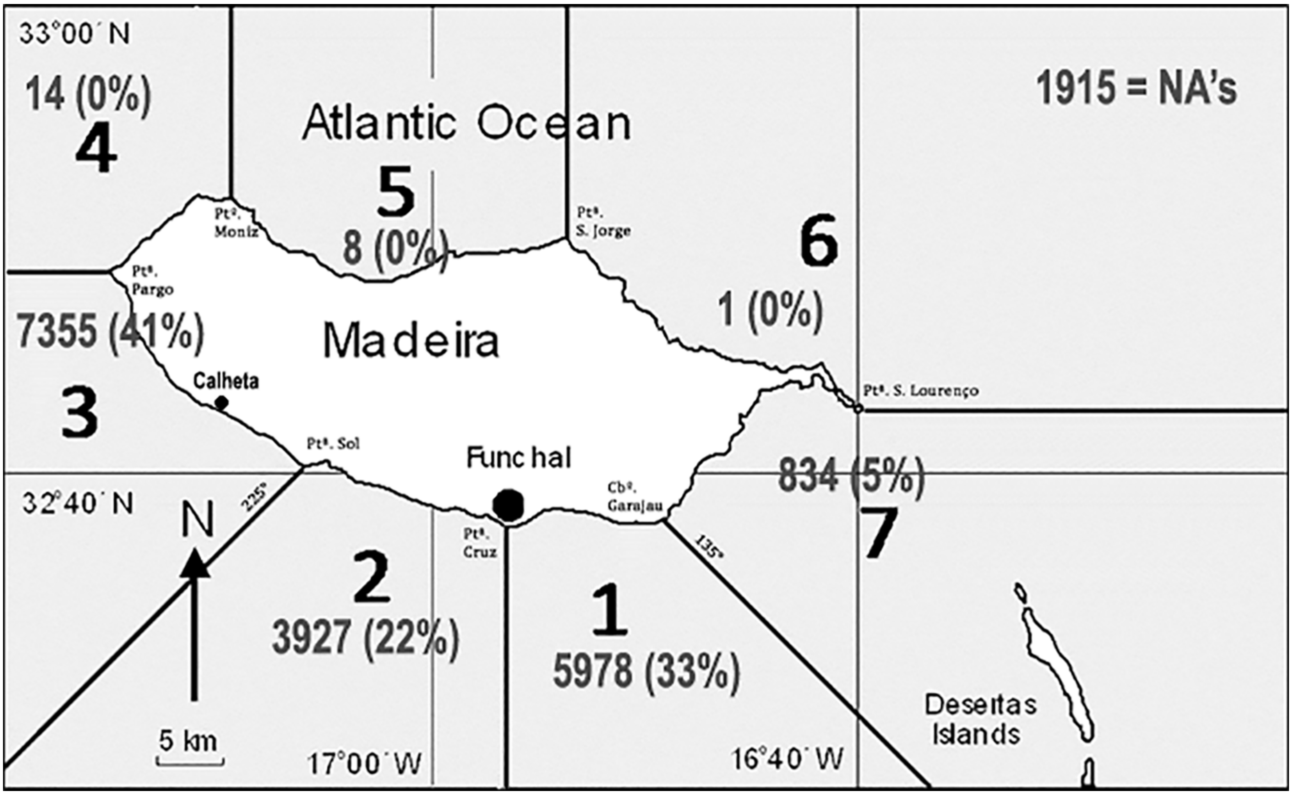

FIGURE 1 | Map of Madeira Island showing the divisions into counting sectors as well as the locations of the marinas of Funchal and Calheta. The numbers represent sampling effort in each sector as number of trips and percent of all trips (NA indicates trips with no recorded sector).

cubic spline interpolation on in-between points (**Figure 2B**). This way we introduced 10-day average points after each succeeding monthly point, thus matching the STS time series format. Due to this, in the analysis of NAO signal we neglected any time periods shorter than the original time resolution of 1 month.

NEST Dataset. This dataset was also obtained from its online repository[2]. The default NEST contained the number of loggerhead turtle nests counted on core index beaches in peninsular Florida. The signal contained yearly plots with sampling during a 109-day time window (May 15 through August 31). Since the dataset is given solely as an image, we used R software to extract the data points from the obtained graph (**Figure 2C**).

2.4 STL Decomposition

We perform an initial signal decomposition using STL (Cleveland et al., 1990), pointing to the limitations of its use in the present case. For the initial data transformations and STL decomposition we used "R" (R Development Core Team, 2021) as well as various packages, i.e.: dplyr (Wickham et al., 2022), reshape (Wickham, 2007), TSA (Chan and Ripley, 2020), car (Fox and Weisberg, 2019). To avoid problems arising from the present zeros, a value of 1 was added to each value of the time series (Cowpertweit and Metcalfe, 2009). Seasonal decomposition and trend extraction was done using STL (Cleveland et al., 1990), a locally weighted loess regression technique (Cowpertweit and Metcalfe, 2009).

2.5 Spectral Analysis

Since STL decomposition is limited, we propose a method of using DSP in signal decomposition. The spectral analysis is conducted on STS, NAO and NEST datasets, including the cross-correlations between them. At first we analyze all signals time series by isolating the most dominant signal periods using DSP. We inspect how they are related to each other, to distinguish whether individually observed periods correspond to higher harmonics of fundamental modes, or whether they appear as independent oscillations in the time series. For that purpose we use Wavelet Transform (WT) allowing us to recognize patterns of most dominant periods, and time intervals of their appearance in the signal. By applying digital filters (high-, low-, and band- pass respectively, hereinafter abbreviated as HP, LP and BP), as well as smoothing average, we isolate characteristic periods from the signal, presented in following section.

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[2] NEST dataset: https://myfwc.com/research/wildlife/sea-turtles/nesting/beach-survey-totals/

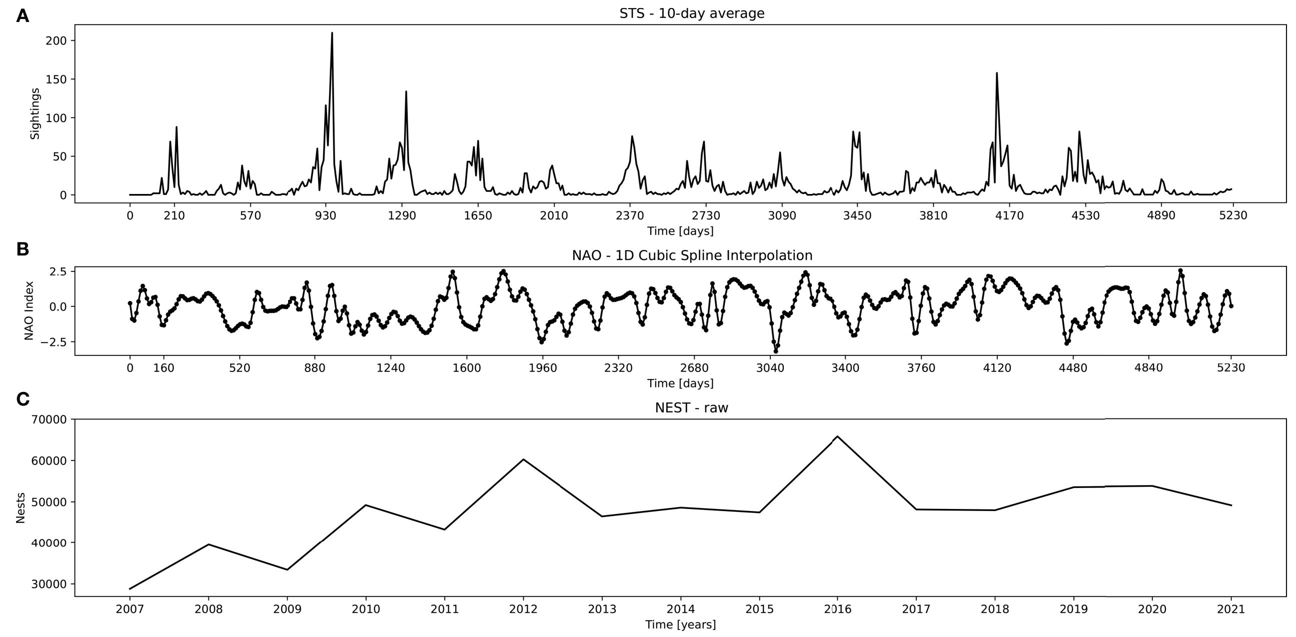

FIGURE 2 | Used datasets, top to bottom: **(A)** STS – 10-day average points of sea turtle sightings, **(B)** NAO – interpolated NAO index average air pressure, and **(C)** NEST – yearly nesting of loggerhead sea turtles in peninsular Florida. Abscissa depicts points matching the sampled STS period (from 2007 - 01 to 2021 - 07).

3 RESULTS

3.1 STL Decomposition

The turtle abundance (STS) has a strong seasonal pattern showing peaks during the summer months. By using STL decomposition on the span of 36 annual 10 day blocks for the loess window for seasonal extraction, the time series was divided into seasonal, trend and remaining components (see **Supplementary Figure 1** in Supplemental Data). To ensure that the sampling effort did not influence our STS signal the same analysis was performed using only boat effort measured as hours-at-sea (**Figure 3**, left plot). The population trend and boat effort are uncorrelated, thus effectively showing a consistent relative population abundance index for oceanic loggerhead turtles off Madeira. Since STL provides solely seasonal components (**Supplementary Figure 1**), it cannot be sensitive to other important modes in the signal which can be modulated. Moreover, STL analysis of STS seasonal mode (T_s^{STS}) provides a monotonic and repetitive signal which is caused by the digital filtering from the libraries that were used. Such signals are typically not found in natural processes, thus we propose the usage of a detailed spectral analysis using the wavelet and Fast Fourier Transforms in combination with DSP techniques.

3.2 Spectral Analysis

STS Signal Components. The wavelet spectra of the STS signal is shown in **Figure 4**. It is possible to notice the strong seasonal component which appears as an oscillation with the fundamental period of T_s ~ 365 *days*, and represents the most dominant component in the signal. This component however includes also the higher harmonic groups around T_s / 2, T_s / 3, and T_s / 4 modes. These higher harmonics are added to the fundamental mode in a way that keeps the integrity of the whole seasonal component. It means that the seasonal component is thus presented (see **Supplementary Figure 2** in Supplemental Data) by a periodic change over one year (the fundamental mode) which has a peaked rather than sine-like shape (due to the distortion induced by its higher harmonics). In **Supplementary Figure 2**, we also show a strong monthly variation (with T_m ~ 30 *days*) that we isolated from the signal (by HP filtering with T_{cut} ~ 50 *days*).

As expected, the seasonal component is amplitude modulated (AM) by longer period components which constitute a general long-periodic trend (see **Figure 3**, right). This trend naturally emerges here as a long period band which is actually the part of the amplitude modulated seasonal component.[3] In **Supplementary Figure 4**, we show the result of cross-correlation between the envelope of the STS seasonal component amplitude change that we get after the demodulation of T_s mode, and, the STS long-period trend. High correlation coefficient (R ~ 0.94) and negligible (relative to T_{cut}) differential phase shift[4] imply that the long-period trend is the modulating signal, and T_s mode is the carrier signal in this case. It means that the original long period trend (the low-

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[3] The spectrum of the amplitude modulated signal whose average value is zero, is composed of a carrier and two side lobes. If the modulated signal has no negative part (thus having the constant and positive average value), the frequency information of the modulating signal (the envelope spectrum) is not only contained in the two side lobes, but it is also present as an additional low-frequency band in its original form.

[4] A time delay introduced between the signals, for which their cross-correlation coefficient reaches its maximum value.

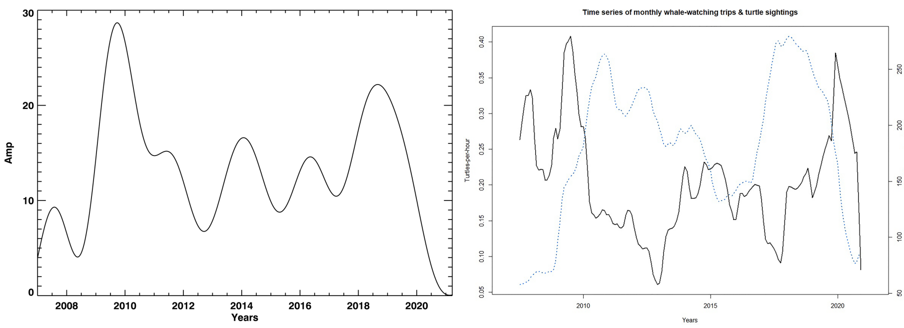

FIGURE 3 | The left plot shows STL decomposition trend lines and boating search effort measured as hour-at-sea (blue) and turtle sightings (black). The right plot shows the trend extracted by using the spectral analysis. It shows a long-period variation in the number of turtle sightings. All trends are shown for the whole interval: 01.01.2007. — 01.07.2021.

frequency band of the envelope) can be simply extracted from the signal by using the LP filtering. The advantage of using the spectral analysis over STL resides in the fact that the STL technique is used to extract the constant amplitude seasonal component, thus pronouncing the remaining long period part as a trend. This however induces the appearance of artificial shorter period components in the trend (as seen in **Figure 3**, left), for which, the spectral analysis is immune. In **Supplementary Figure 3**, we show the trend decomposition to the individual wave modes. One of the trend components has the period T_{nino} ~ 1700 *days* ~ 4.7 *years* which is likely to be caused by El Niño cycle (Trenberth, 1997). It is the same component that we also found in the NAO signal (presented in the following section). Beside the possible El Niño mode, the long-period trend is also composed of one extra long T_{long} ~ 2600 *days* ~ 7 *years*, and one mid-period T_{mid} ~850 *days* period components. Although, the largest period component together with the constant background falls out of the confidence interval (COI) curve (**Figure 4**), it can still be isolated from the trend by applying the LP filter (bottom plot in **Supplementary Figure 3**). Its presence in the signal may be attributed to some long scale climate change which is unknown to us at the present moment. The mode with T_{mid}, though looking like being a first harmonic of T_{nino}, actually appears as superimposed over it.[5] Therefore, we argue that T_{mid} component could possibly be related to some shorter period climate variation such as La Niña, or to some other nature factor.[6]

NAO Signal Components. The WT of NAO signal is depicted in **Figure 5**. As in the STS case, here we also notice the strong seasonal variation T_s ~ 365 *days*, and the mid-period component T_{mid} ~ 850 *days* that is similar to the STS one. Both components are amplitude modulated (AM). The interesting property which shows up in the NAO case is that the modes T_{nino} and T_{long} actually modulate the T_s and T_{mid} components, respectively. The presence of El Niño and extra-long period climate variations in the NAO signal we therefore find by demodulating the seasonal and mid-range components, since the former do not appear directly as independent components in the NAO signal.

The isolated seasonal and mid-period components are shown in **Supplementary Figure 5**, together with their envelopes (the periods T_{nino} and T_{long}, respectively) which are extracted by demodulation. It is interesting to note that T_{long} mode modulates T_{mid} component which, together with T_{nino} mode, both modulate the amplitude of the seasonal component, resulting in the wavelet spectra observed in **Figure 5**.

3.3 Signal Correlations

To find relations between the climate component (NAO) and the measured turtle components (STS, NEST) we use only the strong seasonal components in NAO and STS data, since they show a great statistical significance. Therefore, in STS and NAO signals, we detect and isolate the seasonal carrier signal (the unmodified 1 year period mode), as well as, its envelope (composed of the longer period modes, and represents the rate of change of the carrier mode amplitude), and then cross-correlate them mutually and with NEST data. In this process, we search for the highest obtained correlation coefficients (Pearson's R) found by shifting the STS and NAO signal components in time.[7] Conversely, terms "components", "modes" and "trends" indicate the same word for a filtered signal. Coefficients of determination (R^2) are also depicted including the error in days within 1 σ. All obtained correlations are depicted in **Table 1**.

STS-NAO Correlation (seasonal mode). To verify interdependence between two signals, we apply a linear regression method based on the least squares, to STS (as dependent variable) and NAO (as independent variable). Both STS and NAO signals were filtered to extract their amplitude modulated seasonal components (T_s = 365 *days*). T_s^{STS} and T_s^{NAO}

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[5] The criteria that we used to determine whether some period is a harmonic or an independent mode, lies in the property of the phase of the mode itself, i.e. if the mode is coupled to the observed fundamental period as its harmonic – it thus makes the fundamental oscillation to appear as a more sharp change, or, if the mode is superimposed over that period – it therefore appears as being simply added over the fundamental oscillation.

[6] La Niña has a period of 2–4 years, while El Niño is 2–7 years.

[7] We use terms "shift" and "lag" for the same meaning indicating the delay of the signal by amount of time (Δ_T).

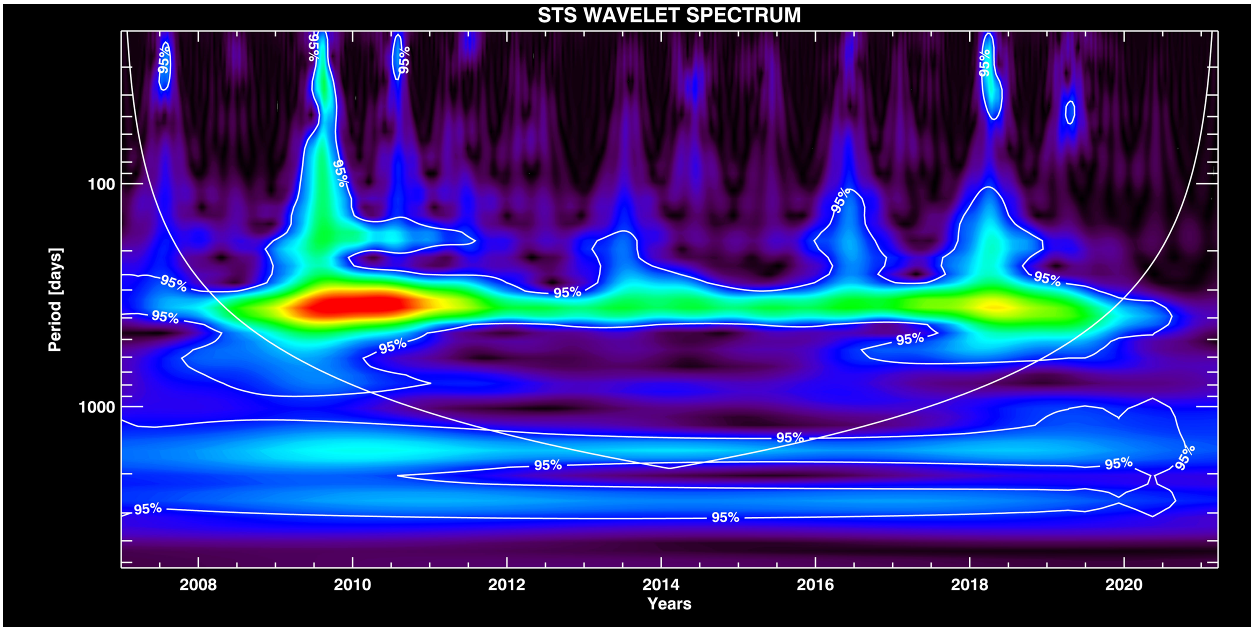

FIGURE 4 | WT of the STS signal with overplotted contours of the significance interval of 0.95 %, and the confidence interval (COI) curve.

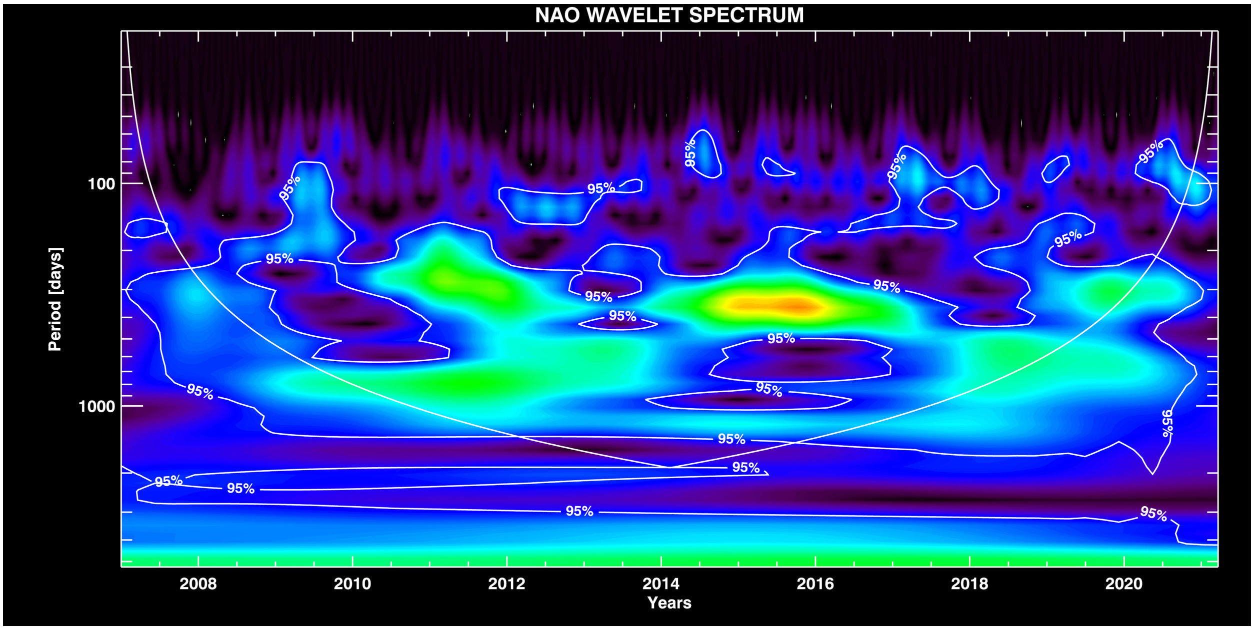

FIGURE 5 | WT of the NAO signal with overplotted contours of the significance interval of 0.95 %, and the confidence interval (COI) curve.

were filtered out by using 1 × *BP* 350 - 380 days. The very narrow band window is used in order to extract the unmodified seasonal components (which does not represent the full signal). The obtained correlation results are depicted in **Table 1** and **Supplementary Figure 6** respectively. The correlation coefficient dependence on the time shift is shown in **Supplementary Figure 6A**. Without any STS shift, a strong negative linear relationship is observed (R = - .96, p < .001,

TABLE 1 | Correlation between sea turtle sightings (STS) in Madeira, Hurrell North Atlantic Oscilation Index (NAO) and nests on core index beaches in peninsular Florida (NEST).

Correlation	Mode	Δ_T	R	p	s	R^2	σ
STS-NAO	Seasonal (365 days)	0 days	**-.96**	<.001	.36	.97	**+/- 24 days**
	T_s^{STS} , T_s^{NAO}	-10 days	-.98	<.001	.22	.97	+/- 22 days
		+170 days	.98	<.001	.25	.96	+/- 22 days
STS-NAO	El Niño (1700 days)	0 days	-.54	<.001	1.29	.60	+/- 64 days
	T_{nino}^{STS}, T_{nino}^{NAO}	**-220 days**	**-.77**	<.001	.97	.60	**+/- 84 days**
		-1110 days	.58	<.001	1.24	.62	+/- 95 days
STS-NEST	Seasonal (1 year)	0 years	-.26	>.05	0	.07	+/-.5 years
		-7 years	**-.52**	<.05	0	.27	**+/-.5 years**
		+7 years	-.26	>.05	0	.27	+/-.5 years

Column names (from left to right): Δ_T - time shift in days or years, R - Pearson's R, p - p-value, s - standard error in days or years, R^2 - Pearson's R (squared) and σ - standard deviation within 1σ. All other bold values are strongest mathematical correlations to which we refer further in text.

Supplementary Figure 6B), where *p* is the p-value statistical significance. Further obtained R-squared was computed (R^2 = .97) with the standard deviation σ = ± 24 *days* (**Supplementary Figure 6C**). The STS time shift Δ_T = -10 *days* (*R* = - .98, *p* < .001, **Supplementary Figure 6D**) does not deviate significantly relative to the non-shifted case. On the other hand, a strong positive correlation was found for Δ_T = + 170 *days* (*R* = 0.98, *p* < .001, **Supplementary Figure 6F**) with uncertainty of 1 σ = ± 22 days. The components used in cross-correlation T_s^{STS} and T_s^{NAO} are shown in **Supplementary Figure 6**. These results indicate that there is a strong anti-correlation present between the STS and NAO signals. The loggerhead sea turtles thus increase traction with the decrease of NAO (T_m), which implies their migration to the locations with calm weather.

STS-NAO Correlation (El Niño mode). As in the previous correlation, we analyze the relation between the seasonal components in STS and NAO data. The difference here is in that we now cross-correlate the El Niño modes (T_{nino} ~ 1700 *days* ~ 4.7 *years*) which we detect in the envelopes of seasonal components. The STS component T_{nino}^{STS} was obtained with the following procedure: (i) 1 × *BP* 240 - 750 days; (ii) 1 × *LP* 1400 days - with demodulation; (iii) 1 × *LP* 1400 days; and (iv) 7 × *HP* 3000 days. Conversely, for the NAO component T_{nino}^{NAO} we used similar steps: (i) 1 × *BP* 260 - 570 days; (ii) *LP* 1400 days - using the envelope of the signal (demodulation); (iii) *LP* 1400 days - additional low-pass to clear further interference from other side lobes; (iv) 5 × *HP* 3000 days - clearing large periods; and (v) 2 × *HP* 1500 days - solving further harmonic issues. Such strict band limits are used in order to encompass all components of the AM seasonal signal (the carrier and both side lobes), and also to filter out the specific mode from the envelope. The correlation coefficients in the case without and with STS shifts of T_{nino} modes are depicted in **Figure 6A**. Obtained correlations are given in **Table 1** and in **Figure 6** respectively. Moderate negative linear relationship was observed (*R* = - .54, *p* < .001, **Figure 6B**) with no STS shift with R^2 = .6, *a* = ± 64 *days* (**Figure 6C**), where again the NAO troughs match the peaks of STS, indicating loggerhead sea turtle increase as a response to lower NAO. Very strong negative relationship is also observed with the time shift of STS signal Δ_T = - 220 *days* (*R* = - .77, *p* < .001 seen in **Figure 6D** and R^2 = .6, σ = ± 84 *days* seen in **Figure 6E**). We also find a moderate strong positive relationship with STS time shift Δ_T = - 1110 *days* (*R* = - .58, *p* < .001 in **Figure 6F** and R^2 = .62, σ = ± 95 *days* in **Figure 6G**). STS peaks are seen as delayed reactions to NAO troughs and vice-versa (**Figure 6H**).

STS-NEST Correlation. Finally, we compare the STS signals with the loggerhead sea turtles nesting from Florida peninsula (NEST) using the yearly points of STS centered at July 1st (as the NEST data collection period). STS signal was filtered with following steps: (i) 1 × *BP* 240 - 750 days; (ii) 1 × *LP* 600 days - with demodulation; (iii) 3 × *LP* 1400 days; and (iv) 3 × *HP* 3000 days. Conversely, NEST signal was filtered with 3 × *HP* 10 *years*. Obtained correlations are depicted in **Supplementary Figure 7** and **Table 1**, with highest correlation coefficient (*R*) shifts with Δ_T = 7 *days* (**Supplementary Figure 7B**). Using linear regression with no time shift (Δ_T = 0), although there is a mild correlation present (*R* = - .26 and R^2 = .07 in **Supplementary Figure 7B, C**), there is no statistically significant correlation (*p* > .5). Such is expected as sea turtles can not travel the greater distance from Florida to Madeira Island. However, 7-year time shift (Δ_T = - 7 *years*) provides statistical significance and strong negative correlation (*R* = - .52, R^2 = .27) as seen in **Supplementary Figures 7D, E**. Such indicates that sea turtles may have 7-year period since nesting until to be observed in Madeira Island. Additional correlation with Δ_T = 7 *years* showed mild negative correlation (*R* = - .26, R^2 = .27), however being not statistically significant (*p* > .05) as seen in **Supplementary Figures 7F, G**. Additional position of default and shifted STS signals, relative to NEST is seen in **Supplementary Figure 7G**, where the troughs of NEST match the STS peaks and vice-versa.

4 DISCUSSION

This study provides a first in-water assessment of relative abundance of oceanic stage loggerhead turtles around Madeira Island, and the second for the North-Atlantic developmental habitats (Vandeperre et al., 2019), though a preliminary version of reported results was already integrated into the 1st Portuguese National Report for the EU Marine Strategy Framework Directive (S.R.A, 2014). Our relative abundance trend spans almost 15 *years* and provides an opportunity to study influencing factors. We show the direct evidence of basin-wide influence of climatic and oceanographic factors on local loggerhead

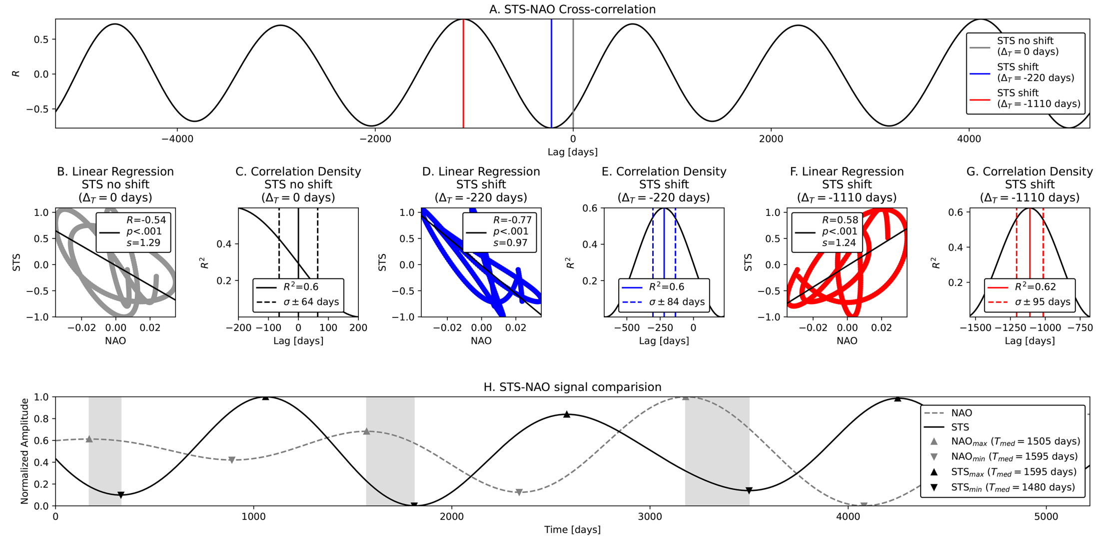

FIGURE 6 | STS-NAO Cross-correlation and linear regression of El Niño modes – T_{nino} ~ 1700 *days* ~ 4.7 *years*. From top to bottom, left to right: **(A)** Correlation coefficients *R* for default STS (no shift) and shifted STS signals; **(B–G)** Linear regression results including coefficients of determination (R^2) and error in days within 1σ; and **(H)** Positions of NAO peaks and STS troughs. Both El Niño modes are anticorrelated.

abundance and distribution, emphasizing the fact that turtle conservation has to be addressed on basin-wide international levels. The oceanic life stage is the least studied life stage among all, where the quantitative assessment of abundance and distribution is key to understand turtle recruitment into subsequent life stages and habitats.

In both STS and NAO datasets, we found the strong seasonal component to be amplitude modulated by the longer (than one year) period modes. We detected the long period trend in STS data, and showed that it is composed of few independent periods of 850, 1700, and 2600 days, which altogether modulate the seasonal change in the number of turtle sightings. By the measured period, the first two components we relate to La Niña and El Niño, respectively. We refer to the longest period one as to some possibly new, still unexplained or undetected climate change trend. We also found the same long period components to appear in the envelope of the seasonal change in NAO index. Apart from the seasonal component and long periodicities, in STS time series we also detected an independent monthly oscillation which is being amplitude modulated by the seasonal and long period components.

The strong anti-correlation between the unmodified and non-shifted STS and NAO seasonal components, implies that loggerhead sea turtles increase traction with the decrease of NAO index (less turtles are sighted when NAO is positive), meaning that their migration is directed toward the warmer weather locations. Indeed, performed cross-correlation analysis between El Niño components which were previously detected in the envelopes of STS and NAO signals, showed the appearance of two maxima – one at the lag of ~ 7 *months*, and the other at the time shift of ~ 3 *years*. The shorter lag implies an anti-correlation between STS and NAO signals, suggesting the larger traction of loggerhead sea turtles with the decrease of air pressure difference. With an average turtle speed of half a knot, one circuit of the midocean North Atlantic Gyre would take around 440 *days* (Carr, 1987). Since Florida to Madeira travel time would be half of this period, it may explain the detected ~ 7 *months* lag. On the other hand, the longer lag which leads to the positive correlation between STS and NAO signals, represents about half the time that turtles spend in oceanic life stage.

Interestingly, the rather strong maximum in the cross-correlation coefficient of cumulative NEST and STS time series reveals the time lag of ~ 7 *years* which finely coincides with the period of 7–9 *years* during which turtles stay in the eastern side of the Atlantic. The oscillation with the same period of ~ 7 *years* is also present in the long period pool of both, STS and NAO time series.

4.1 Index Credibility

Our relative abundance index took advantage of platforms of opportunity and records the number of turtles sighted per time spent searching per island sector, thus configuring a catch-per-unit-effort type of index. Giving that whale-watching companies have often more than 1 daily offshore trip, our temporal sampling density exceeds by greater extent most other applied methodologies, for instance distance sampling as in (Vandeperre et al., 2019), adding to statistical credibility. Since whale-watching trips varied little in their trip time, we have essentially a constant-effort scheme (Quinn and Deriso, 1999) and thus a reliable and cost-effective population sampling methodology, for an otherwise challenging oceanic life stage sampling. For turtles, these types of indices have previously been used mainly to access bycatch rates (Coelho et al., 2013; Carlson et al., 2016) and only recently have citizen science studies addressed population distribution and abundance (Hof et al., 2017; Casale et al., 2020; Hanna et al., 2021). It furthermore represents an example of the contribution of ecotourism to conservation. However, since data recording was done by trained biologists or boat captains, our data cannot be considered citizen science proper (see Vohland et al. (2021) for definitions).

4.2 Population Trend

The population trend was derived using two very different methodologies (**Figure 3**). Both essentially coincided in overall curve shape, showing low population counts between 2010 and 2018 with marked lows in 2013 and 2018. Comparable datasets are from the Azores (Vandeperre et al., 2019) and the Florida nesting (aforementioned NEST). The Azores dataset shows lows between 2005 and 2012 with a 3 year time lag to the Florida nesting data. Given the large distributional area of juvenile oceanic loggerheads from the Great Banks down to Mauritania (Brazner and McMillan, 2008; McCarthy et al., 2010; Varo-Cruz et al., 2016; Freitas et al., 2018; Chambault et al., 2019; Freitas et al., 2019), local changes in population abundance can be caused by two complementary reasons: (1) a lower migration rate to oceanic habitats by juveniles from the production beaches or (2) spatial rearrangements due to oceanic conditions. Furthermore, different populations may use the waters in different ways.

4.3 Ocean-Atmosphere Influences

As widely roaming ectotherms sea turtles are sensitive to temperature variations and thus climate forcing and change (Patrício et al., 2021). Our data indicate a strong STS and NAO seasonal trend components (T_s^{STS} and T_s^{NAO}). Indeed, STS and NAO are anti-correlated, meaning that during positive NAO phases less turtles are sighted around Madeira. The influence of NAO on western Atlantic and Gulf pelagic communities is known (Stenseth et al., 2003; Roberts et al., 2019). Moreover, Johns et al. (2020) showed that *Sargassum* can be transported eastward during negative NAO phases and under extreme anomalous NAO conditions can reach the Canaries and Gibraltar. DuBois et al. (2020) described the influence of hurricanes on turtle hatchling dispersal within the Gulf of Mexico. Positive NAO indices are associated with more storms, where strengthened westerly winds are moved northwards and produce increased temperatures over northern Europe. Such causes dry anomalies and cooler than usual temperatures in the Mediterranean, while negative indices with the roughly the inverse (Stenseth et al., 2003; Herceg-Bulić and Kucharski, 2014). The NAO index thus correlates with sea surface temperature (SST) in specific areas showing the tripole aspect of the NAO with negative correlation centers south of Greenland and in the western subtropics and a positive center off the US east coast (Rodwell et al., 1999). Storm-forced dispersal of loggerheads, though not linked to NAO, was shown by Monzón-Argüello et al. (2012). They are also associated with reduced water surface layer thickness and higher stratification in the western part of the subtropical gyre and the Sargasso Sea (Visbeck et al., 2003). Off New England positive NAO raises SST and affects local cod recruitment (Meng et al., 2016). Warmer SST can induce turtles to migrate further North as found by (Griffin et al., 2019), and thus be prone to a higher probability of cold-stunning when conditions change. Migrating further North may also be a behavioral adaptation to search for more productive colder waters as found by Plotkin (2010) for Olive Ridley's in the eastern tropical Pacific. On the eastern North Atlantic and Mediterranean, positive NAO phases are associated with increased turtle stranding events (Báez et al., 2011). NAO even seems to influence turtles in the eastern tropical Atlantic further south (Báez et al., 2018).

We here found El Niño components in both STS and NAO signals (T_{nino}^{STS} and T_{nino}^{NAO}) using the same WT/FFT spectral analysis and DSP techniques. These components are being lagged at ~ 7 *months* (anti-correlation) and ~ 3 *years* (correlation). The El Niño Southern Oscillation (ENSO) has global effects that also influence the North Atlantic, for instance affecting the path of the Gulf Stream with a time lag of 2 years (Taylor and Stephens, 1998; Taylor et al., 1998). Bjorndal et al. (2017) showed that ecological regime shifts were influenced by unusually strong ENSO events and reduced turtle growth rates in the North and South Atlantic. As DuBois et al. (2020) wrote: "Both subtle differences in the position of oceanographic features (such as meandering currents) and major disturbances (such as hurricanes) can greatly alter dispersal outcomes." As a result this will affect local abundances of sea turtles as those we measured in Madeira waters in the present study, driven by basin wide and larger climatic forcing. This is specially true if we consider that turtles are active swimmers, and not passive dispersers (Dellinger, 1998; McCarthy et al., 2010; Putman and Mansfield, 2015; Freitas et al., 2018; Freitas et al., 2019) and will look up their best habitat given the environmental cues available to them.

4.4 Nesting Data and STS

Our STS data appears to be correlated with the NEST data form the Florida Index Nesting Beaches. However, in contrast to the findings of Vandeperre et al. (2019) who found a time lag of ~ 3 *years*, our time lag was double that amount with its ~ 7 *years*. This coincides with 7+ *year* average duration of the oceanic life stage (Bjorndal et al., 2003a). Why this might be so is unclear to us. The production beaches add on average $1/7^{th}$ each year to the oceanic turtle population, producing a regular turnover, and thus one year's production should not influence overall abundance too much. However, Madeira waters serve as confluence developmental habitat for turtle from other origins as well, namely the Cape Verde Islands (Lino et al., 2010; Marco et al., 2012; Marco, 2013), and these inputs probably influence the sightings at Madeira. Our satellite tracking data (McCarthy et al., 2010; Freitas et al., 2018; Freitas et al., 2019) showed clearly that turtles tagged at summer onset migrated preferentially northward towards the Azores, while those tagged after the summer preferentially migrated SE towards the Canary Islands and Cape Verde. Interestingly enough the oscillation with very similar period of ~ 7 *years* was detected in the long period pool of both, STS and NAO time series.

4.5 Limitations and Future Work

Several planned studies can expand the present analysis. Some potential explanatory variables need testing: (1) the Cape Verde nesting data are needed which we could not secure for our time window, (2) lunar cycles may also prove relevant and (3) we should also check for longer timescale oscillations like the Arctic Oscillation (AO) that influences synchronously the whole Northern Hemisphere (Beaugrand et al., 2015). Furthermore, since estimated turtle size was recorded, it would be important to check if size classes are affected differentially by climatic forcing or if the smallest size class has a stronger influence from nesting beaches (Mansfield et al., 2014). Oceanic stage turtle movements are still poorly understood. Combined individual decisions results in collective movements through the interaction of biological processes and physical processes. Passive drift and active swimming (Polovina et al., 2000; Putman and Mansfield 2015) maintain turtles within appropriate habitat boundaries (Putman et al., 2012). Overall, and mainly for conservation purposes, it would be important to obtain a better picture of more or less synchronous area shifts of oceanic turtles within the North Atlantic which the present paper hints to, and for this more locations should be sampled in comparative ways.

4.6 Conclusions

Turtle populations are typically monitored by using the nesting data, including in-water and remote sensing studies (Kobayashi et al., 2008; National Research Council, 2010). Such species are large organisms with long lifespans which produce large numbers of unnurtured offspring (Hendrickson, 1980). A high mortality seems to occur around the transition to pelagic life (Bjorndal et al., 2003b; Sasso and Epperly, 2007; Salmon and Scholl, 2014), thus making the monitoring of oceanic turtles an important tool to access both, their population status, as well as, the good environmental status of the high seas. To do this effectively, natural causes of the variation have to be understood and separated from anthropogenic causes. The present paper shows that in-water monitoring of juvenile oceanic loggerheads is feasible by using the platforms of opportunity and relative abundances. This points the way toward the implementation of more monitoring programs. Indeed, such programs can cover the wider spatial areas, since relative abundances are much more cost-effective to acquire, compared to the absolute abundances. Our results point to possible natural causes of the detected variation. These different variation time scales were only detectable by using the spectral analysis, a method not typically used in population assessments. Understanding natural causes of the population abundance variation is therefore critical to address anthropogenic factors more directly, e.g. fisheries bycatch or marine litter impact.

DATA AVAILABILITY STATEMENT

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

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because turtles were not handled, only spotted and counted, thus obviating the need for ethics approval according to legislation.

AUTHOR CONTRIBUTIONS

TD designed the study, sampled the data and conducted STL analysis. VZ and MR performed spectral analysis, performing cross-correlation and applying Digital Signal Processing (DSP) techniques. 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.2022.877636/full#supplementary-material

REFERENCES

Alves, J. M., Caldeira, R. M., and Miranda, P. M. (2020). Dynamics and Oceanic Response of the Madeira Tip-Jets. *Q. J. R. Meteorol. Soc.* 146, 3048–3063. doi: 10.1002/qj.3825

Avens, L., Goshe, L., Coggins, L., Snover, M., Pajuelo, M., Bjorndal, K., et al. (2015). Age and Size at Maturation and Adult-Stage Duration for Loggerhead Sea Turtles in the Western North Atlantic. *Mar. Biol.* 162, 1749–1767. doi: 10.1007/s00227-015-2705-x

Avens, L., Goshe, L. R., Pajuelo, M., Bjorndal, K. A., MacDonald, B. D., Lemons, G. E., et al. (2013). Complementary Skeletochronology and Stable Isotope Analyses Offer New Insight Into Juvenile Loggerhead Sea Turtle Oceanic Stage Duration and Growth Dynamics. *Mar. Ecol. Prog. Ser.* 491, 235–251. doi: 10.3354/meps10454

Báez, J. C., Bellido, J. J., Ferri-Yáñez, F., Castillo, J. J., Mart´ın, J. J., Mons, J. L., et al. (2011). The North Atlantic Oscillation and Sea Surface Temperature Affect Loggerhead Abundance Around the Strait of Gibraltar. *Sci. Mar.* 75, 571–575. doi: 10.3989/scimar.2011.75n3571

Ba´ez, J. C., Macías, D., Puerto, M. A., Camin˜ as, J. A., and Ortiz de Urbina, J. M. (2018). North Atlantic Oscillation Leads to the Differential Interannual Pattern Distribution of Sea Turtles From Tropical Atlantic Ocean. *Collect. Vol. Sci. Pap. ICCAT* 74, 3692–3697.

Beaugrand, G., Conversi, A., Chiba, S., Edwards, M., Fonda-Umani, S., Greene, C., et al. (2015). Synchronous Marine Pelagic Regime Shifts in the Northern Hemisphere. *Philos. Trans. R. Soc. B.: Biol. Sci.* 370, 20130272. doi: 10.1098/rstb.2013.0272

Bjorndal, K. A., Bolten, A. B., Chaloupka, M., Saba, V. S., Bellini, C., Marcovaldi, M. A. G., et al. (2017). Ecological Regime Shift Drives Declining Growth Rates of Sea Turtles Throughout the West Atlantic. *Glob. Chang. Biol.* 23, 4556–4568. doi: 10.1111/gcb.13712

Bjorndal, K. A., Bolten, A. B., Dellinger, T., Delgado, C., and Martins, H. R. (2003a). Compensatory Growth in Oceanic Loggerhead Sea Turtles: Response to a Stochastic Environment. *Ecology* 84, 1237–1249. doi: 10.1890/0012-9658(2003)084[1237:CGIOLS]2.0.CO;2

Bjorndal, K. A., Bolten, A. B., and Martins, H. R. (2003b). Estimates of Survival Probabilities for Oceanic-Stage Loggerhead Sea Turtles (*Caretta Caretta*) in the North Atlantic. *Fish. Bull.* 101, 732–736.

Bjorndal, K., Bowen, B., Chaloupka, M., Crowder, L., Heppell, S., Jones, C., et al. (2011). Better Science Needed for Restoration in the Gulf of Mexico. *Science* 331, 537–538. doi: 10.1126/science.1199935

Bolten, A. B. (2003a). "Active Swimmers - Passive Drifters," in *The Oceanic Juvenile Stage of Loggerheads in the Atlantic System (Chapter 4)* (Washington, D.C., USA: Smithsonian Institution Press), 63–78.

Bolten, A. B. (2003b). "Variation in Sea Turtle Life History Patterns," in *Neritic* vs. *Oceanic Developmental Stages(Chpt. 9)*, vol. vol. II. (Boca Raton, USA: CRC Press), 243–257.

Bolten, A. B., Bjorndal, K. A., Martins, H. R., Dellinger, T., Biscoito, M. J., Encalada, S. E., et al. (1998). Transatlantic Developmental Migrations of Loggerhead Sea Turtles Demonstrated by Mtdna Sequence Analysis. *Ecol. Appl.* 8, 1–7. doi: 10.1890/1051-0761(1998)008[0001:TDMOLS]2.0.CO;2

Brazner, J. C., and McMillan, J. (2008). Loggerhead Turtle (*Caretta Caretta*) Bycatch in Canadian Pelagic Longline Fisheries: Relative Importance in the Western North Atlantic and Opportunities for Mitigation. *Fish. Res.* 91, 310–324. doi: 10.1016/j.fishres.2007.12.023

Brigham, E. O., and Morrow, R. (1967). The Fast Fourier Transform. *IEEE Spectr.* 4, 63–70. doi: 10.1109/MSPEC.1967.5217220

Caldeira, R. M. A. (2019). *Island Wakes. 3rd ed* (Oxford: Academic Press), 83–91. doi: 10.1016/B978-0-12-409548-9.11614-8

Caldeira, R. M. A., Groom, S., Miller, P., Pilgrim, D., and Nezlin, N. P. (2002). Sea-Surface Signatures of the Island Mass Effect Phenomena Around Madeira Island, Northeast Atlantic. *Remote Sens. Environ.* 80, 336–360. doi: 10.1016/S0034-4257(01)00316-9

Caldeira, R. M. A., and Sangra, P. (2012). Complex Geophysical Wake Flows. *Ocean. Dyn.* 62, 683–700. doi: 10.1007/s10236-012-0528-6

Carlson, J. K., Gulak, S. J. B., Enzenauer, M. P., Stokes, L. W., and Richards, P. M. (2016). Characterizing Loggerhead Sea Turtle, *Caretta Caretta*, Bycatch in the Us Shark Bottom Longline Fishery. *Bull. Mar. Sci.* 92, 513–525. doi: 10.5343/bms.2016.1022

Carr, A. (1987). New Perspectives on the Pelagic Stage of Sea Turtle Development. *Conserv. Biol.* 1, 103–121. doi: 10.1111/j.1523-1739.1987.tb00020.x

Casale, P., Abbate, G., Freggi, D., Conte, N., Oliverio, M., and Argano, R. (2008). Foraging Ecology of Loggerhead Sea Turtles *Caretta Caretta* In the Central Mediterranean Sea: Evidence for a Relaxed Life History Model. *Mar. Ecol. Prog. Ser.* 372, 265–276. doi: 10.3354/meps07702

Casale, P., Ciccocioppo, A., Vagnoli, G., Rigoli, A., Freggi, D., Tolve, L., et al. (2020). Citizen Science Helps Assessing Spatio-Temporal Distribution of Sea Turtles In Foraging Areas. *Aquat. Conserv.: Mar. Freshw. Ecosyst.* 30, 123–130. doi: 10.1002/aqc.3228

Casale, P., and Tucker, A. D. (2017). *Caretta caretta (amended version of 2015 assessment). The IUCN Red List of Threatened Species 2017* e.t3897a119333622. doi: 10.2305/IUCN.UK.2017-2.RLTS,T3897A119333622.en

Chambault, P., Baudena, A., Bjorndal, K. A., Ar Santos, M., Bolten, A. B., and Vandeperre, F. (2019). Swirling in the Ocean: Immature Loggerhead Turtles Seasonally Target Old Anticyclonic Eddies at the Fringe of the North Atlantic Gyre. *Prog. Oceanogr.* 175, 345–358. doi: 10.1016/j.pocean.2019.05.005

Chan, K.-S., and Ripley, B. (2020). *Tsa: Time Series Analysis. R Package Version 1.3* at https://CRAN.Rproject.org/package=TSA.

Cleveland, R. B., Cleveland, W. S., McRae, J. E., and Terpenning, I. (1990). Stl: A Seasonal-Trend Decomposition Procedure Based on Loess. *J. Off. Stat* 6, 3–73.

Coelho, R., Fernandez-Carvalho, J., and Santos, M. N. (2013). A Review of Methods for Assessing the Impact of Fisheries On Sea Turtles. *Collect. Vol. Sci. Pap. ICCAT* 69, 1828–1859.

Cowpertweit, P. S. P., and Metcalfe, A. V. (2009). *Introductory Time Series With R. Use R!* (Dordrecht, NL: Springer). doi: 10.1007/978-0-387-88698-5

Crouse, D. T., Crowder, L. B., and Caswell, H. (1987). A Stage-Based Population Model for Loggerhead Sea Turtles and Implications for Conservation. *Ecology* 6, 1412–1423. doi: 10.2307/1939225

Delgado, C., Canário, A., and Dellinger, T. (2010). Sex Ratios of Loggerhead Sea Turtles Caretta Caretta During the Juvenile Pelagic Stage. *Mar. Biol.* 157, 979–990. doi: 10.1007/s00227-009-1378-8

Dellinger, T. (1998). The Wandering Turtles of the Atlantic. *Sci. Am. Present.* 9, 88–91.

Dellinger, T., Davenport, J., and Wirtz, P. (1997). Comparisons of Social Structure of Columbus Crabs Living on Loggerhead Sea Turtles and Inanimate Flotsam. *J. Mar. Biol. Assoc. Uni. Kingd.* 77, 185–194. doi: 10.1017/S0025315400033865

DuBois, M. J., Putman, N. F., and Piacenza, S. E. (2020). Hurricane Frequency and Intensity may Decrease Dispersal of Kemp's Ridley Sea Turtle Hatchlings in the Gulf of Mexico. *Front. Mar. Sci.* 7. doi: 10.3389/fmars.2020.00301

Fox, J., and Weisberg, S. (2019). *An R Companion to Applied Regression. 3rd ed* (Thousand Oaks, CA: SAGE Publications).

Freitas, C., Caldeira, R., and Dellinger, T. (2019). Surface Behavior of Pelagic Juvenile Loggerhead Sea Turtles in the Eastern North Atlantic. *J. Exp. Mar. Biol. Ecol.* 510, 73–80. doi: 10.1016/j.jembe.2018.10.006

Freitas, C., Caldeira, R., Reis, J., and Dellinger, T. (2018). Foraging Behavior of Juvenile Loggerhead Sea Turtles in the Open Ocean: From Levy Exploration to Area-Restricted Search. *Mar. Ecol. Prog. Ser.* 595, 203–215. doi: 10.3354/meps12581

Furey, N. B., Armstrong, J. B., Beauchamp, D. A., and Hinch, S. G. (2018). Migratory Coupling Between Predators and Prey. *Nat. Ecol. Evol.* 2, 1846–1853. doi: 10.1038/s41559-018-0711-3

Geldmacher, J., Bogaard, P., Hoernle, K., and Schmincke, H. (2000). The 40ar/39ar Age Dating of the Madeira Archipelago and Hotspot Track (Eastern North Atlantic). *Geochem. Geophys. Geosyst.* 1, 109–122. doi: 10.1029/1999GC000018

Griffin, L. P., Griffin, C. R., Finn, J. T., Prescott, R. L., Faherty, M., Still, B. M., et al. (2019). Warming Seas Increase Cold-Stunning Events for Kemp's Ridley Sea Turtles in the Northwest Atlantic. *PLoS One* 14, e0211503. doi: 10.1371/journal.pone.0211503

Hanna, M. E., Chandler, E. M., Semmens, B. X., Eguchi, T., Lemons, G. E., and Seminoff, J. A. (2021). Citizen-Sourced Sightings and Underwater Photography Reveal Novel Insights About Green Sea Turtle Distribution and Ecology in Southern California. *Front. Mar. Sci.* 8. doi: 10.3389/fmars.2021.671061

Hays, G. C., and Scott, R. (2013). Global Patterns for Upper Ceilings on Migration Distance in Sea Turtles and Comparisons With Fish, Birds and Mammals. *Funct. Ecol.* 27, 748–756. doi: 10.1111/1365-2435.12073

Hendrickson, J. R. (1980). The Ecological Strategies of Sea Turtles. *Am. Zool.* 20, 597–608. doi: 10.1093/icb/20.3.597

Herceg-Bulić, I., and Kucharski, F. (2014). North Atlantic Ssts as a Link Between the Wintertime Nao and the Following Spring Climate. *J. Climate* 27, 186–201. doi: 10.1175/jcli-d-12-00273.1

Hof, C. A. M., Smallwood, E., Meager, J., and Bell, I. P. (2017). First Citizen-Science Population Abundance and Growth Rate Estimates for Green Sea Turtles *Chelonia Mydas* Foraging in the Northern Great Barrier Reef, Australia. *Mar. Ecol. Prog. Ser.* 574, 181–191. doi: 10.3354/meps12173

Houghton, J. D., Callow, M. J., and Hays, G. C. (2003). Habitat Utilization by Juvenile Hawksbill Turtles (Eretmochelys Imbricata, Linnaeus 1766) Around a Shallow Water Coral Reef. *J. Natural Histor.* 37, 1269–1280. doi: 10.1080/00222930110104276

Hurrell, J. W., and Deser, C. (2010). North Atlantic Climate Variability: The Role of the North Atlantic Oscillation. *J. Mar. Syst.* 79, 231–244. doi: 10.1016/j.jmarsys.2009.11.002

IFAW (2009). "Whale Watching Worldwide," in *Tourism Numbers, Expenditures and Expanding Economic Benefits* (Yarmouth Port, MA:International Fund for Animal Welfare). Available at: http://www.ifaw.org/Publications/Program_Publications/Whales/asset_upload_file841_55365.pdf

Johns, E. M., Lumpkin, R., Putman, N. F., Smith, R. H., Muller-Karger, F. E., T. Rueda-Roa, D., et al. (2020). The Establishment of a Pelagic *Sargassum* Population in the Tropical Atlantic: Biological Consequences of a Basin-Scale Long Distance Dispersal Event. *Prog. Oceanogr.* 182, 102269. doi: 10.1016/j.pocean.2020.102269

Kobayashi, D. R., Polovina, J. J., Parker, D. M., Kamezaki, N., Cheng, I.-J., Uchida, I., et al. (2008). Pelagic Habitat Characterization of Loggerhead Sea Turtles, Caretta Caretta, in the North Pacific Ocean, (1997–2006): Insights From Satellite Tag Tracking and Remotely Sensed Data. *J. Exp. Mar. Biol. Ecol.* 356, 96–114. doi: 10.1016/j.jembe.2007.12.019

Krasovskaya, S. (2018). *Economic Contribution of the Whale-Watching Industry for the Madeira Archipelago* (Masters Thesis in Ecotourism, University of Madeira:Funchal, Portugal) at https://digituma.uma.pt/bitstream/10400.13/1852/1/MestradoSvetlana%20Krasovskaya.pdf

Lascelles, B., Notarbartolo Di Sciara, G., Agardy, T., Cuttelod, A., Eckert, S., Glowka, L., et al. (2014). Migratory Marine Species: Their Status, Threats and Conservation Management Needs. *Aquat. Conserv.: Mar. Freshw. Ecosyst.* 24, 111–127. doi: 10.1002/aqc.2512

Lino, S. P. P., Gonc¸alves, E., and Cozens, J. (2010). The Loggerhead Sea Turtle (*Caretta Caretta*) on Sal Island, Cape Verde: Nesting Activity and Beach Surveillance In 2009. *Arquipe´lag - Life Mar. Sci.* 27, 59–63.

Mansfield, K. L., Wyneken, J., Porter, W. P., and Luo, J. (2014). First Satellite Tracks of Neonate Sea Turtles Redefine the 'Lost Years' Oceanic Niche. *Proc. R. Soc. Lond. Ser. B.: Biol. Sci.* 281, 1–9. doi: 10.1098/rspb.2013.3039

Marco, A. (2013). The 2013 Loggerhead Nesting Season in Boavista. *Zool. News* 3, 2.

Marco, A., Abella, E., Liria-Loza, A., Martins, S., Lopez, O., Jimenez-Bordon, S., et al. (2012). Abundance and Exploitation of Loggerhead Turtles Nesting in Boa Vista Island, Cape Verde: The Only Substantial Rookery in the Eastern Atlantic. *Anim. Conserv.* 15, 351–360. doi: 10.1111/j.1469-1795.2012.00547.x

McCarthy, A. L., Heppell, S., Royer, F., Freitas, C., and Dellinger, T. (2010). Identification of Likely Foraging Habitat of Pelagic Loggerhead Sea Turtles (*Caretta Caretta*) in the North Atlantic Through Analysis of Telemetry Track Sinuosity. *Prog. In. Oceanogr.* 86, 224–231. doi: 10.1016/j.pocean.2010.04.009

McClellan, C. M., and Read, A. J. (2007). Complexity and Variation in Loggerhead Sea Turtle Life History. *Biol. Lett.* 3, 592–594. doi: 10.1098/rsbl.2007.0355

Meng, K., Oremus, K., and Gaines, S. (2016). New England Cod Collapse and the Climate. *PLoS One* 11, e0158487. doi: 10.1371/journal.pone.0158487

Monzón-Argüello, C., Dell'Amico, F., Moriniere, P., Marco, A., Lopez-Jurado, L. F., Hays, G. C., et al. (2012). Lost at Sea: Genetic, Oceanographic and Meteorological Evidence for Storm-Forced Dispersal. *J. R. Soc. Interface* 9, 1725–1732. doi: 10.1098/rsif.2011.0788

Monzón-Argüello, C., Rico, C., Carreras, C., Calabuig, P., Marco, A., and Felipe Lopez-Jurado, L. (2009). Variation in Spatial Distribution of Juvenile Loggerhead Turtles in the Eastern Atlantic and Western Mediterranean Sea. *J. Exp. Mar. Biol. Ecol.* 373, 79–86. doi: 10.1016/j.jembe.2009.03.007

Narciso, A., Caldeira, R., Reis, J., Hoppenrath, M., Cacha˜o, M., and Kaufmann, M. (2019). The Effect of a Transient Frontal Zone on the Spatial Distribution of Extant Coccolithophores Around the Madeira Archipelago (Northeast Atlantic). *Estuar. Coast. Shelf. Sci.* 223, 25–38. doi: 10.1016/j.ecss.2019.04.014

National Research Council (2010). *Assessment of Sea-Turtle Status and Trends: Integrating Demography and Abundance* (Washington, DC: National Academies Press). doi: 10.17226/12889

Nunes, N. J., Radeta, M., and Nisi, V. (2020). "Enhancing Whale Watching With Mobile Apps and Streaming Passive Acoustics," in *International Conference on Entertainment Computing* (Springer), 205–222. doi: 10.1007/978-3-030-65736-9_18

Patrício, A. R., Hawkes, L. A., Monsinjon, J. R., Godley, B. J., and Fuentes, M. (2021). Climate Change and Marine Turtles: Recent Advances and Future Directions. *Endang. Specie. Res.* 44, 363–395. doi: 10.3354/esr01110

Peltier, H., and Ridoux, V. (2015). Marine Megavertebrates Adrift: A Framework for the Interpretation of Stranding Data in Perspective of the European Marine Strategy Framework Directive and Other Regional Agreements. *Environ. Sci. Policy* 54, 240–247. doi: 10.1016/j.envsci.2015.07.013

Pipa, T., Atchoi, E., Silva, C., Be´cares, J., Gil, M., Freitas, L., et al. (2019). "MISTIC SEAS II: Applying a Subregional Coherent and Coordinated Approach to the Monitoring and Assessment of Marine Biodiversity in Macaronesia for the Second Cycle of the MSFD. Final Technical Report (TRWP1): Workpackage 1 - Monitoring Programs and Data Gathering," in *Tech. Rep., European Commission*, pp.339. doi: 10.13140/RG.2.2.17231.10407

Plotkin, P. T. (2010). Nomadic Behaviour of the Highly Migratory Olive Ridley Sea Turtle *Lepidochelys Olivacea* in the Eastern Tropical Pacific Ocean. *Endang. Specie. Res.* 13, 33–40. doi: 10.3354/esr00314

Polovina, J. J., Kobayashi, D. R., Parker, D. M., Seki, M. P., and Balazs, G. H. (2000). Turtles on the Edge: Movement of Loggerhead Turtles (Caretta Caretta) Along Oceanic Fronts, Spanning Longline Fishing Grounds in the Central North Pacific 1997–1998. *Fish. Oceanogr.* 9, 71–82. doi: 10.1046/j.1365-2419.2000.00123.x

Putman, N., and Mansfield, K. (2015). Direct Evidence of Swimming Demonstrates Active Dispersal in the Sea Turtle "Lost Years". *Curr. Biol.* 25, 1221–1227. doi: 10.1016/j.cub.2015.03.014

Putman, N. F., Seney, E. E., Verley, P., Shaver, D. J., Lo´ pez-Castro, M. C., Cook, M., et al. (2020). Predicted Distributions and Abundances of the Sea Turtle 'Lost Years' in the Western North Atlantic Ocean. *Ecography* 43, 506–517. doi: 10.1111/ecog.04929

Putman, N. F., Verley, P., Shay, T. J., and Lohmann, K. J. (2012). Simulating Transoceanic Migrations of Young Loggerhead Sea Turtles: Merging Magnetic Navigation Behavior With an Ocean Circulation Model. *J. Exp. Biol.* 215, 1863–1870. doi: 10.1242/jeb.067587

Quinn, T. J., and Deriso, R. B. (1999). "Quantitative Fish Dynamics," in *Biological Resource Management Series* (New York, NY: Oxford University Press).

Radeta, M., Nunes, N. J., Vasconcelos, D., and Nisi, V. (2018). "Poseidon-Passive-Acoustic Ocean Sensor for Entertainment and Interactive Data-Gathering in Opportunistic Nautical-Activities," in *Proceedings of the2018 Designing Interactive Systems Conference*. 999–1011. doi: 10.1145/3196709.3196752

R Development Core Team (2021). *R Language Definition, Version 4.1.2 (2021-11-01.* R Foundation for Statistical Computing. http://cran.r-project.org/doc/manuals/R-lang.pdf

Regional da Madeira, A. (2013). Decreto Legislativo Regional N.° 15/2013/M De 14 De Maio: Aprova O Regulamento Da Atividade De Observac¸A˜o De Vertebrados Marinhos Na Regia˜o Auto´ Noma Da Madeira. *Jorn. Oficial. Da. Regia˜. O. Auto´. Noma. Da. Madeira. I. Se´rie.* 57, 2–12.

Roberts, S. M., Boustany, A. M., Halpin, P. N., and Rykaczewski, R. R. (2019). Cyclical Climate Oscillation Alters Species Statistical Relationships With Local Habitat. *Mar. Ecol. Prog. Ser.* 614, 159–171. doi: 10.3354/meps12890

Rodwell, M., Rowell, D., and Folland, C. (1999). Oceanic Forcing of the Wintertime North Atlantic Oscillation and European Climate. *Nature* 398, 320–323. doi: 10.1038/18648

Saavedra, C., Begoña Santos, M., Valcarce, P., Freitas, L., Silva, M., Pipa, T., et al. (2018). "MISTIC SEAS Ii," in *Macaronesia Roof Report. Tech. Rep., European Commission*, pp. 116 at https://misticseas3.com/sites/default/files/materialdivulgativo/macaronesian_roof_report_en.pdf

Salmon, M., and Scholl, J. (2014). Allometric Growth in Juvenile Marine Turtles: Possible Role as an Antipredator Adaptation. *Zoology* 117, 131–138. doi: 10.1016/j.zool.2013.11.004

Sambolino, A., Alves, F., Fernandez, M., Krakauer, A. B., Ferreira, R., and Dinis, A. (2022). Spatial and Temporal Characterization of the Exposure of Island-Associated Cetacean Populations To Whale- Watching in Madeira Island (Ne Atlantic). *Reg. Stud. Mar. Sci.* 49, 102084. doi: 10.1016/j.rsma.2021.102084

Sasso, C. R., and Epperly, S. P. (2007). Survival of Pelagic Juvenile Loggerhead Turtles in the Open Ocean. *J. Wildl. Manage.* 71, 1830–1835. doi: 10.2193/2006-448

Sequeira, M., Elejabeitia, C., Silva, M., Dinis, A., Stephanis, R., Urquiola, E., et al. (2009). Review of Whalewatching Activities in Mainland Portugal, the Azores, Madeira and Canary Archipelagos and the Strait of Gibraltar *J Cetacean Res. Manage SC61/WW11*

S.R.A (2014). *Diretiva Quadro Estratégia Marinha: Estratégia Marinha Para a Subdivisão Da Madeira* (Funchal:Secretaria Regional do Ambiente e dos Recursos Naturais), pp. 463. Available at: https://www.dgrm.mm.gov.pt/as-pem-diretiva-quadro-estrategiamarinha#collapse__com_liferay_journal_content_web_portlet_JournalContentPortlet_INSTANCE_QFjQWpm5JsNv__3

Stenseth, N. C., Ottersen, G., Hurrell, J. W., Mysterud, A., Lima, M., Chan, K. S., et al. (2003). Studying Climate Effects on Ecology Through the Use of Climate Indices: The North Atlantic Oscillation, El Niño Southern Oscillation and Beyond. *Proc. R. Soc. Lond. Ser. B.: Biol. Sci.* 270, 2087–2096.

Taylor, A. H., Jordan, M. B., and Stephens, J. A. (1998). Gulf Stream Shifts Following Enso Events. *Nature* 393, 638. doi: 10.1038/31380

Taylor, A. H., and Stephens, J. A. (1998). The North Atlantic Oscillation and the Latitude of the Gulf Stream. *Tellu. A.: Dyn. Meteorol. Oceanogr.* 50, 134–142. doi: 10.3402/tellusa.v50i1.14517

Torrence, C., and Compo, G. P. (1998). A Practical Guide to Wavelet Analysis. *Bull. Amer. Meteor. Soc* 79, 61–78. doi: 10.1175/1520-0477(1998)079<0061:APGTWA>2.0.CO;2

Trenberth, K. E. (1997). The Definition of El Nino. *Bull. Am. Meteorol. Soc.* 78, 2771–2778. doi: 10.1175/1520-0477(1997)078<2771:TDOENO>2.0.CO;2

Turtle Expert Working Group (2009). *An Assessment of the Loggerhead Turtle Population in the Western Northern Atlantic Ocean, a Report of the Turtle Expert Working Group*. NOAA Technical Memorandu NMFS-SEFSC 575, pp.1–131. https://repository.library.noaa.gov/view/noaa/3714.

Vandeperre, F., Parra, H., Pham, C. K., Machete, M., Santos, M., Bjorndal, K. A., et al. (2019). Relative Abundance of Oceanic Juvenile Loggerhead Sea Turtles in Relation to Nest Production at Source Rookeries: Implications for Recruitment Dynamics. *Sci. Rep.* 9, 13019. doi: 10.1038/s41598-019-49434-0

Varo-Cruz, N., Bermejo, J. A., Calabuig, P., Cejudo, D., Godley, B. J., López-Jurado, L. F., et al. (2016). New Findings About the Spatial and Temporal Use of the Eastern Atlantic Ocean by Large Juvenile Loggerhead Turtles. *Diversity Distri.* 22, 481–492. doi: 10.1111/ddi.12413

Visbeck, M., Chassignet, E. P., Curry, R., Delworth, T., Dickson, B., and Krahmann, G. (2003). *The Ocean's Response to North Atlantic Oscillation Variability* (Washington, DC: American Geophysical Union), 113–145. doi: 10.1029/GM134

Vohland, K., Land-Zandstra, A., Ceccaroni, L., Lemmens, R., Perelló, J., Ponti, M., et al. (2021). *The Science of Citizen Science* (Cham, Switzerland: Springer). doi: 10.1007/978-3-030-58278-4

Wallace, B. P., DiMatteo, A. D., Bolten, A. B., Chaloupka, M. Y., Hutchinson, B. J., Abreu-Grobois, F. A., et al. (2011). Global Conservation Priorities for Marine Turtles. *PLoS One* 6(9), 1–14. doi: 10.1371/journal.pone.0024510

Wallace, B. P., DiMatteo, A. D., Hurley, B. J., Finkbeiner, E. M., Bolten, A. B., Chaloupka, M. Y., et al. (2010). Regional Management Units for Marine Turtles: A Novel Framework for Prioritizing Conservation and Research Across Multiple Scales. *PLoS One* 5, 15465. doi: 10.1371/journal.pone.0015465

Wickham, H. (2007). Reshaping Data With the Reshape Package. *J. Stat. Softw.* 21, 1–20. doi: 10.18637/jss.v021.i12

Wickham, H., François, R., Henry, L., and Müller, K. (2022). *Dplyr: A Grammar of Data Manipulation. R Package Version 1.0.8.*

Witherington, B., Herren, R. M., and Bresette, M. (2006). *Caretta Caretta – Loggerhead Sea Turtle* (Lunenburg, MA: Chelonian Research Foundation), 74–89.

World Meterological Organization (2012). *Manual on Marine Meteorological Services. Vol. 2 – Regional Aspects* (Geneva, Switzerland: WMO).

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EDITED BY
Patrick Jodice,
United States Geological Survey
(USGS), United States

REVIEWED BY
Luke Bower,
United States Geological Survey
(USGS), United States
Patricia Mancini,
Federal University of Rio de Janeiro,
Brazil

*CORRESPONDENCE
Guillermo Luna-Jorquera
gluna@ucn.cl

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Oceanographic gradients explain changes in the biological traits of nesting seabird assemblages across the south-eastern Pacific

Joao B. Gusmao[1,2], Guillermo Luna-Jorquera[1,3]* and Marcelo M. Rivadeneira[3,1,4]

[1]Departamento de Biologia Marina, Centre for Ecology and Sustainable Management of Oceanic Islands (ESMOI), Facultad Ciencias del Mar, Universidad Católica del Norte, Coquimbo, Chile, [2]Programa de Pós-Graduação em Geoquímica: Petróleo e Meio Ambiente (POSPETRO), Institute of Geosciences, Federal University of Bahia (UFBA), Salvador, Brazil, [3]Centro de Estudios Avanzados en Zonas Aridas (CEAZA), Coquimbo, Chile, [4]Departamento de Biología, Universidad de La Serena, La Serena, Chile

Seabirds are top predators in coastal and pelagic ecosystems that forage at sea but return to land regularly during the breeding season (i.e., central place foragers). This unique life history strategy is directly related to their biological traits and helps define their role as top predators in marine systems. We analysed the effects of physiographic characteristics of nesting islands (area, elevation, and distance from the continent, as predicted by the General Dynamic Model of Oceanic Island Biogeography) and oceanographic variables from waters surrounding nesting islands that tend to be characterised by steep gradients (temperature, salinity, and primary productivity) on the trait diversity of nesting seabird assemblages on islands of the south-eastern Pacific Ocean. Four biological traits related to species' life history and feeding strategy were used to calculate two indices, the Functional Richness and Rao's Quadratic entropy. We used fourth-corner and RLQ analysis to determine the relationship between biological traits and environmental variables. Island physiography and primary productivity in the waters surrounding nesting islands significantly affected seabird trait diversity, which gradually decreased from Chilean coastal islands to the distant Polynesian Islands. The traits for body mass and clutch size showed a significant positive relationship with primary productivity. We identified three assemblages of seabirds that had contrasting trait structures. These were defined as the Galapagos, Coastal Chile, and south-eastern Oceanic islands assemblages, and reflected the adaptations of three different species pools to specific oceanographic conditions. Our results suggest that food-related constraints might be one of the most critical environmental filters that shaped the current trait structure of nesting seabird assemblages on the islands in the eastern South Pacific Ocean.

KEYWORDS

macroecology, functional diversity (FD), trait diversity, oceanic islands, coastal islands, RLQ, fourth-corner analysis

Introduction

Seabirds represent a global group of vertebrates that are relevant top predators in marine food webs (Schreiber and Burger, 2002). Their distribution ranges from tropical to polar systems, and they occur in estuarine, coastal, and open oceanic waters (González-Solís and Shaffer, 2009; Jungblut et al., 2017). During the breeding season, seabirds regularly move between their reproductive habitat, mainly located on islands, to their foraging habitat at sea. This transboundary movement makes them essential drivers of nutrient cycling, transferring nutrients from their marine feeding grounds to the various habitats located on the islands on which they roost and breed. The islands on which seabirds breed (i.e., the distribution of breeding seabirds) are highly constrained by the availability of quality habitat to support nest sites and, for most seabirds, colonies. Habitat quality for breeding seabirds is often related to local factors such as the presence of terrestrial predators, distance from foraging grounds, and availability of suitable nest sites (Schreiber and Burger, 2002). Other factors, such as competition both for food and nest sites, also play a role in determining the distribution of breeding seabirds (Furness and Monaghan, 1987; Schreiber and Burger, 2002).

The role of seabirds as predators in marine ecosystems is directly related to biological traits that reflect life history and feeding strategies (Keith et al., 2001; Shealer, 2001; Schreiber and Burger, 2002). Body mass is an essential component of the avian condition, reflecting the inherent energy reserve available to survive and breed (Bennett and Owens, 2002). Differences in body size (i.e., structural size) among seabirds may result in differences in prey type or prey size, foraging behavior, and distance traveled during foraging (Quillfeldt et al., 2011; Cook et al., 2013). Similarly, it has been proposed that body mass and clutch size primarily reflect adaptations related to energy allocation, in which geographic regions with low food supply would favor small body size and small clutches given the energetic demands of a large offspring (Bennett and Owens, 2002; McNab, 2003). Furthermore, regions with low levels of food resources often support seabird assemblages that are comprised of species with smaller body masses (Ashmole and Ashmole, 1967; McNab, 2003). Exceptions have been observed, however, in high productivity areas of the Atlantic (e.g., São Pedro and São Paulo Archipelago, Mancini and Bugoni, 2014) and Pacific oceans (e.g., coastal islands of north central Chile, Luna-Jorquera et al., 2012), in which seabird assemblages are comprised of species with body mass ranging from a few grams to several kilograms.

The diversity of species traits is an essential driver of ecosystem functioning and responses in terrestrial and aquatic environments (Petchey and Gaston, 2006). Accordingly, an increasing number of studies that examine trait diversity have applied analytical approaches to assess the structure of species assemblages (Jiguet et al., 2007; Ding et al., 2013; Luck et al., 2013; Rayner et al., 2014). For example, the relationship between traits of a species and environmental characteristics is expected to shape communities (Mouillot et al., 2013; Gravel et al., 2016). Furthermore, studies have highlighted the role of trait diversity in modulating ecosystem functioning (Cerrano et al., 2009; Brose and Hillebrand, 2016). Thus, trait-based approaches have been applied to different marine and terrestrial systems to analyze community-level responses to environmental factors and disturbances (Levin et al., 2001; Boyer and Jetz, 2010; Mouillot et al., 2013; Dehling et al., 2014; Morais et al., 2019).

Factors that influence the distribution of seabirds can be considered within both their foraging habitat (i.e., at sea) and the breeding habitat (i.e., on land). In the south-eastern Pacific Ocean, seabirds form assemblages at sea and display biogeographic patterns at different temporal and spatial scales in response to the oceanographic features of the areas where they typically forage (Weichler et al., 2004; Serratosa et al., 2020). In contrast to studies such as these that seek to explain the drivers of seabird assemblages at sea, the factors explaining the diversity patterns of seabirds nesting on islands have seldom been studied. In oceanic islands, local species diversity is unlikely to be at equilibrium, so the classic theory of island biogeography (i.e., island area and isolation; MacArthur and Wilson, 1963; MacArthur and Wilson, 1967) may not be sufficient to explain the observed patterns. Instead, the General Dynamic Model of Oceanic Island Biogeography, GDM (Whittaker et al., 2008; Borregaard et al., 2017) provides a broader conceptual framework for studying diversity in oceanic islands. For example, Gusmao et al. (2020) may be the only study that examines the influence of island physiography (as predicted by the GDM) and oceanographic factors on the spatial variation in species richness and diversity of nesting seabird assemblages in south-eastern Pacific islands, an area that supports an extensive community of nesting seabirds. That study reported that island physiography and oceanographic factors strongly explain changes in species richness and composition across the south-eastern Pacific (Gusmao et al., 2020). However, it is still unclear whether the diversity of biological traits of nesting seabird assemblages would change across islands located in a wide spatial gradient that covers from Galapagos to southern Chile and from the Chilean coast to Pitcairn. Considering the ecological role that seabirds play in insular ecosystems and their current conservation threats, it is essential to identify patterns of biological trait diversity to understand the role of environmental factors in structuring seabird nesting assemblages in coastal and oceanic islands.

We use a trait-based approach to analyze seabird assemblages across islands of the south-eastern Pacific to elucidate how environmental factors may shape the nesting assemblages in such insular systems. Based on the GDM, we hypothesize that if the availability of nesting habitats within an island is a key driver of the trait structure of seabird assemblages, then physiographic characteristics of islands such as area and elevation would be the main predictors of seabird trait diversity. In contrast, if food availability is the main driver of the trait structure of seabird assemblages, then oceanographic variables that influence food availability (i.e., salinity, temperature, and primary productivity) would be the main predictors of seabird trait diversity. We also posited that if environmental gradients across biogeographical realms shaped seabird trait diversity, then the most notable differences in seabird trait diversity would be associated with the largest spatial scales.

Methods

Study area

We compiled information on the occurrence (i.e., presence or absence) of 53 species (Data sheet 1) of seabird nesting on 41 coastal and oceanic islands (Data sheet 2) of contrasting climate and geological history (Spalding et al., 2007; Costello et al., 2017). Although we were primarily interested in the south-eastern Pacific, we also included data from the Galápagos to increase the data set's latitudinal gradient. The final dataset accounted for six main archipelagos (Data sheet 2): Juan Fernández, Desventuradas, Rapa Nui, Pitcairn, Galápagos, and Chilean coastal islands, which range from ~23°S to ~38°S (Figure 1).

We compiled information about the oceanographic features around each island by sampling raster maps from the Bio-ORACLE online database (Tyberghein et al., 2012; Assis et al., 2018) (Data sheet 2). Each Bio-ORACLE global-scale raster map (resolution of 5 arcmins; ~9.2 km at latitude zero) was sampled considering a 50 km buffer around the center of each island using tools of the R packages *raster* (Hijmans, 2021) and *geosphere* (Hijmans, 2019). After excluding highly collinear variables (Pearson's correlation > |0.8|), six environmental variables were considered in our analyses (Data sheet 2): island area (km^2), elevation (m), sea surface temperature (°C), sea surface salinity (SSS), primary productivity (g m^{-3} day^{-1}), and distance to the mainland (km).

Seabird assemblages

We gathered information on nesting seabird occurrences on each island. This information was extracted from the literature and unpublished reports (Data sheet 1). For most Chilean islands, the information on seabirds is from our field records collected intermittently for 20 years (1999-2019) for the coastal islands and five years (2013-2018) for the oceanic islands.

We also compiled information on four biological traits for each seabird species (Data sheet 3): (1) feeding stratum within the water column, defined as below the water surf zone, around the water surf zone, and on the ground; (2) diet based on predominant prey types defined as feeding on invertebrates, vertebrate endotherms [mammals and birds], vertebrate ectotherms [reptiles and amphibians], fishes, scavenger, and unknown; (3) clutch size, average for the species, and (4) body mass in grams, average for the species. These traits were selected since they are related to species' life history and foraging ecology (Boyer and Jetz, 2010; Ding et al., 2013; Luck et al., 2013). Data on seabird feeding stratum and diet were extracted from Wilman et al. (2014), who provided the information on feeding stratum and diet as percentages of multiple trait subcategories (e.g., % diet comprised of fish, % foraging below the water surf zone, respectively). Thus, we used principal components analyses to reduce the full set of categories (three for feeding stratum and six for diet) to fewer vectors (i.e., PCA axes) that, in all cases, explained more than 90% of the variation for each trait (see Supplementary Material Table S1). Hence, we accounted for the information on feeding stratum and diet in our trait-based analysis without unnecessarily increasing the number of dimensions in our trait space. The final trait matrix with four columns was then standardized by centering and scaling the trait values. Information about body mass and clutch size was compiled from the literature and online databases; complete table of species traits and cited references are included in the Data sheet 3.

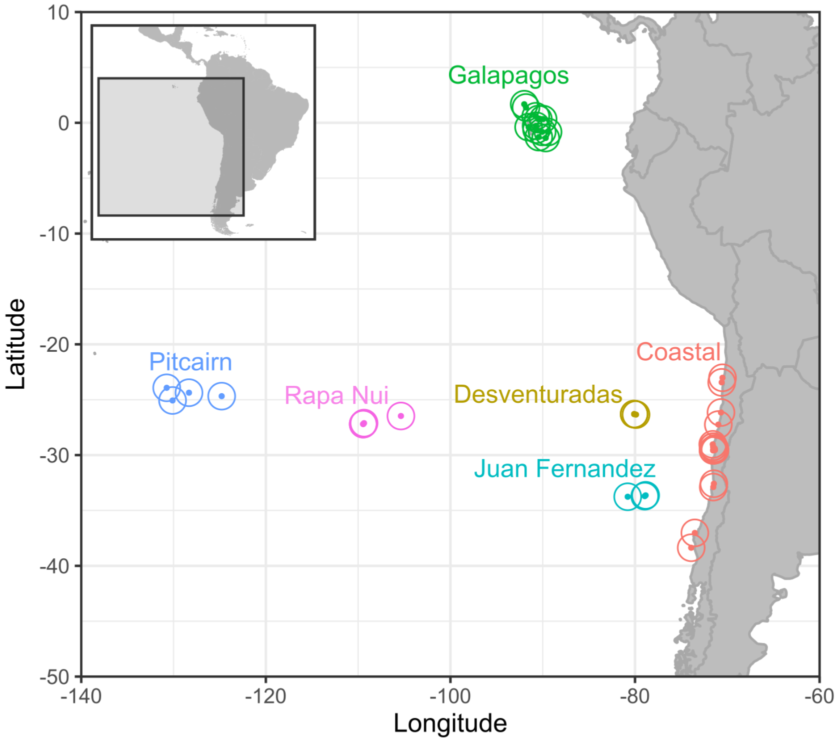

FIGURE 1
Location of the oceanic and coastal islands considered in the study. Islands are represented with a dot and a surrounding circle. The latter does not represent the 50 km buffer to obtain the oceanographic data.

Trait diversity

We selected two trait-based metrics to estimate seabird trait diversity, Functional Richness (FRic, Laliberté and Legendre, 2010) and Rao's Quadratic entropy (Rao's Q; Botta-Dukát, 2005; Ricotta and Szeidl, 2009). These indices were chosen because they reflect different aspects of the multivariate trait space formed by the trait values of all seabird species. Both metrics are distance-based multivariate indices that can be calculated using species' occurrences and trait scores. FRic measures the convex hull hypervolume of the trait space, reflecting the general range of the trait values within a community (Mason et al., 2005; Laliberté and Legendre, 2010). Thus, increasing the range of trait values within a community would increase FRic. This index tends to be highly influenced by species richness and is very sensitive to species with particularly unique trait values (Mason et al., 2013). Rao's Q accounts for the general differences in traits among all species observed in each assemblage. Thus, the more the species in an assemblage differ in trait values (in this case, estimated as the Euclidean distances comparing all species regarding their traits), the higher the Rao's Q value. Although Rao's Q is relatively independent of species richness when the number of species is high, its values can vary widely when calculated for species-poor communities (Mouchet et al., 2010; de Bello et al., 2016). Although we only considered species occurrences, Rao's Q can also weight species abundances in the calculations. We did not use other distance-based functional diversity indices, such as Functional Evenness (FEve) and Functional Divergence (FDiv), due to their dependence on abundance data (Laliberté and Legendre, 2010), which are not available for all the species in our dataset. Both FRic and Rao's Q were calculated using the R package *FD* (Laliberté and Legendre, 2010; Laliberté and Shipley, 2011).

Data analysis

The relationship between trait diversity and environmental variables was analyzed by fitting linear models. Since the empirical error distributions were similar to the theoretical normal probability distribution (visual inspection of Q-Q plots), models were fit considering a Gaussian error structure. Two types of environmental predictors were considered in the models, (*i*) oceanographic: salinity, primary productivity, and sea surface temperature, and (*ii*) island feature: area, elevation, and distance to the continent. The island elevation and the distance from the continent were square root-transformed, and the island area was transformed as $\log_{10}$. All covariates were scaled and centered before fitting the models. Models were validated *via* likelihood ratio tests comparing the fitted model to a null model with no predictors but the intercept. Additionally, we tested whether the model residuals were spatially autocorrelated by applying the Moran's I test implemented in the R package *ape* (Paradis et al., 2004).

We used fourth-corner analysis (Legendre et al., 1997; Dray and Legendre, 2008; Peres-Neto et al., 2017) and RLQ analysis (Dolédec et al., 1996) to assess the relationship between seabird traits and island characteristics. These trait-based analyses have been applied to different biological models, including marine worms (Wouters et al., 2018), insects (Luiza-Andrade et al., 2017), fishes (Keck et al., 2014), and birds (Barbaro and Van Halder, 2009; Azeria et al., 2011; Hartel et al., 2014). The fourth-corner analysis assesses how assemblage trait structure is related to environmental gradients based on the information of species occurrences, environmental variables, and species' traits (Peres-Neto et al., 2017). This analysis was performed using the function *fourthcorner()* in the R package *ade4* (Dray and Dufour, 2007), considering Chessel's correlations (Peres-Neto et al., 2017), 9999 permutations on sites and species (permutation methods 2 and 4, respectively), and Holm's p-value corrections. We used RLQ-analysis to relate seabird traits to environmental factors (i.e., oceanographic factors and island physiography), considering species occurrence nesting on islands. The RLQ procedure performs a double inertia analysis of an environmental-variables-by-islands (R-table) and a species-by-traits (Q-table) matrix, with a link expressed by a species-nesting-by-islands matrix (L-table). RLQ-analysis combines three unconstrained separate ordinations, correspondence analysis of L-table and centered normed principal component analyses of Q- and R-tables, to maximize the covariance between environmental factors and trait data by using co-inertia analysis (Bernhardt-Römermann et al., 2008). First, a correspondence analysis (CA) was performed on the L-occurrence matrix, in which axis scores were used as row weights of a principal components analysis (PCA) of the R-environment matrix. Then, a principal components analysis (PCA) was performed on the Q-trait matrix using the CA site scores as column weights. These steps resulted in a constrained ordination depicting the variation patterns in trait composition across islands, with vectors indicating how environmental variables relate to each ordination axis. RLQ analysis was performed using the R package *ade4* (Dray and Dufour, 2007).

All analyses were performed using R 4.1 (R Core Team, 2017), and all graphs were constructed using the R package *ggplot2* (Wickham, 2009).

Results

Seabird trait diversity, expressed by FRic and Rao's Q, varied markedly across archipelagos and islands (Figure 2). This variation was not dependent on the species richness for Rao's Q ($p > 0.05$, Figure 2A) but was confirmed for FRic (Figure 2B). The highest trait diversity levels were observed on the Chilean coastal islands (median: Rao's Q = 3.26, FRic 3.34) and Galapagos islands (Rao's Q = 2.55, FRic = 4.05), followed by Desventuradas (Rao's Q = 2.58, FRic = 3.18), Rapa Nui (Rao's Q = 1.92, FRic = 2.89), Pitcairn (Rao's Q = 2.32, FRic = 3.42), and Juán Fernández (Rao's Q = 0.7, FRic = 0.36; Figures 2C, D).

The linear model results indicated that environmental predictors explained 50% of total variation in Rao's Q. Rao's Q was negatively related to island elevation and positively related to primary productivity in surrounding waters (Table 1). FRic was positively related to island area and negatively related to island elevation. We detected no evidence of significant spatial autocorrelation on the residuals of the fitted models (Moran's I test, $p>0.05$). See Supplementary Material Figure S1 for individual raw relationships between each environmental variable and diversity index.

The results of the ordinations of the traits diet and feeding stratum are shown in Table S1 (Supplementary Material). For diet, PC1, which explained 90% of the total variation, described a gradient from a *fish-based* diet to an *invertebrate-based* diet. For the feeding stratum, PC1, which explained 95% of the total variation, described a gradient from the feeding stratum around the surf zone to the feeding stratum below the surf zone.

The RLQ analysis and the fourth-corner analysis indicated significant effects of environmental variables on the trait structures we assessed (Figures 3, 4). The RLQ axes explained 70% (Axis 1 = 60%, Axis 2 = 19%) of the correlation between environmental variables (matrix R) and species traits (matrix Q). Most of the variance in environmental gradients (>77%) and biological traits (>94%) was explained by the first two axes. The traits that contributed to most inertia were clutch size (45%) and body mass (25.8%); for environmental variables, primary productivity (37.2%), SST (22.9%), and island distance to the continent (21.9%) contributed to most inertia (Table 2). Gradients in environmental variables along the first axis were mostly related to increases in SST, salinity, island distance, and decreases in primary productivity (Figure 3C). All traits but diet were negatively correlated to the first axis (Figure 3D). Environmental gradients along the second axis were mostly related to increases in salinity and decreases in SST (Figure 3C). Two traits, clutch size, and diet were positively correlated to the second axis (Figure 3D).

The RLQ ordination (Figure 3) depicted four main clusters of islands with contrasting seabird trait structures: (1) Pitcairn and Rapa Nui archipelagos, restricted to quadrant I; (2) Coastal Chilean islands, concentrated in quadrant II; (2) Galapagos archipelago, restricted to quadrants III and IV; and (4) Desventuradas and Juan Fernández archipelagos, restricted to the center of the ordination. The distant Pitcairn and Rapa Nui archipelagos were characterized predominantly by seabirds with a diet based in invertebrates and with small body sizes. The cluster of

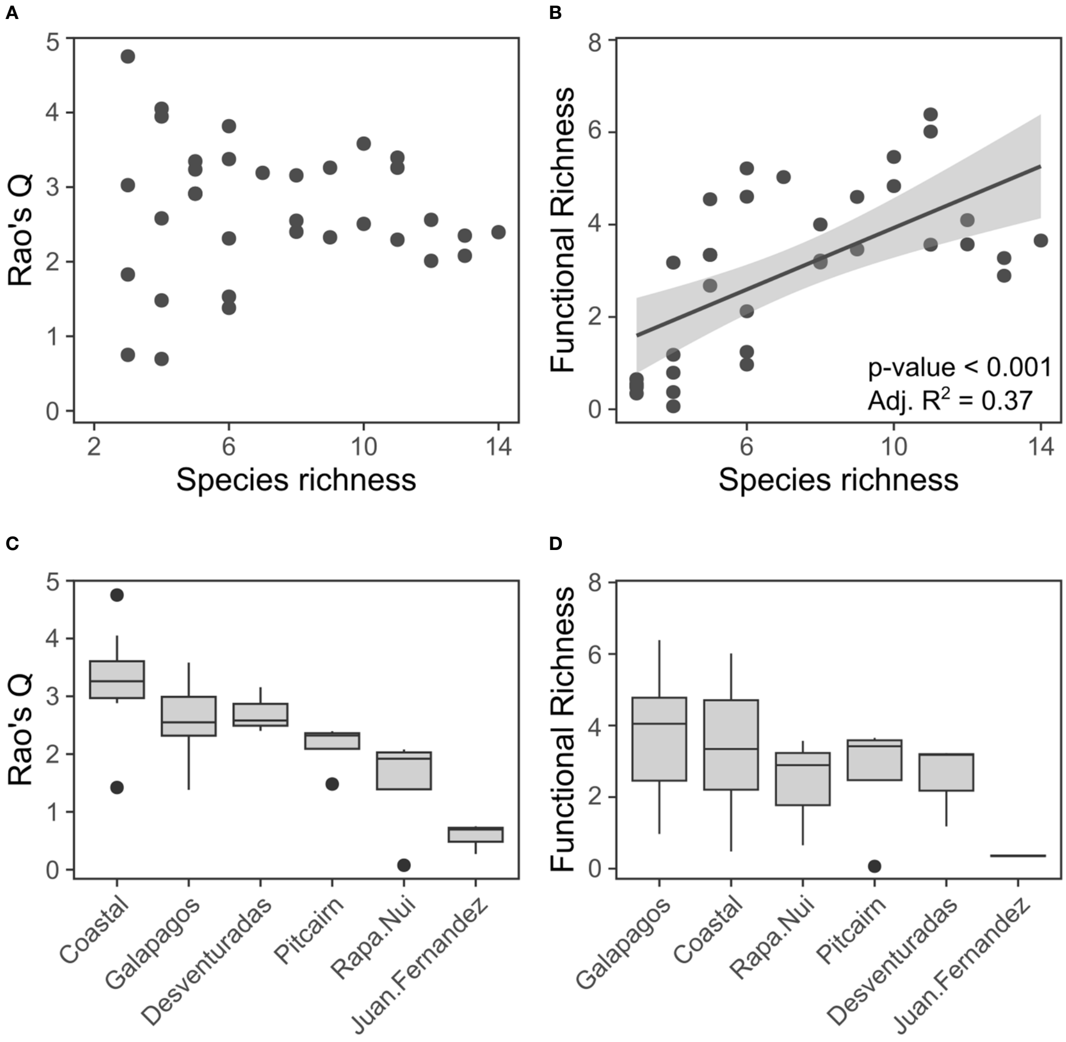

FIGURE 2

Changes in trait diversity of seabird assemblages across islands of the southeastern Pacific. Relationship between species richness and **(A)** Rao's Q, and **(B)** FRic. The linear fit (black line), its associated 95% CI (gray area), and respective-value and adjusted R^2 are shown for the significant fit for the FRic model. Boxplots depicting changes in trait diversity across archipelagos for **(A)** Rao's Q, and **(B)** FRic. Midlines represent medians, boxes represent the interquartile range between quartiles 1 and 3, whiskers represent minimum and maximum non-outlier values, and dots represent outliers.

Coastal Chilean islands was characterized by predominantly piscivorous seabirds with larger clutch size and body mass. Galapagos' seabird assemblages were characterized by small clutch size, fish-based diet, and feeding in the deep water stratum. Desventuradas and Juan Fernández were located at the center of the ordination, depicting an assemblage structure intermediary to the other island clusters.

The results of the fourth-corner analysis (Supplementary Material Table S2) were similar to the RLQ analysis (Figure 4). Island distance, salinity, and primary productivity were significantly correlated to body mass and clutch size ($p<0.01$; Figure 4). Clutch size was negatively related to SST, salinity, and island distance, and positively related to primary productivity. The latter result was mainly forced by the Galápagos archipelago, whose SST is on average ~9.1°C higher than the SST of the Humboldt Current System, where the Chilean coastal islands are located. Finally, body mass was positively correlated with primary productivity but negatively with island distance and salinity. This reflects changes in community structure along the longitudinal gradient, separating the distant Polynesian islands from the other archipelagos near the South American continent (Figure 3).

TABLE 1 Results of the linear models testing the effects of environmental variables on seabird trait diversity (Rao's Q and FRic indices).

Rao's quadratic entropy (Rao's Q)

	Estimate	SE	t-value	p-value	
(Intercept)	1.769	0.636	2.78	0.009	**
Isl. area[1]	0.598	0.716	0.84	0.4	
Isl. Elevation[2]	-1.654	0.807	-2.05	0.05	*
Isl. Distance[2]	-0.813	1.256	-0.65	0.5	
SST	0.719	0.739	0.97	0.3	
Salinity	0.482	0.818	0.59	0.6	
Primary prod.	2.069	0.734	2.82	0.008	**
Adjusted R^2 = 0.50					

Functional richness (FRic)[3]

	Estimate	SE	t-value	p-value	
(Intercept)	1.014	0.453	2.24	0.03	*
Isl. area[1]	1.586	0.548	2.89	0.007	**
Isl. Elevation[2]	-1.301	0.604	-2.16	0.04	*
Isl. Distance[2]	-0.518	0.949	-0.55	0.6	
SST	0.228	0.557	0.41	0.7	
Salinity	0.364	0.636	0.57	0.6	
Primary prod.	0.175	0.532	0.33	0.7	
Adjusted R^2 = 0.20					

Significant coefficient estimates ($p < 0.05$) are highlighted in bold and * indicate extent of significance.

[1] transformed to log10(x)

[2] transformed to the $\sqrt{x}$

[3] transformed to ln(x+1)

Discussion

Our results show that increases in trait diversity of nesting seabird assemblages in the south-eastern Pacific are explained by increases in island area, island elevation, and distances from nesting islands to the South American continent, results that are consistent with the predictions of the GDM (Whittaker et al., 2008; Borregaard et al., 2017). Our results are also consistent with a recent study demonstrating that physiographic factors explain the species diversity of seabird assemblages nesting on islands of the south-eastern Pacific (Gusmao et al., 2020). That study found that large islands contain a high number of nesting species, reflecting a positive species-area relationship that allows for the establishment of colonies of different species. Thus, the GDM is a useful conceptual model for understanding the influence of island physiography in determining seabird trait diversity; however, oceanographic factors also play a major role shaping the seabird assemblages on oceanic and coastal islands. Indeed, we found that trait diversity among the seabird assemblages on islands was explained by the primary productivity of the waters surrounding the island. Changes in the composition of seabird assemblages observed across archipelagos reflected differences in species traits, indicating that seabird assemblages with contrasting trait structures characterize different zones of the south-eastern Pacific. In general, the greater the distance from the South American continent, the higher the predominance of an invertebrate-based diet and the smaller the body mass and clutch size. Of all the variables we assessed, primary productivity was significantly correlated with all traits but feeding strategy, suggesting that food-related constraints might be one of the most critical environmental filters that shaped the current trait structure of seabird assemblages in the south-eastern Pacific.

No significant relationship was detected between species richness and Rao's Q, indicating that assemblages with high species richness do not necessarily present increased trait diversity (Rao's Q index is independent of species richness; Botta-Dukát, 2005; Schleuter et al., 2010). According to the information analyzed in this study, the island elevation and the island area, variables related to local spatial scales, significantly affect trait diversity. This is consistent with theoretical models predicting that large islands with high elevations would provide a wider range of habitat types and increased topographic complexity, thus providing a range of habitats for different seabird species (Roth, 1976; Lomolino and Weiser, 2001; González-Megías et al., 2007). The significant effect of primary productivity in waters surrounding nesting islands on Rao's Q suggests that variables related to large spatial scales also influence changes in seabird trait diversity. Differences in trait diversity across large spatial scales were observed in the Pacific

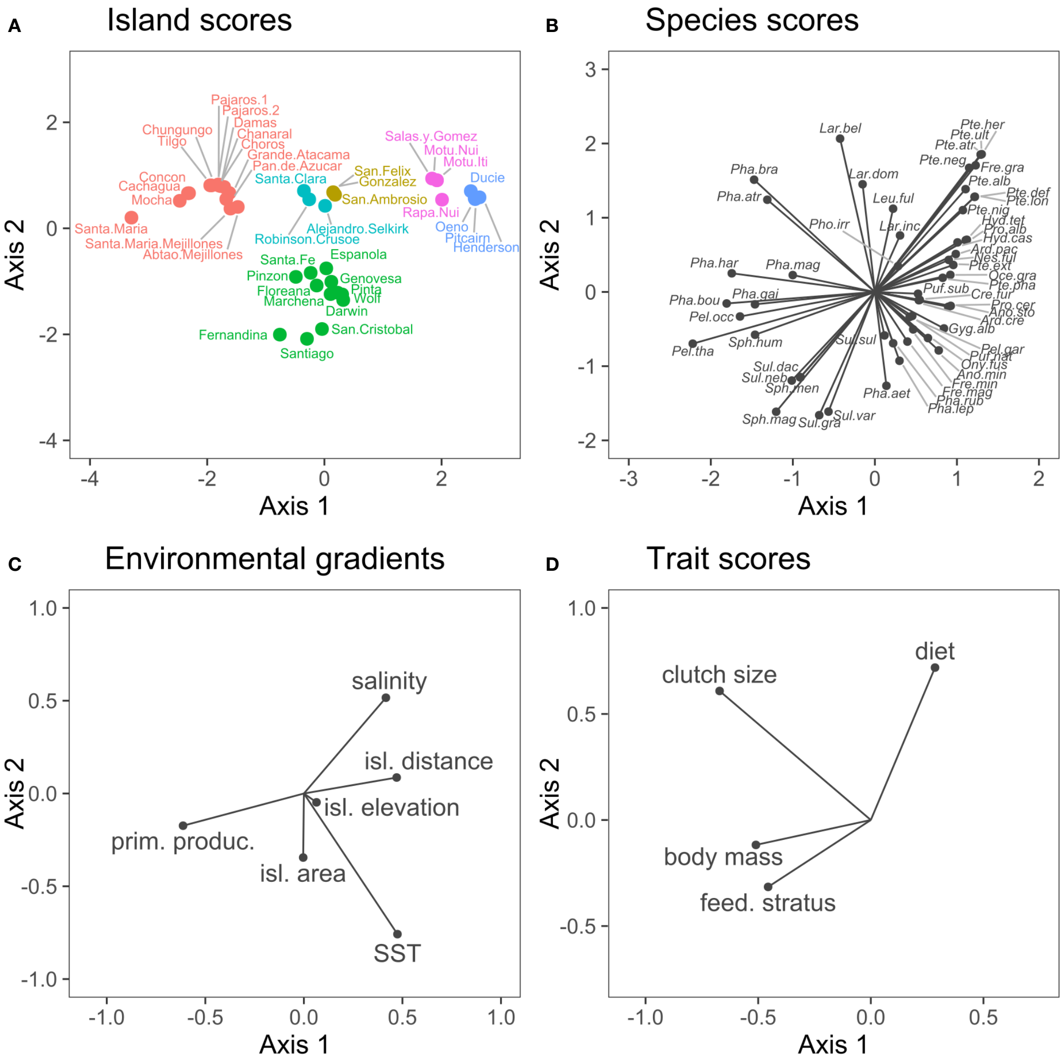

FIGURE 3
RLQ analysis showing the scores obtained after correspondence and principal component analysis (see Data analysis for details) for **(A)** islands, **(B)** species, **(C)** environmental variables, and **(D)** traits. Species abbreviations are defined in Data sheet 1.

for other taxonomic groups (e.g., fishes and corals; Yeager et al., 2017). Variations in trait diversity across large spatial scales are explained mainly by variables with steep environmental gradients, such as sea surface temperature and productivity (Fisher et al., 2010; Barton et al., 2013; Stuart-Smith et al., 2013). Our results suggest that the variation in trait diversity across large spatial scales is related to the environmental differences observed between Chilean coastal islands and distant oceanic islands such as Pitcairn and Rapa Nui archipelagos. Chilean coastal islands are distributed along the Humboldt Current, one of the most productive upwelling systems in the world (Penven et al., 2005; Thiel et al., 2007), while Pitcairn and Rapa Nui archipelagos are located in the oligotrophic waters of the center of the South Pacific gyre (Loret and Tanacredi, 2003). This contrast in environmental conditions indicates that productivity may be a significant environmental filter for seabirds nesting on islands of the south-eastern Pacific Ocean.

Lack (1947) proposed that food availability and quality represent a major energetic constraint for avian clutch size. Lack suggested that low food availability would favor individuals with small clutch sizes given the low energetic demand to raise a small brood. Although this hypothesis was initially proposed to explain latitudinal changes in clutch size, it could also apply to gradients in food availability, such as those that occur across oligotrophic and eutrophic marine systems. Thus, the food gradient observed from ultra-oligotrophic waters of the center of the south-eastern Pacific gyre to the eutrophic waters of the

TABLE 2 Contributions (%) of individual traits and environmental variables to the total inertia to both RLQ axes.

Variables	Inertia (%)	Axis 1 (%)	Axis 2 (%)
Biological traits			
Body mass	25.76	26.02	1.38
Clutch size	44.97	45.07	37.02
Diet	8.57	8.12	51.65
Feeding stra.	20.70	20.79	9.95
Environmental variables			
Isl. Area	0.13	0.00	11.92
Isl. Elevation	0.41	0.41	0.23
Isl. Distance	21.95	22.16	0.74
SST	22.87	22.54	57.46
Salinity	17.41	17.32	26.64
Primary prod.	37.23	37.57	3.01

Ordination results are shown in Figure 3.

Humboldt current may modulate the observed changes in clutch size among the seabirds in the assemblages we studied. The increase in clutch size we observed with the decreasing distance from the South American continent also suggests that nest predation has little effect on explaining the seabird trait structure. A conceptual model states that birds with small clutch sizes would be favored in zones with high nest predation since the energy allocation in a single reproduction attempt is relatively small compared to birds with large clutch sizes (Martin, 1995). However, this model does not apply to our study system since the number of terrestrial predators decreases from the South American continent to the Polynesian Islands

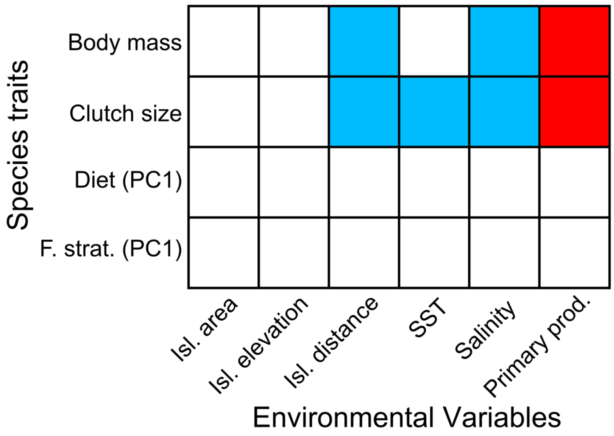

FIGURE 4
Results of the fourth-corner statistics analysis depicting the significant ($p < 0.05$) correlation between seabird traits (rows) and environmental variables (columns). Cell colors indicates if the correlations were positive (red) or negative (blue). Isl. = islands; SST = Sea surface temperature; prod. = productivity; F. strat. = Feeding stratum; PC1 = a vector after principal component analysis (see 2.2. for details and Supplementary Material Table S2).

(excluding invasive species; Simeone and Luna-Jorquera, 2012; Luna et al., 2018). Therefore, the smaller body mass and clutch size of the Polynesian seabird assemblages, represented mainly by species of the Family Procellariidae, possibly reflect an energy-saving adaptation.

The RLQ analysis separated the structure of the seabird assemblage from the Galapagos, Polynesian, and Chilean coastal islands. This separation reflects the three biogeographical realms proposed by Spalding et al. (2007) in this region; the Tropical Eastern Pacific, the Eastern Indo-Pacific, and the Temperate South American realms, respectively. The correlations of specific seabird traits with particular marine realms are consistent with the fourth corner analysis results, highlighting the adaptations of seabirds to cope with the environmental characteristics of each realm. For instance, for the seabird assemblages of Pitcairn and Rapa Nui, their small body mass and clutch sizes are consistent with relatively lower energetic demand for breeding compared to species with larger body mass and larger clutch sizes, and possibly represent an adaptation to the filtering influence of the oligotrophic waters of the center of the Pacific gyres. For highly productive systems of the provinces of the Warm Temperate south-eastern Pacific and along the Humboldt Current, increased marine productivity is positively correlated with large body mass and clutch size. The Tropical Eastern Pacific realm (Galapagos) was associated with high sea surface temperature and characterized by species with small clutch sizes. The negative relationship between clutch size and sea surface temperature is consistent with Rensch's rules, which suggest larger clutch sizes in colder environments (Gaston et al., 2008). No evidence of Bergmann's rule, which posits that larger body sizes of endotherms are expected in colder climates (Olson et al., 2009), was observed for our study system. The negative correlation observed between body mass and distance from the continent is also consistent with Olson et al. (2009), who suggest that birds tend to have larger median body mass on the mainland compared to oceanic islands. Thus, the trait structure of seabird assemblages of the south-eastern Pacific is a product of the local effects of island characteristics and the primary environmental filters established by the gradients observed among different biogeographical realms, which agrees with the finding of Nunes et al. (2017), i.e., that spatial phenotypic variation in seabirds may be strongly linked to oceanographic conditions.

Our study highlighted the marked differences in nesting assemblages of seabirds across different oceanic and coastal systems, reflecting the three marine biogeographical realms described in this region (Spalding et al., 2007). Since assemblages differ in species and trait structure, our results elucidate differences in the ecological roles of seabirds in these systems and the vulnerability of local seabirds colonies to the effects of climate change. In general, trait diversity is considered a better predictor of ecosystem function than species richness because traits are assumed to reflect the relationship of each species with its environment (Díaz and Cabido, 2001). Even though trait diversity metrics do not describe the direct relationship between species and functions, it is intuitive that species depicting high trait similarities tend to have similar niches (Villéger et al., 2011; Mason and De Bello, 2013). Considering the high species richness observed in Pitcairn and Rapa Nui (Gusmao et al., 2020) and the relatively low trait diversity observed in the Polynesian islands, we posit that these islands have high functional redundancy (i.e., species performing similar ecological roles; Luck et al., 2013; Pillar et al., 2013). This does not necessarily mean that the system is impoverished, but rather that these assemblages have a high chance of conserving functions when species are locally extinct (Luck et al., 2013). Assuming that the traits considered in this study are a fair representation of species niches, marine managers should be aware of islands with low species richness and high trait diversity since the local extinction of any species in such systems may have a greater probability of causing a significant loss in ecosystem functioning.

There is growing evidence showing the negative impact of anthropogenic activities on the functional diversity of birds (Matuoka et al., 2020; Stewart et al., 2022), particularly in archipelagos (Sayol et al., 2021). A recent meta-analysis demonstrated that human disturbances consistently reduce the functional diversity of bird assemblages and that impacts are higher in tropical areas (Matuoka et al., 2020). We cannot rule out these effects on our study systems. For instance, Rapanui is a textbook case of human ecocide, as the prehistoric human populations collapsed the fragile local ecosystem, leading to the extinction of most native birds and the further post-colonial invasion of other species (Plaza et al., 2021). It is likely that such species turnover leads to changes in the local functional diversity of Rapanui seabirds, as seen in other systems (Sayol et al., 2021). However, baseline information on the human impacts on other islands from our study archipelagos is unavailable.

Conclusion

Our results indicated that the trait diversity of seabird assemblages in our study system was explained by both local factors (e.g., island physiography) and large-scale environmental gradients (e.g., primary productivity as it related to the increasing distance from the South American continent). The latter also corresponded to gradients observed across three different marine biogeographical realms. Our findings reflect the adaptations of the species of seabirds in our study area to the oceanographic conditions surrounding their nesting islands.

Seabirds with lower body mass and a small clutch size were associated with the distant Pitcairn and Rapa Nui archipelagos, suggesting energy-saving adaptations to cope with the oligotrophic conditions in that area. In contrast, seabirds nesting at Chilean coastal islands along the highly productive Humboldt Current were characterized by large body mass and large clutch sizes. The gradient in trait diversity observed from Polynesian islands to the Chilean coastal islands suggests the influence of environmental filters limiting trait diversity in the most distant archipelagos.

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

GL-J and JG designed and conceived the study. JG analyzed the data and wrote first version 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.

Publisher's Note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.897947/full#supplementary-material

SUPPLEMENTARY DATA SHEET 1
Compiled data on the occurrence of seabird colonies nesting on islands of the southeastern Pacific Ocean. The consulted literature and sources are shown in the metadata tab.

SUPPLEMENTARY DATA SHEET 2
Compiled data on the physiography of islands of the southeastern Pacific Ocean. It also includes data on the oceanography of the surrounding waters. The consulted literature and sources are shown in the metadata tab.

SUPPLEMENTARY DATA SHEET 3
Compiled data on the biological traits of seabirds nesting on islands of the southeastern Pacific Ocean. The consulted literature and sources are shown.

References

Ashmole, N. P., and Ashmole, M. J. (1967). Comparative feeding ecology of sea birds of a tropical oceanic island. *Peabody Museum Nat. Hist. Bull. Yale Univ.* 24, 1–131. doi: 10.2307/4511544

Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E. A., and De Clerck, O. (2018). Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. *Glob. Ecol. Biogeogr.* 27, 277–284. doi: 10.1111/geb.12693

Azeria, E. T., Ibarzabal, J., Hébert, C., Boucher, J., Imbeau, L., and Savard, J. P. L. (2011). Differential response of bird functional traits to post-fire salvage logging in a boreal forest ecosystem. *Acta Oecologica* 37, 220–229. doi: 10.1016/j.actao.2011.02.005

Barbaro, L., and Van Halder, I. (2009). Linking bird, carabid beetle and butterfly life-history traits to habitat fragmentation in mosaic landscapes. *Ecography (Cop.).* 32, 321–333. doi: 10.1111/j.1600-0587.2008.05546.x

Barton, A. D., Pershing, A. J., Litchman, E., Record, N. R., Edwards, K. F., Finkel, Z. V., et al. (2013). The biogeography of marine plankton traits. *Ecol. Lett.* 16, 522–534. doi: 10.1111/ele.12063

Bennett, P. M., and Owens, I. P. F. (2002). *Evolutionary ecology of birds: Life histories, mating systems, and extinction* (New York, U.S.A: Oxford University Press).

Borregaard, M. K., Amorim, I. R., Borges, P. A. V., Cabral, J. S., Fernández-Palacios, J. M., Field, R., et al. (2017). Oceanic island biogeography through the lens of the general dynamic model: Assessment and prospect. *Biol. Rev.* 92, 830–853. doi: 10.1111/brv.12256

Botta-Dukát, Z. (2005). Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *J. Veg. Sci.* 16, 533–540. doi: 10.1111/j.1654-1103.2005.tb02393.x

Boyer, A. G., and Jetz, W. (2010). Biogeography of body size in pacific island birds. *Ecography (Cop.).* 33, 369–379. doi: 10.1111/j.1600-0587.2010.06315.x

Brose, U., and Hillebrand, H. (2016). Biodiversity and ecosystem functioning in dynamic landscapes. *Philos. Trans. R. Soc B Biol. Sci.* 371, 20150267. doi: 10.1098/rstb.2015.0267

Cerrano, C., Danovaro, R., Gambi, C., Pusceddu, A., Riva, A., and Schiaparelli, S. (2009). Gold coral (Savalia savaglia) and gorgonian forests enhance benthic biodiversity and ecosystem functioning in the mesophotic zone. *Biodivers. Conserv.* 19, 153–167. doi: 10.1007/s10531-009-9712-5

Cook, T. R., Lescroël, A., Cherel, Y., Kato, A., and Bost, C.-A. (2013). Can foraging ecology drive the evolution of body size in a diving endotherm? *PloS One* 8, e56297. doi: 10.1371/journal.pone.0056297

Costello, M. J., Tsai, P., Wong, P. S., Cheung, A. K. L., Basher, Z., and Chaudhary, C. (2017). Marine biogeographic realms and species endemicity. *Nat. Commun.* 8, 1–9. doi: 10.1038/s41467-017-01121-2

de Bello, F., Carmona, C. P., Lepš, J., Szava-Kovats, R., and Pärtel, M. (2016). Functional diversity through the mean trait dissimilarity: resolving shortcomings with existing paradigms and algorithms. *Oecologia* 180, 933–940. doi: 10.1007/s00442-016-3546-0

Dehling, D. M., Töpfer, T., Schaefer, H. M., Jordano, P., Böhning-Gaese, K., and Schleuning, M. (2014). Functional relationships beyond species richness patterns: Trait matching in plant-bird mutualisms across scales. *Glob. Ecol. Biogeogr.* 23, 1085–1093. doi: 10.1111/geb.12193

Díaz, S., and Cabido, M. (2001). Vive la différence: plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.* 16, 646–655. doi: 10.1016/S0169-5347(01)02283-2

Ding, Z., Feeley, K. J., Wang, Y., Pakeman, R. J., and Ding, P. (2013). Patterns of bird functional diversity on land-bridge island fragments. *J. Anim. Ecol.* 82, 781–790. doi: 10.1111/1365-2656.12046

Dolédec, S., Chessel, D., Ter Braak, C. J. F., and Champely, S. (1996). Matching species traits to environmental variables: A new three-table ordination method. *Environ. Ecol. Stat.* 3, 143–166. doi: 10.1007/BF02427859

Dray, S., and Dufour, A. B. (2007). The ade4 package: implementing the duality diagram for ecologists. *J. Stat. Software* 22, 1–20. doi: 10.18637/jss.v022.i04

Dray, S., and Legendre, P. (2008). Testing the species traits–environment relationships: the fourth-corner problem revisited. *Ecology* 89, 3400–3412. doi: 10.1890/08-0349.1

Fisher, J. A. D., Frank, K. T., and Leggett, W. C. (2010). Global variation in marine fish body size and its role in biodiversity-ecosystem functioning. *Mar. Ecol. Prog. Ser.* 405, 1–13. doi: 10.3354/meps08601

Furness, R. W., and Monaghan, P. (1987). *Seabird ecology* (New Your, U.S.A: Chapman and Hall). doi: 10.1007/978-1-4613-2093-7

Gaston, K. J., Chown, S. L., and Evans, K. L. (2008). Ecogeographical rules: Elements of a synthesis. *J. Biogeogr.* 35, 483–500. doi: 10.1111/j.1365-2699.2007.01772.x

González-Megías, A., María Gómez, J., and Sánchez-Piñero, F. (2007). Diversity-habitat heterogeneity relationship at different spatial and temporal scales. *Ecography (Cop.).* 30, 31–41. doi: 10.1111/j.2006.0906-7590.04867.x

González-Solís, J., and Shaffer, S. A. (2009). Introduction and synthesis: Spatial ecology of seabirds at sea. *Mar. Ecol. Prog. Ser.* 391, 117–120. doi: 10.3354/meps08282

Gravel, D., Albouy, C., and Thuiller, W. (2016). The meaning of functional trait composition of food webs for ecosystem functioning. *Philos. Trans. R. Soc B Biol. Sci.* 371, 20150268. doi: 10.1098/rstb.2015.0268

Gusmao, J. B., Luna-Jorquera, G., Fernández, C., Luna, N., Plaza, P., Portflitt-Toro, M., et al. (2020). The role of island physiography and oceanographic factors in shaping species richness and turnover of nesting seabird assemblages on islands across the south-eastern pacific. *J. Biogeogr.* 47, 2611–2621. doi: 10.1111/jbi.13973

Hartel, T., Hanspach, J., Abson, D. J., Máthé, O., Moga, C. I., and Fischer, J. (2014). Bird communities in traditional wood-pastures with changing management in Eastern Europe. *Basic Appl. Ecol.* 15, 385–395. doi: 10.1016/j.baae.2014.06.007

Hijmans, R. J. (2021). raster: Geographic Data Analysis and Modeling. *R package version 3.4-13.* Available at: https://CRAN.R-project.org/package=raster.

Hijmans, R. J. (2019). geosphere: Spherical Trigonometry.*R package version 1.5-10.* Available at : https://CRAN.R-project.org/package=geosphere.

Jiguet, F., Gadot, A.-S., Julliard, R., Newson, S. E., and Couvet, D. (2007). Climate envelope, life history traits and the resilience of birds facing global change. *Glob. Change Biol.* 13, 1672–1684. doi: 10.1111/j.1365-2486.2007.01386.x

Jungblut, S., Nachtsheim, D. A., Boos, K., and Joiris, C. R. (2017). Biogeography of top predators – seabirds and cetaceans – along four latitudinal transects in the Atlantic ocean. *Deep. Res. Part II Top. Stud. Oceanogr.* 141, 59–73. doi: 10.1016/j.dsr2.2017.04.005

Keck, B. P., Marion, Z. H., Martin, D. J., Kaufman, J. C., Harden, C. P., Schwartz, J. S., et al. (2014). Fish functional traits correlated with environmental variables in a temperate biodiversity hotspot. *PloS One* 9, e93237. doi: 10.1371/journal.pone.0093237

Keith, C. H., Schreiber, E. A., and Burger, J. (2001). "Breeding biology, life histories, and life history-environment interactions in seabirds," in *Biology of marine birds*. Eds. E. A. Schreiber and J. Burger (New York, U.S.A: CRC Press), 722.

Laliberté, E., and Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91, 299–305. doi: 10.1890/08-2244.1

Laliberté, E., Legendre, P., and Shipley, B. (2014). FD: measuring functional diversityfrom multiple traits, and other tools for functional ecology. *R package version 1.0-12.*

Legendre, P., Galzin, R. G., and Harmelin-Vivien, M. L. (1997). Relating behavior to habitat: Solutions to the fourth-corner problem. *Ecology* 78, 547–562. doi: 10.2307/2266029

Levin, L. A., Etter, R. J., Rex, M. A., Gooday, A. J., Smith, C. R., Pineda, J., et al. (2001). Environmental influences on regional deep-sea species diversity. *Annu. Rev. Ecol. Syst.* 32, 51–93. doi: 10.1146/annurev.ecolsys.32.081501.114002

Lomolino, M. V., and Weiser, M. D. (2001). Towards a more general species-area relationship: diversity on all islands, great and small. *J. Biogeogr.* 28, 431–445. doi: 10.1046/j.1365-2699.2001.00550.x

Loret, J., and Tanacredi, J. T. (2003). *Easter Island: Scientific exploration into the world's environmental problems in microcosm*. Eds. J. Loret and J. T. Tanacredi (Boston, MA: Springer U). doi: 10.1007/978-1-4615-0183-1

Luck, G. W., Carter, A., and Smallbone, L. (2013). Changes in bird functional diversity across multiple land uses: interpretations of functional redundancy depend on functional group identity. *PloS One* 8, e63671. doi: 10.1371/journal.pone.0063671

Luiza-Andrade, A., Brasil, L. S., Benone, N. L., Shimano, Y., Farias, A. P. J., Montag, L. F., et al. (2017). Influence of oil palm monoculture on the taxonomic and functional composition of aquatic insect communities in eastern Brazilian Amazonia. *Ecol. Indic.* 82, 478–483. doi: 10.1016/j.ecolind.2017.07.006

Luna-Jorquera, G., Fernández, C. E., and Rivadeneira, M. M. (2012). Determinants of the diversity of plants, birds and mammals of coastal islands of the Humboldt current systems: implications for conservation. *Biodivers. Conserv.* 21, 13–32. doi: 10.1007/s10531-011-0157-2

Luna, N., Varela, A. I., Brokordt, K., and Luna-Jorquera, G. (2018). Assessing potential predation risk by introduced predators on unattended eggs in the red-tailed tropicbird, phaethon rubricauda, on rapa nui (Easter island). *Trop. Conserv. Sci.*, 1–8. doi: 10.1177/1940082918785079

MacArthur, R. H., and Wilson, E. O. (1963). An equilibrium theory of insular zoogeography. *Evol. (N. Y).* 17, 373–387. doi: 10.1111/j.1558-5646.1963.tb03295.x

MacArthur, R. H., and Wilson, E. O. (1967). *The theory of island biogeography* (Princeton, N.J.: Princeton University Press), 203 p.

Mancini, P. L., and Bugoni, L. (2014). Resources partitioning by seabirds and their relationship with other consumers at and around a small tropical archipelago. *ICES J. Mar. Sci.* 71, 2599–2607. doi: 10.1093/icesjms/fsu105

Martin, T. E. (1995). Avian life history evolution in relation to nest sites, nest predation, and food. *Ecol. Monogr.* 65, 101–127. doi: 10.2307/2937160

Mason, N. W. H., and De Bello, F. (2013). Functional diversity: A tool for answering challenging ecological questions. *J. Veg. Sci.* 24, 777–780. doi: 10.1111/jvs.12097

Mason, N. W. H. H., De Bello, F., Mouillot, D., Pavoine, S., and Dray, S. (2013). A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. *J. Veg. Sci.* 24, 794–806. doi: 10.1111/jvs.12013

Mason, N. W. H., Mouillot, D., Lee, W. G., and Wilson, J. B. (2005). Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* 111, 112–118. doi: 10.1111/j.0030-1299.2005.13886.x

Matuoka, M. A., Benchimol, M., Almeida-Rocha, J. M. de, and Morante-Filho, J. C. (2020). Effects of anthropogenic disturbances on bird functional diversity: A global metaanalysis. *Ecol. Indic.* 116, 106471. doi: 10.1016/j.ecolind.2020.106471

McNab, B. K. (2003). The physiological ecology of vertebrates: A view from energetics. *J. Mammal.* 84, 774–775. doi: 10.1644/1545-1542(2003)084<0774:TPEOVA>2.0.CO;2

Morais, G. C., Gusmao, J. B., Oliveira, V. M., and Lana, P. (2019). Macrobenthic functional trait diversity at multiple scales along a subtropical estuarine gradient. *Mar. Ecol. Prog. Ser.* 624, 23–37. doi: 10.3354/meps13033

Mouchet, M. A., Villéger, S., Mason, N. W. H., and Mouillot, D. (2010). Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Funct. Ecol.* 24, 867–876. doi: 10.1111/j.1365-2435.2010.01695.x

Mouillot, D., Graham, N. A. J., Villéger, S., Mason, N. W. H., and Bellwood, D. R. (2013). A functional approach reveals community responses to disturbances. *Trends Ecol. Evol.* 28, 167–177. doi: 10.1016/j.tree.2012.10.004

Nunes, G. T., Mancini, P. L, and Bugoni, L. (2017). When Bergmann's rule fails: evidences of environmental selection pressures shaping phenotypic diversification in a widespread seabird. *Ecography* 40, 365–375. doi: 10.1111/ecog.02209

Olson, V. A., Davies, R. G., Orme, C. D. L., Thomas, G. H., Meiri, S., Blackburn, T. M., et al. (2009). Global biogeography and ecology of body size in birds. *Ecol. Lett.* 12, 249–259. doi: 10.1111/j.1461-0248.2009.01281.x

Paradis, E., Claude, J., and Strimmer, K. (2004). APE: Analyses of phylogenetics and evolution in r language. *Bioinformatics* 20, 289–290. doi: 10.1093/bioinformatics/btg412

Penven, P., Echevin, V., Pasapera, J., Colas, F., and Tam, J. (2005). Average circulation, seasonal cycle, and mesoscale dynamics of the Peru current system: A modeling approach. *J. Geophys. Res. C Ocean.* 110, 1–21. doi: 10.1029/2005JC002945

Peres-Neto, P. R., Dray, S., and Braak, C. J. F. (2017). Linking trait variation to the environment: critical issues with community-weighted mean correlation resolved by the fourth-corner approach. *Ecography (Cop.).* 40, 806–816. doi: 10.1111/ecog.02302

Petchey, O. L., and Gaston, K. J. (2006). Functional diversity: back to basics and looking forward. *Ecol. Lett.* 9, 741–758. doi: 10.1111/j.1461-0248.2006.00924.x

Pillar, V. D., Blanco, C. C., Müller, S. C., Sosinski, E. E., Joner, F., and Duarte, L. D. S. (2013). Functional redundancy and stability in plant communities. *J. Veg. Sci.* 24, 963–974. doi: 10.1111/jvs.12047

Plaza, P., Serratosa, J., Gusmao, J. B., Duffy, D. C., Arce, P., and Luna-Jorquera, G. (2021). Temporal changes in seabird assemblage structure and trait diversity in the rapa nui (Easter island) multiple-use marine protected area. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 31, 378–388. doi: 10.1002/aqc.3501

Quillfeldt, P., Schroff, S., van Noordwijk, H., Michalik, A., Ludynia, K., and Masello, J. (2011). Flexible foraging behaviour of a sexually dimorphic seabird: large males do not always dive deep. *Mar. Ecol. Prog. Ser.* 428, 271–287. doi: 10.3354/meps09058

Rayner, L., Lindenmayer, D. B., Wood, J. T., Gibbons, P., and Manning, A. D. (2014). Are protected areas maintaining bird diversity? *Ecography (Cop.).* 37, 43–53. doi: 10.1111/j.1600-0587.2013.00388.x

R Core Team (2021). *R: A language and environment for statistical computing.* (Vienna, Austria: R Foundation for Statistical Computing). Available at: https://www.R-project.org/.

Ricotta, C., and Szeidl, L. (2009). Diversity partitioning of rao's quadratic entropy. *Theor. Popul. Biol.* 76, 299–302. doi: 10.1016/j.tpb.2009.10.001

Roth, R. R. (1976). Spatial heterogeneity and bird species diversity. *Ecology* 57, 773–782. doi: 10.2307/1936190

Sayol, F., Cooke, R. S.C., Pigot, A. L., Blackburn, T. M., Tobias, J. A., Steinbauer, M. J., et al. (2021). Loss of functional diversity through anthropogenic extinctions of island birds is not offset by biotic invasions. *Sci. Adv.* 7. doi: 10.1126/sciadv.abj5790

Schleuter, D., Daufresne, M., Massol, F., and Argillier, C. (2010). A user's guide to functional diversity indices. *Ecol. Monogr.* 80, 469–484. doi: 10.1890/08-2225.1

Schreiber, E. A., and Burger, J. (2002). *Biology of marine birds* (Boca Raton: CRC Press). doi: 10.1201/9781420036305

Serratosa, J., Hyrenbach, K. D., Miranda-Urbina, D., Portflitt-Toro, M., Luna, N., and Luna-Jorquera, G. (2020). Environmental drivers of seabird At-Sea distribution in the Eastern south pacific ocean: Assemblage composition across a longitudinal productivity gradient. *Front. Mar. Sci.* 6. doi: 10.3389/fmars.2019.00838

Shealer, D. (2001). "Foraging behavior and food of seabirds," in *Biology of marine birds*. Eds. E. A. Schreiber and J. Burger (Boca Raton: CRC Press), 137–178. doi: 10.1201/9781420036305.ch6

Simeone, A., and Luna-Jorquera, G. (2012). Estimating rat predation on Humboldt penguin colonies in north-central Chile. *J. Ornithol.* 153, 1079–1085. doi: 10.1007/s10336-012-0837-z

Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdaña, Z. A., Finlayson, M., et al. (2007). Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. *Bioscience* 57, 573–583. doi: 10.1641/B570707

Stewart, P. S., Voskamp, A., Santini, L., Biber, M. F., Devenish, A. J. M., Hof, C., et al. (2022). Global impacts of climate change on avian functional diversity. *Ecol. Lett.* 25, 673–685. doi: 10.1111/ele.13830

Stuart-Smith, R. D., Bates, A. E., Lefcheck, J. S., Duffy, J. E., Baker, S. C., Thomson, R. J., et al. (2013). Integrating abundance and functional traits reveals new global hotspots of fish diversity. *Nature* 501, 539–542. doi: 10.1038/nature12529

Thiel, M., Macaya, E. C, Acuña, E., Arntz, W. E, Bastias, H., Brokordt, K., et al. (2007). The Humboldt current system of northern and central Chile: oceanographic processes, ecological interactions and socioeconomic feedback. In: R. N. Gibson, R. J. A. Atkinson and J. D. M. Gordon (Eds.), *Oceanography and Marine Biology an Annual Review* 45 (Taylor and Francis), 195–344. doi: 10.1201/9781420050943

Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F., and De Clerck, O. (2012). Bio-ORACLE: A global environmental dataset for marine species distribution modelling. *Glob. Ecol. Biogeogr.* 21, 272–281. doi: 10.1111/j.1466-8238.2011.00656.x

Villéger, S., Novack-Gottshall, P. M., and Mouillot, D. (2011). The multidimensionality of the niche reveals functional diversity changes in benthic marine biotas across geological time. *Ecol. Lett.* 14, 561–568. doi: 10.1111/j.1461-0248.2011.01618.x

Weichler, T., Garthe, S., Luna-Jorquera, G., and Moraga, J. (2004). Seabird distribution on the Humboldt current in northern Chile in relation to hydrography, productivity, and fisheries. *ICES J. Mar. Sci* 61, 148–154. doi: 10.1016/j.icesjms.2003.07.001

Whittaker, R. J., Triantis, K. A., and Ladle, R. J. (2008). A general dynamic theory of oceanic island biogeography. *J. Biogeogr.* 35, 977–994. doi: 10.1111/j.1365-2699.2008.01892.x

Wickham, H. (2009). *ggplot2: Elegant graphics for data analysis* (New York, NY: Springer New York). doi: 10.1007/978-0-387-98141-3

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. M., and Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology* 95, 2027–2027. doi: 10.1890/13-1917.1

Wouters, J. M., Gusmao, J. B., Mattos, G., and Lana, P. (2018). Polychaete functional diversity in shallow habitats: Shelter from the storm. *J. Sea Res.* 135, 18–30. doi: 10.1016/j.seares.2018.02.005

Yeager, L. A., Deith, M. C. M., McPherson, J. M., and Williams, I. D. (2017). And baum, J Scale dependence of environmental controls on the functional diversity of coral reef fish communities. *K. Glob. Ecol. Biogeogr.* 26, 1177–1189. doi: 10.1111/geb.12628

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Phenological divergence, population connectivity and ecological differentiation in two allochronic seabird populations

Fernando Medrano[1,2]*, Teresa Militão[1,2], Ivandra Gomes[3], Mariona Sardà-Serra[1,2], Mònica de la Fuente[1,2], Herculano A. Dinis[3] and Jacob González-Solís[1,2]

[1]Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Facultat de Biologia, Universitat de Barcelona (UB), Barcelona, Spain, [2]Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona (UB), Barcelona, Spain, [3]Associação Projecto Vitó, São Filipe, Cape Verde

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EDITED BY
Patrick Jodice,
Clemson University, United States

REVIEWED BY
Daniel Paul Costa,
University of California, Santa Cruz,
United States
Ingrid L. Pollet,
Acadia University, Canada
Cecilia Soldatini,
Center for Scientific Research and
Higher Education in Ensenada
(CICESE), Mexico

*CORRESPONDENCE
Fernando Medrano
fernandomedranomartinez@
gmail.com

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Phenological divergence between conspecific populations breeding sympatrically is increasingly recognized as an important evolutionary process that may lead to allochronic speciation. However, the extent to which adaptation to differences in the timing of breeding may contribute to this process remains unclear. In this study, we assessed breeding phenology, population connectivity, and niche differentiation of two allochronic populations we of the Cape Verde Storm-petrel (Hydrobates jabejabe). We monitored nesting activity, marked individuals, tracked individuals during both the breeding and nonbreeding periods, and determined the trophic niche during both the breeding and nonbreeding periods. Timing of breeding for the two allochronic populations segregated into a hot (March-August) and cool (September-February) season (hereafter, hot and cool populations). These periods matched the two annual pulses of oceanic productivity around Cabo Verde, suggesting allochrony was primarily driven by a biannual cyclicity in food availability. Despite their allochronic breeding, there was, however, low differentiation between the hot and cool populations in spatial use, daily activity patterns, and trophic niche during both the breeding and nonbreeding periods. Further, the exchange of breeders between seasons, as documented through the recapture of marked individuals, may hinder seasonal adaptation by each population and ultimately, allochronic speciation. Consequently, allochrony alone may not be sufficient to drive speciation unless reproductive isolation between populations is complete or populations become strongly adapted to the environmental conditions associated with their timing of breeding.

KEYWORDS

allochrony, sympatric speciation, petrels, storm-petrel, adaptation-by-time, sympatry, hydrobatidae

1 Introduction

Allochrony refers to the temporal divergence of breeding between populations that can occur at different timescales, i.e. in daily activity (e.g. butterflies, Devries et al., 2008), seasonally (e.g. oaks, Juri and Premoli, 2021; toads, Thomé et al., 2021) or in different years (e.g. cicadas Marshall et al., 2011; Sota et al., 2013). The most common form of allochrony is the phenological divergence in the timing of annual phenophases, which can limit population connectivity (i.e., the exchange of breeders among populations), promote assortative mating, and may ultimately result in reproductive isolation (Hendry and Day, 2005; Taylor and Friesen, 2017). Allochronic populations may experience different environmental conditions and subsequently, adapt the timing of breeding, thus enabling ecological differentiation to operate on multiple axes of the ecological niche, such as diet, habitat, space use, or daily activity (Taylor and Friesen, 2017). This differentiation may act concurrently with allochrony and ultimately lead to sympatric speciation by allochrony, a well-recognized process with increasing relevance in evolutionary biology (Hendry and Day, 2005; Taylor and Friesen, 2017).

Several genetic studies across multiple taxa have demonstrated that limited gene-flow between allochronic populations may result in a sympatric speciation process (e.g., fruit flies, Doellman et al., 2019; butterflies, Gradish et al., 2018; seaweeds, Homma et al., 2020; whitefish, Bitz-Thorsen et al., 2020). However, there is little understanding or empiric evidence of how population connectivity and ecological differentiation between allochronic populations may drive this evolutionary process, particularly in tetrapods. For example, phenological divergence may operate synergistically with seasonal differences in food resources, thus promoting spatial differentiation in foraging areas or non-breeding distributions (Friesen, 2015). To develop a more complete understanding of how allochrony may operate, we need to understand what traits are differentiated between the allochronic populations and subsequently how environmental drivers may promote allochrony. However, detailed comparative studies on phenological divergence, population connectivity, and ecological differentiation between allochronic populations are scarce. Furthermore, it is still unclear how phenological divergence may be associated with temporal pulses in food availability (Monteiro and Furness, 1998; Barros et al., 2019; Taylor et al., 2019), breeding habitat availability (Monteiro and Furness, 1998) or predation pressure (Monteiro and Furness, 1998). Phenology of predators is usually associated with pulses of food availability, which in marine systems may be indicated by oceanographic productivity (e.g. bony fish, Cushing, 1990; Schweigert et al., 2013; Malick et al., 2015, seabirds, Hipfner, 2008), and which in turn relates to oceanographic conditions such as changes in sea temperature, nutrient supply, salinity, or ocean mixing (Ji et al., 2013; Hernández-León et al., 2020). Seabirds have often been employed as study models to understand how marine organisms match their breeding phenology to pulses of ocean productivity, while also avoiding seasonally adverse weather conditions such as storms (e.g. temperate Ramírez et al., 2016 and polar systems, Moe et al., 2009; Ramírez et al., 2017). In tropical oceans, the intra-annual stability of conditions allows some seabirds to breed throughout the year (e.g., frigatebirds (*Fregata* spp.), tropicbirds (*Phaeton* spp.) and boobies (*Sula* spp. Furness and Monaghan, 1987)). Interestingly, several tropical and sub-tropical petrels show two annual phenological peaks, and these can occur either in nearby localities (e.g. Bulwer's Petrel *Bulweria bulwerii*, Megysi & O'Daniel, 2020), or on the same breeding site (e.g. Trindade Petrel *Pterodroma arminjoniana*, Leal & Bugoni, 2021). Indeed, allochrony has been recognized as a major driver of speciation in small pelagic seabirds, i.e. storm-petrel species breeding in Guadalupe (Townsend's storm-petrel, *Hydrobates socorroensis* and Ainley's storm-petrel *Hydrobates cheimnomnestes*, Power and Ainley, 1986; Taylor et al., 2018), Iwo (Swinhoe's storm-petrel *Hydrobates monorhoi* and Matsudaira's storm-petrel *Hydrobates matsudairae*, Warham, 1992), and Azores Islands (Monteiro's storm-petrel *Hydrobates monteiroi* and Band-rumped storm-petrel *Hydrobates castro*, Friesen et al., 2007; Taylor et al., 2019). Whether allochrony might be a driver of speciation in other systems such as the Galapagos or the Atacama Desert is still unclear (Band-rumped storm-petrel in Galapagos *Hydrobates castro*, Smith and Friesen, 2007; Taylor et al., 2019; Markham's storm-petrel in Atacama, *Hydrobates markhami*, Barros et al., 2019).

The Cape Verde storm-petrel (*Hydrobates jabejabe*) is an endemic seabird of the Cabo Verde archipelago (Alexander, 1898; Murphy, 1924; Semedo et al., 2020). It is often considered a year-round breeder, but the occurrence of two breeding peaks, one in summer and one in winter, suggests the existence of two populations. These have been usually referred to as a hot (i.e., summer breeding) and a cool (i.e., winter breeding) population and preliminary evidence indicates genetic connectivity (Φ_{st}>0.35, Taylor et al., 2019). However, detailed studies on the phenology, population connectivity, spatial ecology, trophic ecology, and daily activity patterns of these hot and cool breeding populations have not been conducted to date. In this study, we sought to (i) determine the phenology of each population, (ii) assess population connectivity between the two populations, (iii) measure the degree of differentiation across multiple axes of the ecological niche in each population, (iv) assess divergence in ecological traits of each population, and (v) evaluate the role of the environment as a driver of allochrony in this species. Considering that a recent study did not identify a clear genetic structure between the hot and cool populations (Taylor et al., 2019), we predicted that some population connectivity would occur between the two populations, and therefore that differentiation along different axes of the ecological niche may occur but be relatively low.

2 Methods

2.1 Study species and area

Cape Verde storm-petrel was formerly considered a conspecific of the Band-rumped storm-petrel (*Hydrobates castro*) (Murphy, 1924), but has recently been recognized as a full species based on bioacoustics and genetic evidence (Bolton, 2007; Friesen et al., 2007; Sangster et al., 2012; Taylor et al., 2019). It is considered a year-round breeder, but with preliminary evidence of breeding peaks in summer (hot population) and winter (cool population) (Taylor et al., 2019). This study was conducted in Cima Islet (14.971°N, 24.637°W; see Appendix S1), an islet of the tropical volcanic archipelago of Cabo Verde located off tropical Western Africa. Fieldwork was conducted between 2018-2021. Sample sizes of all the analyses are summarized in Appendix S2.

2.2 Breeding phenology

To assess the phenology of Cape Verde storm-petrels, we actively searched for nests year-round and, once located, checked the contents of the known nests every 2-3 days, monitoring 27-56 nests each year from 2018-2021. We obtained hatching and fledging dates from monitoring data. Considering that in most of the nests we did not know the exact laying date, we inferred it from hatching dates assuming a 42-day incubation period (Harris, 1969). We used geolocators (see more details below in the spatial overlap section) to define departure and arrival dates in waters surrounding Cabo Verde, defined as waters within 400 km of the nesting island. We chose this buffer distance around the colony island to accommodate the potential error of the geolocators (Halpin et al., 2021). We also used geolocators to establish the first day individuals spent in the nest burrow (i.e., no light data recorded for a continuous 24-hour period indicating the bird spent the day inside a burrow). Sample size of phenological dates varied because geolocators were recovered at different breeding stages or because some nests were found after hatching. We used these phenological data to define the breeding period but also any period of time when birds of the hot and cool populations were present in Cima Islet. We plotted trip data using boxplots in R through the package "ggplot2" (Wickham, 2016), and calculated the median and quartiles using the quantil.circular function of the package "circular" (Lund et al., 2017).

2.3 Population connectivity

To evaluate the population connectivity between the hot and cool populations, we used capture-mark-recapture data from adults and chicks found in burrows as well as from 1,777 individuals mist-netted from 2009 to 2021. We assessed connectivity by analyzing: (1) birds ringed as chicks in the nest and recaptured in mist nets as prospectors in subsequent years; (2) breeders captured in their nest and recaptured breeding in the following years; and (3) birds captured in mist nets and recaptured in mist nets. We assessed the level of connectivity between both populations through chord diagrams, with the function chordDiagram of the "circlize" package in R (Gu et al., 2014).

2.4 Ecological differentiation between the two allochronic populations (hot-cool populations)

2.4.1 Spatial differentiation during the breeding period

We measured the differentiation between the hot and cool populations in foraging areas during the breeding period by deploying Pathtrack$^{®}$ Nanofix-mini GPSs on breeders (~0.95g, representing an average of 2.4% of the bird's body weight, with a range of 1.80-3.13%) between 2018-2020. These devices were used successfully for studying the spatial ecology of lower-weighted species in the Northern Atlantic and the Mediterranean (Rotger et al., 2020; Bolton, 2021; Pascalis et al., 2021). The temporal resolution for location acquisition was one fix every 3 hours in 2018 and one fix every 2 hours in 2019 and 2020. GPS tags were attached to the base of the four central tail feathers with Tesa$^{®}$ tape and recovered on average after 10 days (range: 3-50 days). We did not deploy GPS on both parents of a nest simultaneously to avoid potentially impacting the success of the nest. We deployed 162 GPS tags and recovered 144 tags. We used data from recovered tags to describe space use and estimate 5%, 20%, 50%, 75%, and 95% kernel densities. We also calculated the overlap of the whole population (using complete and incomplete trips) between the first and the second year of data (i.e., between 2018/19 and 2019/20), between sexes, and between breeding stages (incubation/brooding/chick-rearing) in all sampled birds. We used the "adehabitatHR" package of R to calculate the kernels, and used the kernelUD and getverticeshr functions to create kernel contours and the kerneloverlap function to calculate their overlap (Calenge, 2006). For creating the kernel unit densities, we used the "href" smoothing factor and a grid of 1000.

We also calculated metrics from complete foraging trips, including trip duration, total distance covered, maximum distance from the colony. We compared these metrics and the 50% kernel size between hot and cool populations through Generalized Linear Mixed Models (GLMM). Our models included population, sex (birds were sexed molecularly, see methods in Appendix S3) and breeding stage (incubation/brooding/chick rearing) as fixed factors, and, year, and individual as random factors. We assigned Gaussian or

Gamma distributions depending on the variable. We measured differences in the departure bearing of the foraging trip by calculating the bearing angle from the colony to the first position that was at least 72 km from the colony (maximum distance covered between the colony and the first GPS fix, 3h apart). To account for differences in environmental conditions between populations, we obtained wind direction and intensity before the departure of each trip. For extracting the wind data, we used the wind.dl function of the "rWind" package in R (Fernández-López and Schliep, 2019), which extract the data from the Global Forecast System of the USA's National Weather Service. We used a spatial resolution of 0.5 degrees and temporal resolution of 3 hours. We compared the bearing and the wind data between allochronic populations using the Watson-Williamson test, with the watson.williams function of the "circular" package in R (Lund et al., 2017).

2.4.2 Spatial differentiation during the non-breeding period

We measured the differentiation between the hot and cool populations during the non-breeding period by deploying W65A9-Sea Migrate Technology geolocators (~0.8g, representing an average of 2% of the bird's body weight, with a range of 1.5%-2.6%) on breeders at the end of chick-rearing, between 2018-2020. We deployed 60 devices and recovered 19, 11 from the hot population and 8 from the cool population. We attached the geolocators to the tibia using a metallic ring with stainless steel cable. These devices have been used for studying individuals of similar-weighted species in the Northern Atlantic and Northern Pacific without generating significant impacts (e.g. *Hydrobates leucorhous* and *Hydrobates furcatus* Pollet et al., 2014; Halpin et al., 2018; Hedd et al., 2018). Geolocators were programmed to provide light levels every minute, and recorded maximum light levels every 5 minutes, providing two positions per day at a spatial error of up to 400 km (Halpin et al., 2021). To process the geolocator data, we used the IntiProc software of Migrate Technology to obtain the sun angle for calibrating the positions. This angle was obtained by calibrating the geolocators in an open location with known coordinates, and far from any artificial light for at least one week. Subsequently, we used the preprocessLight function of the "TwGeos" package in R (Lisovski et al., 2020) to process the light. With this function, we estimated the hour of sunrise and sunset, inspected the integrity of the light curve of each day, and manually corrected the transitions of sunrise or sunset with clear interferences. After that, we filtered and removed positions ± 20 days near the equinoxes, and those with quadratic speeds over the 0.95 quantile (43.14 km/h).

We assessed the degree of spatial overlap between the hot and cool populations for several parameters during the nonbreeding season, estimating the kernel densities at 5%, 20%, 50%, 75% and 95%. We also calculated the spatial overlap between the first and the second year of data (i.e., between 2018/19 and 2019/20), between sexes (male/female). We used the "adehabitatHR" package of R to calculate the kernels, and used the kernelUD and getverticeshr functions to create kernel contours and the kerneloverlap function to calculate their overlap (Calenge, 2006). To create the kernel unit densities, we used the "href" smoothing factor, and a grid of 1000. We also calculated some trip metrics, including the duration of the non-breeding period (since the departure until the arrival from the Cabo Verde waters); distance from the centroid of the core kernel density (50% density) during the nonbreeding period to the colony, and individual core kernel size. Comparisons between hot and cool populations were conducted through Generalized Linear Mixed Models (GLMM). Our models included population, and sex (birds were sexed molecularly, see methods in Appendix S3) as fixed factors, and year and individual as random factors. We assigned Gaussian or Gamma distributions depending on the variable.

2.4.3 Trophic differentiation

To assess the trophic differentiation between the hot and cool populations during both the breeding and non-breeding period, we analysed the carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic values for blood and feather samples collected during the breeding period and for feathers inferred to have grown during the non-breeding period (Ramos and González-Solís, 2012). All samples were collected from breeding birds. Specifically, we sampled the innermost primary (P1) and innermost secondary (S1) as indicators of the stable isotopes integrated at the end of the breeding season, and the eighth secondary (S8), outermost rectrix (R6), and body feathers as indicators of the non-breeding season (see details on the molting patterns in the Appendix S4, and Lab procedures for isotopes analyses in the Appendix S5).

We tested for differences in carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic values through a Generalized Linear Mixed Model, with season and sex as fixed factors and year and individual as random factors. We assigned a Gaussian or Gamma distribution, and a log or identity link function depending on the distribution of each variable. We calculated the isotopic niche amplitude using Stable Isotope Bayesian Ellipses (SIBER) and assessed resource differentiation and isotopic niche width by calculating the overlap and size of the ellipses, respectively. To calculate the isotopic niche amplitude and visualizing Stable Isotopic values of both populations we used the "SIBER" package in R (Jackson et al., 2011)

2.4.4 Daily activity differentiation

We assessed differences in the daily proportion of time spent on the water (resting periods) during the non-breeding period based on wet-dry data which was recorded by the geolocators every six seconds and subsequently packed in five minutes blocks. Because moon illumination can affect activity levels in some petrels (Harris, 1969; Watanuki, 2002), we obtained moon illumination from the function moonAngle in the "oce" package (Kelley, 2018). We also checked whether there were differences in the proportion of time spent on the water in the non-breeding period by dividing the activity into day-time and night-time, determined by the sunrise and sunset time of the geolocators, obtained with preprocessLight function of the "TwGeos" package in R (Lisovski et al., 2020). To test for differences in daily activity patterns between the hot and cool populations, we built Generalized Additive Mixed Models (GAMMs) with the proportion of time on the water as the response variable, and the hour, population, sex, day/night, and moon illumination as fixed factors. We included year and trip nested into the individual birds as random factors.

2.4.5 Habitat differentiation and potential environmental drivers of the allochronic process

To assess the potential influence of environmental variability on allochrony, we built an extended time series of three environmental variables thought to be potential drivers of foraging and nesting behavior for this species. The time series extended from 2001 – 2019 and each variable was collected at a temporal resolution of 10 days. To determine whether pulses in oceanic productivity might drive allochrony, and whether differentiation occurred in the oceanic features between both populations, we obtained primary productivity (mg m^{-3}) values from the Global Ocean Biogeochemistry Hindcast of Copernicus (https://resources.marine.copernicus.eu/) at 0.25° resolution. We extracted daily primary productivity year-round values for each GPS position obtained during the chick-rearing period, as this is the breeding stage with the highest energetic requirement for parents. For the non-breeding period, we extracted the year-round primary productivity by using the daily average using a 50% density kernel. To assess if rainfall could be a driver of the phenology (since nests can be flooded), we also extracted rainfall data (mm) from Copernicus (https://climate.copernicus.eu/). Finally, we also compared the hours of light (i.e., night length) that birds experienced during nesting in the hot and cool seasons, since night length might influence on the amount of time available for foraging in this nocturnal species. For extracting the day length for both populations, we used the day length function of the "insol" package (Corripio, 2014). To determine if differences occurred between the hot and cool populations in primary productivity, rainfall, or day length, we performed GAMMs with the day of the year as a fixed factor, and the year and trip nested into the individual birds as a random factor.

2.5 Ecological traits

Breeding success: We assessed the proportion of successful and failed nests from nest monitoring, excluding suspected failures that happened after handling procedures (i.e., nests abandoned by one parent after deploying/recovering a tag, corresponding to 1-14 nests per season). After this exclusion, we analyzed data of 12-42 nests per season (75% of the nests monitored). We analyzed breeding success, defined as the proportion of nests were the chick fledged, using a logistic regression, with year and population as explanatory variables and breeding success as the response variable.

Foraging efficiency: We calculated the foraging efficiency for all the birds tagged with a GPS as the daily mass gain. We obtained mass gain by weighing parents with a Pesola® scale prior to colony departure (i.e., as part of the regular monitoring activities). In the case birds left the colony one or two days after the last weighing, we inferred their mass at departure by using the average daily loss of mass obtained from the population of incubating birds which were weighed in three-day intervals. Birds were always weighed within 3 days of colony departure (range: 1-3 days). Our models included population and sex (to account for potential dimorphism) as fixed factors, and the year, and individual as random factors. We used a Gamma distribution link function.

2.6 Model building, selection, and assumptions

We did all the comparisons through Generalized Linear Mixed Models (GLMM) using the functions lmer and glmer of the "lme4" package in R (Bates et al., 2015). In the case of Generalized Additive Mixed Models (GAMM), we conducted the analysis through the gamm function, in the "mgcv" package of R (Wood, 2001). We did a backward selection, dropping variables and selected the best models based on corrected AIC values. Sample sizes of all the analyses are included in Appendix S2. We checked the selected model' normality of the residuals through a Q-Q plot and the homogeneity of the residuals through Cleveland dotplots (Zuur et al., 2010).

3 Results

Phenology of hot and cool populations: We found two clearly segregated breeding phenologies for successful breeders, with no temporal overlap within any given phase of breeding, although some overlap occurred between different phases (i.e., range of laying, hatching, and fledging dates based on nest monitoring; see Figure 1). Also, there were two failed breeding attempts that did not fit within the hot or cool population phenologies, because they bred between summer and winter (August). One of the nests failed flooded by the rain. Although two breeding phenologies were defined, geolocators data indicated that the arrival and departure dates from Cabo Verde waters of birds from each population overlapped extensively, thus defining intermediate periods in which birds from the two populations occurred within the waters near the breeding area (Figure 1).

Based on nest monitoring and geolocation dates, we define the hot population as those birds breeding from the end of March to the end of August and the cool populations as those breeding from the beginning of September to the end of March. The data gathered from mist-netting generally support the seasons we propose, but the exact details differ slightly. For example, our mist-netting data indicated that the birds from one population can arrive at the colony and initiate breeding before the other population finishes breeding and departs the colony. This results in a reproductive season that is shorter than that defined solely from tracking data. Thus, the period in which mist-netting birds can be assigned to one season spans from early April to mid-May for the hot season, and from early September to early January for the cool season. There are two intermediate periods when the birds captured through mist-netting could correspond to any of the populations, spanning from early January to early April and from mid-May and late August. Details on the phenology are provided in Appendix S6.

3.1 Population connectivity

Population connectivity between hot and cool populations: From 2018 to 2021, we ringed 145 chicks (n = 58 cool season, n = 87 hot season). We recaptured eight of these chicks after an average of 1.9 years (range: 1.7—2.6 years). Five chicks ringed in the cool season were recaptured in mist-nets also during the cool season. Of the three chicks ringed in the hot season, one was recaptured in the cool period, and two were recaptured in the intermediate periods (Figure 2A). We ringed 276 breeders from 2018 to 2021 (n = 156 cool season, n = 120 hot season), and 67 were subsequently recaptured as breeders (n = 50 cool season, n = 17 hot season). Of the 156 individuals ringed in the cool season, 49 were recaptured as breeders in the cool season, while one

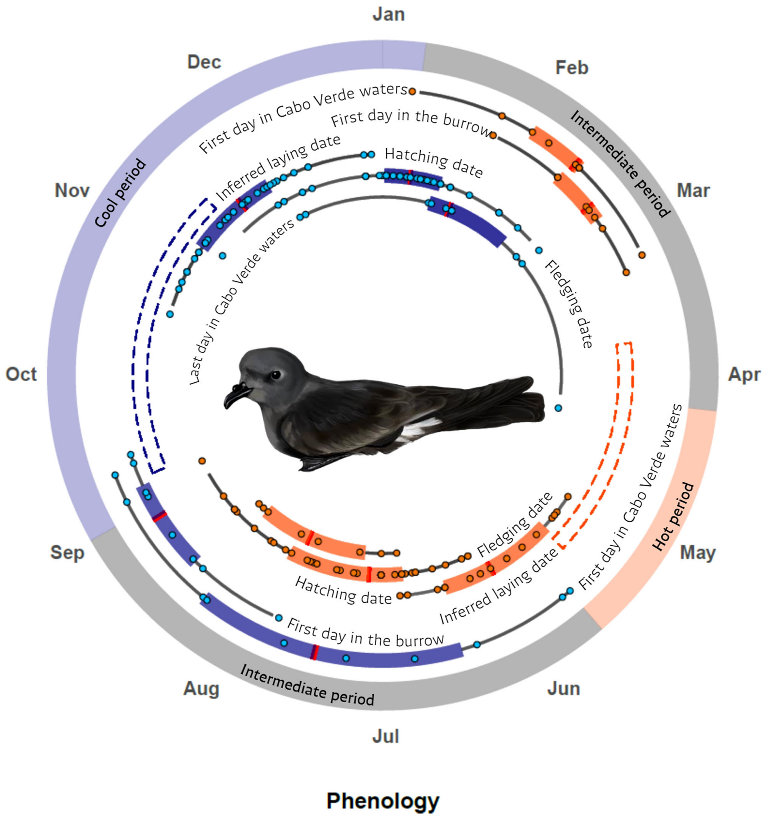

FIGURE 1
Phenology of the hot and cool populations of the Cape Verde storm-petrel in Cima Islet (Cabo Verde) based on nest monitoring and light-level geolocators. Blue shading indicates the phenology for the cool population while red/orange shading indicates the phenology of the hot population. Laying dates were inferred from hatching dates based on an incubation period of 42 days. Hot and cool seasons correspond to periods when only hot or cool breeders can be found in the colony whereas intermediate periods correspond to periods when birds from both populations can be found in the colony. Each boxplot shows the median, the first and third quartiles at the end of the box, and the first and 99th quantiles on the tails. Artwork by María Jesús Mallea S.

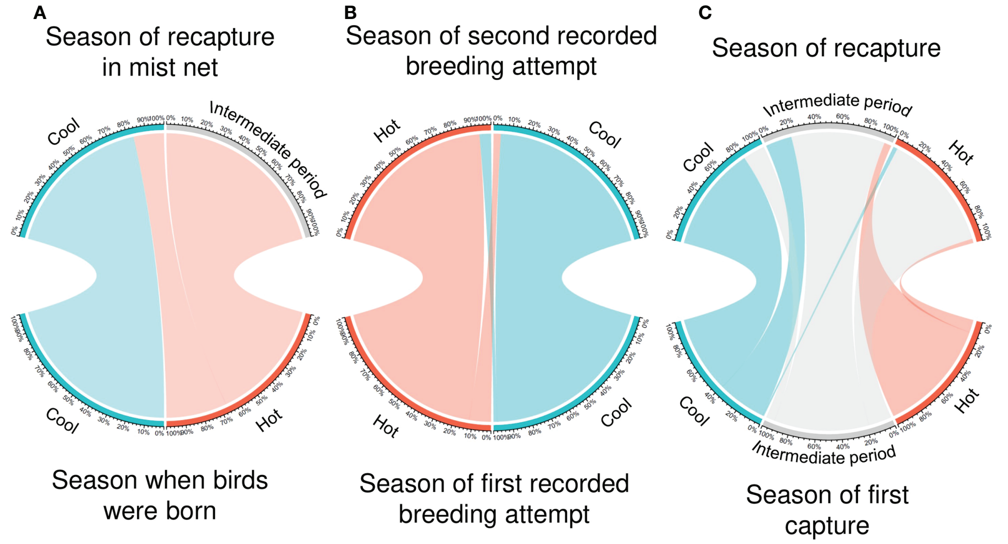

FIGURE 2
Chord diagrams assessing connectivity between hot and cool populations of the Cape Verde storm-petrel in Cima Islet (Cabo Verde). Hot season is depicted in orange, cool season in blue, and intermediate periods in grey. The bottom of the diagram shows the percentage of individuals that were initially captured in each season while the top shows the percentage of individuals during the period when they were recaptured for **(A)** birds ringed as chicks; **(B)** birds ringed as breeding adults and; **(C)** birds ringed in mist-nets. Sample sizes are summarized in Table 1.

individual was recaptured in the hot season. Of the 120 individuals ringed in the hot season, 15 were recaptured as breeders in the hot season, while two individuals were recaptured as breeders in the cool season (Figure 2B). All the three breeders that switched seasons were unsuccessful breeders in the first breeding attempt, but one breeder that failed in the hot season was successful in the subsequent cool season. Also, we ringed a total of 1,222 birds in mist-nets, of which we recaptured 79. Of the birds initially captured in the cool season, 43 were subsequently recaptured in the cool season, 1 bird in the hot season, and 26 birds in the intermediate period (Figure 2C). Of the birds initially captured in the hot season, one was subsequently recaptured in the hot season and 8 in the intermediate period. Ringing and recapture data are summarized in Table 1.

3.2 Ecological differentiation

3.2.1 Spatial differentiation during the breeding period

We compared foraging areas of breeding birds within years between populations and within populations between years. The mean (± SD) of spatial overlap of foraging areas within years between the hot and cool populations for each kernel density was 55.4 ± 21.9 (Figure 3A). The mean (± SD) of spatial overlap of foraging areas between years within populations was 65.5 ± 19.5 (Appendix S7), and therefore appeared to be slightly higher than that within years between populations. The maximum distance ($\bar{x}$:225 km; range: 40—738 km; p-value = 0.48), duration ($\bar{x}$: 2.7 days; range: 0.7—10.6 days; p-value = 0.59), distance covered ($\bar{x}$: 728 km; range: 107—2,167 km; p-value = 0.37) and the individual core kernel size ($\bar{x}$: 18,585 km^2; range: 1,365—151,781 km^2; p-value = 0.55) do not differ significantly between the two populations (boxplots available in Appendix S8, statistics available in Appendix S9). The bearing angle of departure from the colony during the breeding season differs significantly between the two seasons by 77.9° (F=58.18, df=184, p-value<0.01), with birds of the hot population heading North-West ($\bar{x}$: 261.9°; range: 46.5° — 346.8°), while birds of the cool population head mainly to the South-East ($\bar{x}$: 184°; range: 107.7° —316.2°) (see Appendix S10). Wind direction was to the South-West in both seasons, but differed significantly by 4.7° (F=6.44, df=184, p-value<0.01), with an average wind direction of 226.7° for the hot population and 231.06° for the cool population. Wind intensity did not differ significantly between the two seasons, with a mean of 7.3 km/h (p-value>0.05).

3.2.2 Spatial differentiation during the non-breeding period

We compared areas of non-breeding birds within years between populations and within populations between years. The mean (± SD) of spatial overlap of non-breeding areas within years between the hot and cool populations for each kernel density was 60.7 ± 20.1 (Figure 3B). The mean (± SD) of spatial overlap of non-breeding areas between years within populations was 53.6 ± 25.3 (Appendix S11), and therefore

TABLE 1 Summary of the captures and recaptures made for (a) chicks, captured as prospectors in subsequent years; (b) breeders and (c) birds captured through mist-netting.

	First ringing season	Number of ringed birds	Recaptured hot season	Recaptured cool season	Recaptured indetermined period
Ringed chicks	Hot	58	0	1	2
	Cool	77	0	5	0
Ringed breeders	Hot	120	15	2	–
	Cool	156	1	49	–
Ringed mist-netted birds	Hot	62	1	0	8
	Cool	416	1	43	26

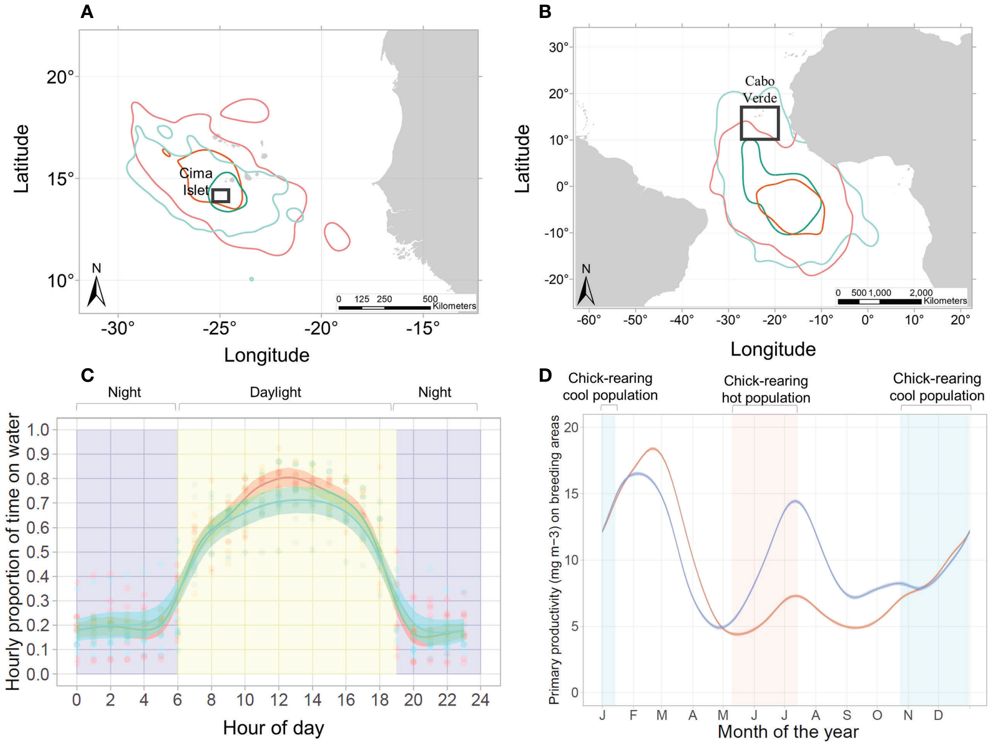

FIGURE 3
Niche overlap of both populations (cool population indicated by blue/green shading and hot population by orange/red shading) across different niche axes: **(A)** home-range and core area (95% and 50% kernel densities, respectively) during the breeding season for birds from the hot (N=95) and cool (N=122) populations; **(B)** home-range and core area during the non-breeding season for birds from the hot (N=11) and cool (N=8) populations; **(C)** daily activity patterns of birds from hot and cool populations, as determined from wet/dry data from geolocators and indicated by the proportion of time spent on the water during the non-breeding season (yellow background indicates day time and purple background indicated night time); GAMM shows the mean and the standard deviation interval, and **(D)** primary productivity in the marine areas used during the breeding season by the hot and cool populations; red background indicates the chick-rearing period of the hot season population, and blue background indicates the chick-rearing period of the cool season population. Sample sizes are summarized in Appendix S2.

appeared to be higher than that within years between populations. Duration of the non-breeding period (x̄: 168.8 days; range: 7.0—266.5 days; p-value = 0.69), distance of the centroid of the non-breeding area to the colony (x̄: 2,155.6 km, range: 650.8—3,033.2 km; p-value = 0.34) and 50% individual core kernel density size (x̄: 1,296,086 km^2, range: 391,232.5 — 3,105,773 km^2; p-value = 0.29) per non-breeding trip did not differ between the two populations (Appendix S12, statistics in Appendix S13).

Trophic differentiation between hot and cool populations: We found a high overlap of the Stable Isotopes Bayesian Ellipses between the hot and cool populations for both the first primary feather and for blood, but a lower overlap for the first and eighth secondary feathers, and no overlap for the sixth rectrix, and body feathers (Figure 4).

Nitrogen values were higher for the hot than for the cool population for the sixth rectrix (GLM estimate =-0.0006, p-value<0.01), eighth secondary (GLM estimate=-0.003, p-value<0.05), and body feathers (GLM estimate=-0.0001, p-value<0.01), but no difference was found for blood (p-value=0.220), first primary (p-value=0.375) and first secondary (p-value=0.111). Carbon values did not differ between populations in any of the tissues. Furthermore, the standard Bayesian ellipses areas were larger for the cool population, particularly for blood samples (Appendix S14).

Daily activity differentiation between hot and cool populations: Overall, we found that birds from the hot population spent more time on the water than birds of the cool population (Figure 3C) during daylight (GAMM estimate=-0.05, p-value<0.05) and night period (GAMM estimate=-0.19, p-value<0.01). Birds of the hot population spent on average 42.3% of the time on the water (range: 0—95.7% of the time per hour), while birds of the cool population spent on average 40.4% of the time on the water (range: 0—92.9% of the time per hour). Furthermore, we found no association between the night activity and the moon illumination (p-value=0.7).

3.2.3 Habitat niche and potential environmental drivers of the allochronic process

We identified two annual pulses of productivity in the foraging areas used by the Cape Verde storm-petrel during chick-rearing (Figure 3D; Appendix S15). The first pulse of the year occurred during the months of February-March, while the second occurred during the months of July-August. Productivity pulses in the areas visited by the hot population were overall significantly higher than for the areas visited by the cool population (GAMM estimate: 1.42, p-value<0.01; Figure 3D; Appendix S15). In addition, the areas visited during the non-breeding season only showed one productivity pulse that matched the period when the hot population were in that areas (Appendix S16). Rainfall in Cabo Verde was concentrated in September (Appendix S17). The number of hours available for foraging at night in the waters surrounding the colony was greater for the cool population, with up to 2 more hours per night, than for the hot population (Appendix S17).

3.3 Ecological traits

Breeding success: We found no differences in the breeding success between the two populations (GLM p-value=0.7, Appendix S18), but there was an interannual difference within populations.

Foraging efficiency: The daily weight gain per trip (x̄: 0.6 g; range:-0.9—2 g) did not differ between the two populations (Linear Model p-value =0.8).

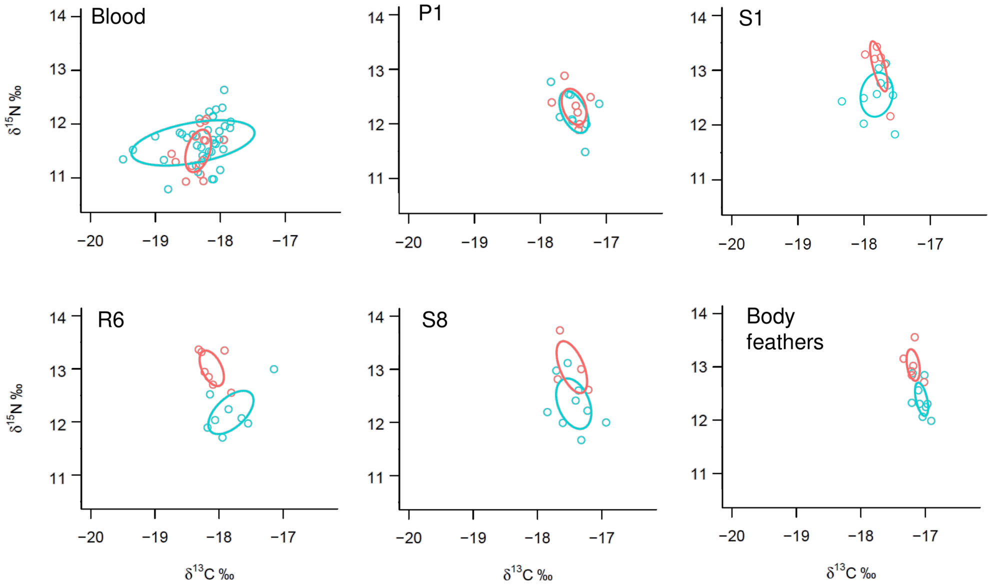

FIGURE 4
Comparison of the Bayesian Ellipses for stable isotopes of carbon and nitrogen for the hot (orange) and cool (blue) populations of Cape Verde storm-petrels. Stable isotopes were sampled for the breeding areas from blood and the first primary feather (P1), and for the non-breeding areas from the first secondary feather (S1), sixth rectrix (R6), eighth secondary feather (S8) and body feathers. Sample sizes are summarized in Appendix S2.

4 Discussion

In this study, we assess the phenological divergence, population connectivity, and ecological differentiation of two allochronic populations of seabird breeding at the same site. Our data indicated that two reproductive seasons occurred during the year, and that the peaks of reproductive activity in each of these seasons did not overlap temporally. We posit that these two distinct reproductive seasons are driven by two annual pulses of productivity in the waters around the breeding area. We identified facets of population connectivity between the two allochronic populations, including individuals that switched from one breeding season to the other. Further, we also found that, for the most part, the extent of differentiation between the two allochronic populations in space use, daily-use patterns, habitat use, and trophic ecology was relatively low during the breeding and non-breeding periods. These data indicate that the two allochronic populations (i.e., hot and cool populations) of Cape Verde storm-petrels appear to have not developed specific adaptations despite breeding during different periods of the year, and as such the exchange of individuals between populations may continue to be facilitated.

Cape Verde storm-petrels have long been assumed to breed year-round (Friesen et al., 2007; Taylor et al., 2019). Based on three years of continuous nest monitoring, we consistently found that there are two seasonal peaks of reproduction within the year, with no temporal overlap between them for any given breeding phase, similar to those described for the closely related storm-petrels breeding in the Azores (*Hydrobates castro/monteiroi* Bolton et al., 2008; Taylor et al., 2018). Seasonal peaks of reproduction suggest a disruptive selection towards two optimum environmental conditions in two different periods, driving birds to center their breeding activity on one of these two periods of the year (Monteiro and Furness, 1998; Barros et al., 2019; Taylor et al., 2019). Indeed, environmental conditions in Cabo Verde waters also show two annual pulses of productivity, and the hot and cool populations we defined appear to match their chick-rearing stage with these two periods. Although a time lag of about three months does occur between each pulse in the primary productivity and the respective peak in the breeding phenology of each population after the pulse, we posit this is related to the time needed for the biomass and energy to be transferred from phytoplankton productivity to zooplankton productivity, the latter being a primary food source for the storm-petrels (Ramírez et al., 2016). This disruptive selection process could be reinforced by rainy conditions during one of the intermediate periods. That is, birds may avoid rainfall in August and September to reduce the risk of flooding at the nest site. Indeed, one out of the two breeding attempts occurring in the intermediate period failed due to heavy rains.

When assessing allochrony among populations, it is critical to determine the extent of connectivity, i.e. whether there is any exchange of breeders between populations. Based on three years of continuous and intensive monitoring, we found that two out of 15 recaptured breeders (~13.3%) switched from breeding during the hot to the cool season, while one out of 50 breeders (2%) switched from breeding during the cool to the hot season. Thus, birds occasionally changed their breeding season, particularly after a breeding failure. Despite breeding phenology in birds typically being considered to be under genetic control (Liedvogel et al., 2009; Wilczek et al., 2009; Tang et al., 2016), our results show some phenotypic plasticity in breeding phenology, which might be driven by individual breeding performance. A similar pattern has been described among albatrosses, where the timing of breeding is driven by the past breeding success (Lewis et al., 2012). In cases where individuals switched breeding seasons, it is still unclear the extent to which switching the timing of breeding could affect other aspects of the annual cycle, such as molting and subsequent breeding attempts. For example, failed breeders of a past breeding season might advance their timing of molting (Ramos et al., 2018). Further, in our study the populations show a higher level of connectivity than one exchange per generation, which may explain the gene-flux between both populations (Taylor et al., 2019), and consequently the conditions under which speciation is unlikely to happen (Frankham et al., 2002).

Given the divergence in phenology between the hot and cool populations, we expected to find some seasonal adaptations and ecological divergence between populations, a pattern observed in other seabirds (e.g., penguins Thiebot et al., 2012; Green et al., 2022; Giant-petrels Granroth-Wilding & Phillips, 2019). However, we found low spatial differentiation between the hot and cool populations during both the breeding and non-breeding seasons. During the breeding season, the high spatial overlap may be mediated by the wind direction, which is similar between the two seasons. Consistent wind patterns during each breeding season may result in a similar foraging direction of each population as individuals seek to avoid headwinds and take advantage of crosswinds (Spear and Ainley, 2008; Paiva et al., 2010; Ventura et al., 2022). We also observed similar space use during the non-breeding seasons and posit this may be due to food availability in that area, although the current data are insufficient to assess this hypothesis.

We also found that isotope values in tissues generated during the breeding season (blood and P1) did not differ between the two populations, suggesting both populations were exploiting similar resources. This result contrasts with what was found in two allochronic species of storm-petrels in a temperate archipelago (Azores), where DNA metabarcoding data revealed that the two populations had different diets (Carreiro et al., 2022). In contrast, the isotopic values of the tissues regenerated during the non-breeding period (R6, S8, and body feathers) showed significant differences between the two populations. One mechanism underlying this difference may be that diet differs between the two populations during this phase of the annual cycle. Alternatively, isotopic differences during the non-breeding period may arise from seasonal changes in the isotopic baseline related to seasonal differences in the productivity and the nutrient dynamics of the Canary, North Equatorial and South Equatorial currents throughout the year (Stramma and Schott, 1999). Our understanding of the meaning of the isotopic overlap could be enhanced by measuring the trophic niche through other approaches, either analyzing the diet with DNA metabarcoding (e.g. Carreiro et al., 2022), or collecting baseline samples from the oceanic system to better understand annual fluctuations (e.g. Price et al., 2014).

It also appears that there are few environmental differences in the ocean (i.e., the foraging habitat) during the time periods it is occupied by each population. Consequently, differences in ecological traits between populations may be limited. For example, the productivity pulse occurring before the breeding season of the hot population is generally higher than that occurring before the breeding season of the cool population, suggesting the hot population may benefit from greater food availability. However, birds of both populations show a similar mass gain after a foraging trip, which indicates that food acquisition in terms of mass is similar between the two seasons. We also found that productivity was higher in waters visited during the non-breeding period by birds from the hot population, which may explain why birds from the hot population spent slightly more time on the water (i.e., presumably resting) compared to flying during the non-breeding season than those from the cool population. Our data also demonstrate that the breeding phenology of the hot population matches that of other small seabirds that nest in our study area (i.e., in the Cima Islet; white-faced storm-petrels, Bulwer's petrels and Boyd's shearwaters). Having multiple species breeding simultaneously may impose interspecific competition for breeding cavities, as it has been documented in an analogous seabird community in the Azores (Ramos et al., 1997). Indeed, the avoidance of competition for nesting cavities was one of the mechanisms suggested to cause the onset of the allochronic process between Monteiro's and Band-rumped storm-petrels (Monteiro and Furness, 1998). Finally, given that Cape Verde storm-petrels are mainly nocturnal, birds of the cool population may benefit from the longer period of darkness in Cabo Verde during winter (with 2 more hours than the hot population; Appendix S17), providing them more opportunities for foraging than birds from the hot season (Monteiro and Furness, 1998). The influence of each factor on different life-history traits requires further research but we did not find differences in the breeding success between the two populations.

In summary, despite a clear divergence in the timing of breeding, we did not find high levels of ecological differentiation, raising the question of whether allochrony can drive phenotypic divergence alone (genetic drift), or if allochrony needs to be coupled with adaptation to seasonal conditions (natural selection) to culminate in allochronic speciation (Dieckmann et al., 2004). Ultimately, systems with relatively little seasonal differentiation, such as those occurring in tropical oceanic environments, may not differ enough throughout the year to promote specific seasonal adaptations to the environment. In contrast, seasonal environments were conducive to allochronic speciation of the Band-rumped storm-petrel and the Monteiro's storm-petrel in the Azores (Monteiro and Furness, 1998; Friesen et al., 2007) and Townsend storm-petrel and Ainley's storm-petrel in the Guadalupe Island (Taylor et al., 2019), and presumably promoted ecological differentiation and ultimately speciation. Alternatively, considering that in our study population connectivity occurs, gene flow might be high enough to maintain the homogeneity of the ecological traits in both populations, preventing differentiation to take place until reproductive isolation increases. For better insights in both topics, new studies of ecological differentiation in other allochronic species are key to get a deeper understanding on how ecological differentiation could reinforce speciation, and which types of systems are more likely to generate differentiation, and consequently speciation.

Data availability statement

Data presented in the study are deposited in different repositories. Tracking data (GPS and geolocators) is available in the Seabird Tracking Database repository, identifiers: 1568, 1569, 1778, 1779. Isotopic data is deposited in the Figshare repository, accession number 10.6084/m9.figshare.21388869.

Ethics statement

All procedures involving animal manipulations were in accordance with required European legislation. Deployment and recovery of GPSs and geolocators, and associated sampling procedures, were accomplished in < 10 minutes per bird and did not have any visible detrimental effects on individuals (e.g., external signs of panting or weakness). Additionally, we did not detect any differences in the breeding success between nests where a parent carried a GPS (N=60) and control nests (N=87) in a chi-squared test (c2 = 2.37, p=0.12, df=1) nor in return rates between birds that carried a geolocator (N=60) and breeders with no geolocators (N=235) in a chisquared test (c2 = 0.01, p=0.89, df=1). All research and monitoring was conducted under permission from the Direção Nacional do Ambiente from Cabo Verde "Autorização N.°91/2018; Autorização N.°107/2019; Autorização N.°016/DNA/2020".

Author contributions

FM conceived the study, carried out fieldwork, data curation and analysis, lab analyses, and wrote the first draft. TM coordinated and carried out fieldwork, supervised the analyses, and reviewed the draft. IG led fieldwork. MS-S coordinated fieldwork and conducted lab analyses. MF carried out fieldwork and lab analyses. HD coordinated logistics and resources. JG-S led fieldwork, designed the study, supervised analyses, and helped drafting 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.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.975716/full#supplementary-material

References

Alexander, B. (1898). VII.–an ornithological expedition to the cape Verde islands. *Ibis* 40, 74–118. doi: 10.1111/j.1474-919X.1898.tb05509.x

Barros, R., Medrano, F., Norambuena, H. V., Peredo, R., Silva, R., de Groote, F., et al. (2019). Breeding phenology, distribution and conservation status of markham's storm-petrel *Oceanodroma markhami* in the atacama desert. *Ardea* 107, 75–84. doi: 10.5253/arde.v107i1.a1

Bates, D., Mächler, M., Bolker, B. M., and Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Software* 67, 1–48. doi: 10.18637/jss.v067.i01

Bitz-Thorsen, J., Häkli, K., Bhat, S., and Præbel, K. (2020). Allochrony as a potential driver for reproductive isolation in adaptive radiations of European whitefish ecomorphs. *Ecol. Freshw. Fish* 29, 40–49. doi: 10.1111/EFF.12486

Bolton, M. (2007). Playback experiments indicate absence of vocal recognition among temporally and geographically separated populations of madeiran storm-petrels *Oceanodroma castro*. *Ibis* 149, 255–263. doi: 10.1111/j.1474-919X.2006.00624.x

Bolton, M. (2021). GPS Tracking reveals highly consistent use of restricted foraging areas by European storm-petrels *Hydrobates pelagicus* breeding at the largest UK colony: implications for conservation management. *Bird Conserv. Int.* 31, 35–52. doi: 10.1017/S0959270920000374

Bolton, M., Smith, A. L., Gómez-Díaz, E., Friesen, V. L., Medeiros, R., Bried, J., et al. (2008). Monteiro's storm-petrel *Oceanodroma monteiroi*: A new species from the Azores. *Ibis* 150, 717–727. doi: 10.1111/j.1474-919X.2008.00854.x

Calenge, C. (2006). The package "adehabitat" for the r software: A tool for the analysis of space and habitat use by animals. *Ecol. Modell.* 197 (3-4), 516–519. doi: 10.1016/j.ecolmodel.2006.03.017

Carreiro, A. R., Bried, J., Deakin, Z., Jones, K. B., Thomas, R. J., Symondson, W. O. C., et al. (2022). First insights into the diet composition of madeiran and monteiro's storm petrels (*Hydrobates castro* and *H. monteiroi*) breeding in the Azores. *Waterbirds* 44, 300–307. doi: 10.1675/063.044.0304

Corripio, J. P. (2014). Package "insol". r package version, 1(1). *CRAN Repository*.

Cushing, D. H. (1990). Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis. *Adv. Mar. Biol.* 26, 249–293. doi: 10.1016/S0065-2881(08)60202-3

Devries, P. J., Austin, G. T., and Martin, N. H. (2008). Diel activity and reproductive isolation in a diverse assemblage of Neotropical skippers (Lepidoptera: Hesperiidae). *Biol. Journ. Linn. Soc* 94, 723–736. doi: 10.1111/j.1095-8312.2008.01037.x

Dieckmann, U., Doebeli, M., Metz, J., and Tautz, D. (2004). *Adaptative speciation* (Cambridge: Cambridge University Press).

Doellman, M. M., Egan, S. P., Ragland, G. J., Meyers, P. J., Hood, G. R., Powell, T. H. Q., et al. (2019). Standing geographic variation in eclosion time and the genomics of host race formation in *Rhagoletis pomonella* fruit flies. *Ecol. Evol.* 9, 393–409. doi: 10.1002/ECE3.4758

Fernández-López, J., and Schliep, K. (2019). rWind: download, edit and include wind data in ecological and evolutionary analysis. *Ecography* 42, 804–810. doi: 10.1111/ecog.03730

Frankham, R., Ballou, J. D., and Briscoe, D. A. (2002). *Introduction to conservation genetics* (Cambridge: Cambridge University Press).

Friesen, V. L. (2015). Speciation in seabirds: why are there so many species … and why aren't there more? *J. Ornithol.* 156, 27–39. doi: 10.1007/s10336-015-1235-0

Friesen, V. L., Smith, A. L., Gómez-Díaz, E., Bolton, M., Furness, R. W., González-Solís, J., et al. (2007). Sympatric speciation by allochrony in a seabird. *Proc. Natl. Acad. Sci. U.S.A.* 104, 18589–18594. doi: 10.1073/pnas.0700446104

Furness, R. W., and Monaghan, P. (1987). *Seabird ecology* (Michigan: Springer).

Gradish, A. E., Keyghobadi, N., Sperling, F. A. H., and Otis, G. W. (2018). Population genetic structure and assessment of allochronic divergence in the macoun's Arctic (*Oeneis macounii*) butterfly. *Can. J. Zool.* 97, 121–130. doi: 10.1139/CJZ-2018-0117

Granroth-Wilding, H. M. V., and Phillips, R. A. (2019). Segregation in space and time explains the coexistence of two sympatric sub-Antarctic petrels. *Ibis* 161, 101–116. doi: 10.1111/IBI.12584

Green, C. P., Ratcliffe, N., Mattern, T., Thompson, D., Lea, M. A., Wotherspoon, S., et al. (2022). The role of allochrony in influencing interspecific differences in foraging distribution during the non-breeding season between two congeneric crested penguin species. *PloS One* 17, e0262901. doi: 10.1371/JOURNAL.PONE.0262901

Gu, Z., Gu, L., Eils, R., Schlesner, M., and Brors, B. (2014). Circlize implements and enhances circular visualization in r. *Bioinformatics* 30, 2811–2812. doi: 10.1093/bioinformatics/btu393

Halpin, L. R., Pollet, I. L., Lee, C., Morgan, K. H., and Carter, H. R. (2018). Year-round movements of sympatric fork-tailed (*Oceanodroma furcata*) and leach's (*O. leucorhoa*) storm-petrels. *J. Field Ornithol.* 89, 207–220. doi: 10.1111/jofo.12255

Halpin, L. R., Ross, J. D., Ramos, R., Mott, R., Carlile, N., Golding, N., et al. (2021). Double-tagging scores of seabirds reveals that light-level geolocator accuracy is limited by species idiosyncrasies and equatorial solar profiles. *Methods Ecol. Evol.* 12, 2243–2255. doi: 10.1111/2041-210X.13698

Harris, M. P. (1969). The biology of storm petrels in the Galapagos islands. *Proc. Calif. Acad. Sci.* 4, 95–166.

Hedd, A., Pollet, I. L., Mauck, R. A., Burke, C. M., Mallory, M. L., McFarlane Tranquilla, L. A., et al. (2018). Foraging areas, offshore habitat use, and colony overlap by incubating leach's storm-petrels *Oceanodroma leucorhoa* in the Northwest Atlantic. *PloS One* 13, 1–18. doi: 10.1371/JOURNAL.PONE.0194389

Hendry, A. P., and Day, T. (2005). Population structure attributable to reproductive time: Isolation by time and adaptation by time. *Mol. Ecol.* 14, 901–916. doi: 10.1111/j.1365-294X.2005.02480.x

Hernández-León, S., Koppelmann, R., Fraile-Nuez, E., Bode, A., Mompeán, C., Irigoien, X., et al. (2020). Large Deep-sea zooplankton biomass mirrors primary production in the global ocean. *Nat. Commun* 6048, 1–8. doi: 10.1038/s41467-020-19875-7

Hipfner, J. M. (2008). Matches and mismatches: Ocean climate, prey phenology and breeding success in a zooplanktivorous seabird. *Mar. Ecol. Prog. Ser.* 368, 295–304. doi: 10.3354/meps07603

Homma, Y., Okuda, S., Kasahara, M., Takahashi, F., Yoshikawa, S., and Uwai, S. (2020). Phenological shifts and genetic differentiation between sympatric populations of *Sargassum horneri* (Fucales, phaeophyceae) in Japan. *Mar. Ecol. Prog. Ser.* 642, 103–116. doi: 10.3354/MEPS13332

Jackson, A. L., Inger, R., Parnell, A. C., and Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER - stable isotope Bayesian ellipses in r. *J. Anim. Ecol.* 80, 595–602. doi: 10.1111/j.1365-2656.2011.01806.x

Ji, R., Jin, M., and Varpe, Ø. (2013). Sea Ice phenology and timing of primary production pulses in the Arctic ocean. *Glob. Chang. Biol.* 19, 734–741. doi: 10.1111/gcb.12074

Juri, G., and Premoli, A. C. (2021). Allochrony of neighbour ecological species: Can isolation by time maintain divergence? the natural experiment of sympatric *Nothofagus*. *For Ecol. Manage.* 497, 119466. doi: 10.1016/J.FORECO.2021.119466

Kelley, D. E., Richards, C., and Layton, C. (2022). Oce: an R package for Oceanographic Analysis. *Journal of Open Source Software* 7, 1–5. doi: 10.21105/joss.03594

Leal, G. R., and Bugoni, L. (2021). Individual variability in habitat, migration routes and niche used by trindade petrels, *Pterodroma arminjoniana*. *Mar. Biol.* 68, 1–14. doi: 10.1007/S00227-021-03938-4

Lewis, S., Nussey, D. H., Wood, A. G., Croxall, J. P., and Phillips, R. A. (2012). Intrinsic determinants of a population trend in timing of breeding in the wandering albatross. *Oikos* 121, 2061–2071. doi: 10.1111/J.1600-0706.2012.20293.X

Liedvogel, M., Szulkin, M., Knowles, S. C. L., Wood, M. J., and Sheldon, B. C. (2009). Phenotypic correlates of clock gene variation in a wild blue tit population: evidence for a role in seasonal timing of reproduction. *Mol. Ecol.* 18, 2444–2456. doi: 10.1111/J.1365-294X.2009.04204.X

Lisovski, S., Bauer, S., Briedis, M., Davidson, S. C., Dhanjal-Adams, K. L., Hallworth, M. T., et al. (2020). Light-level geolocator analyses: A user's guide. *J. Anim. Ecol.* 89, 221–236. doi: 10.1111/1365-2656.13036

Lund, U., Agostinelli, C., Arai, H., Gagliardi, A., Garcia Portuges, E., Giunchi, D., et al (2017). R package "circular": Circular statistics *R package.*

Malick, M. J., Cox, S. P., Mueter, F. J., and Peterman, R. M. (2015). Linking phytoplankton phenology to salmon productivity along a north-south gradient in the northeast pacific ocean. *Can. J. Fish. Aquat. Sci.* 72, 697–708. doi: 10.1139/cjfas-2014-0298

Marshall, D. C., Cooley, J. R., and Hill, K. B. R. (2011). Developmental plasticity of life-cycle length in thirteen-year periodical cicadas (Hemiptera: Cicadidae). *Ann. Entomol. Soc. Am.* 104, 443–450. doi: 10.1603/AN10087

Megysi, J. L., and O'Daniel, D. L. (2020). "Bulwer's petrel (Bulweria bulwerii)," in *Birds of the world* (Ithaca, NY, USA: Cornell Lab of Ornithology). doi: 10.2173/bow.bulpet.01

Moe, B., Stempniewicz, L., Jakubas, D., Angelier, F., Chastel, O., Dinessen, F., et al. (2009). Climate change and phenological responses of two seabird species breeding in the high-Arctic. *Mar. Ecol. Prog. Ser.* 393, 235–246. doi: 10.3354/meps08222

Monteiro, L. R., and Furness, R. W. (1998). Speciation through temporal segregation of madeiran storm petrel (*Oceanodroma castro*) populations in the Azores? *Phi. Trans. Roy. Soc. B.: Biol. Sci.* 353, 945–953. doi: 10.1098/rstb.1998.0259

Murphy, R. C. (1924). The marine ornithology of the cape Verde islands, with a list of all the birds of the archipelago. *Bull. Am. Mus. Nat. Hist.* 50, 211–278.

Paiva, V. H., Guilford, T., Meade, J., Geraldes, P., Ramos, J. A., and Garthe, S. (2010). Flight dynamics of cory's shearwater foraging in a coastal environment. *Zoology* 113, 47–56. doi: 10.1016/j.zool.2009.05.003

Pascalis, F., Pala, D., Pisu, D., Morinay, J., Benvenuti, A., Spano, C., et al. (2021). Searching on the edge: dynamic oceanographic features increase foraging opportunities in a small pelagic seabird. *Mar. Ecol. Prog. Ser.* 668, 121–132. doi: 10.3354/MEPS13726

Pollet, I. L., Ronconi, R. A., Jonsen, I. D., Leonard, M. L., Taylor, P. D., and Shutler, D. (2014). Foraging movements of leach's storm-petrels *Oceanodroma leucorhoa* during incubation. *J. Av. Biol.* 45, 305–314. doi: 10.1111/jav.00361

Power, D. M., and Ainley, D. G. (1986). Seabird geographic variation: Similarity among populations of leach's storm-petrel. *Auk* 103, 575–585. doi: 10.1093/auk/103.3.575

Price, T. D., Frei, K. M., and Naumann, E. (2014). Isotopic baselines in the north Atlantic region. *J. North Atlantic.* 2014, 103–136. doi: 10.3721/037.002.sp707

Ramírez, F., Afán, I., Tavecchia, G., Catalán, I. A., Oro, D., and Sanz-Aguilar, A. (2016). Oceanographic drivers and mistiming processes shape breeding success in a seabird. *Proc. Roy. Soc. B.: Bio Sci.* 283 (1826), 1–9. doi: 10.1098/rspb.2015.2287

Ramírez, F., Tarroux, A., Hovinen, J., Navarro, J., Afán, I., Forero, M. G., et al. (2017). Sea Ice phenology and primary productivity pulses shape breeding success in Arctic seabirds. *Sci. Rep.* 7, 1–9. doi: 10.1038/s41598-017-04775-6

Ramos, R., and González-Solís, J. (2012). Trace me if you can: The use of intrinsic biogeochemical markers in marine top predators. *Front. Ecol. Environ.* 10, 258–266. doi: 10.1890/110140

Ramos, R., Llabrés, V., Monclús, L., López-Béjar, M., and González-Solís, J. (2018). Costs of breeding are rapidly buffered and do not affect migratory behavior in a long-lived bird species. *Ecology* 99, 2010–2024. doi: 10.1002/ECY.2435

Ramos, J. A., Monteiro, L. R., Sola, E., and Moniz, Z. (1997). Characteristics and competition for nest cavities in burrowing procellariiformes. *Condor* 99, 634–641. doi: 10.2307/1370475

Rotger, A., Sola, A., Tavecchia, G., and Sanz-Aguilar, A. (2020). Foraging far from home: Gps-tracking of Mediterranean storm-petrels *Hydrobates pelagicus melitensis* reveals long-distance foraging movements. *Ardeola* 68, 3–16. doi: 10.13157/arla.68.1.2021.ra1

Sangster, G., Collinson, J. M., Crochet, P. A., Knox, A. G., Parkin, D. T., and Votier, S. C. (2012). Taxonomic recommendations for British birds: Eighth report. *Ibis* 154, 874–883. doi: 10.1111/j.1474-919X.2012.01273.x

Schweigert, J. F., Thompson, M., Fort, C., Hay, D. E., Therriault, T. W., and Brown, L. N. (2013). Factors linking pacific herring (*Clupea pallasi*) productivity and the spring plankton bloom in the strait of Georgia, British Columbia, Canada. *Prog. Oceanogr.* 115, 103–110. doi: 10.1016/j.pocean.2013.05.017

Semedo, G., Paiva, V. H., Militaõ, T., Rodrigues, I., Dinis, H. A., Pereira, J., et al. (2020). Distribution, abundance, and on-land threats to cabo Verde seabirds. *Bird Conserv. Int.* 31, 53–76. doi: 10.1017/S0959270920000428

Smith, A. L., and Friesen, V. L. (2007). Differentiation of sympatric populations of the band-rumped storm-petrel in the Galapagos islands: An examination of genetics, morphology, and vocalizations. *Mol. Ecol.* 16, 1593–1603. doi: 10.1111/j.1365-294X.2006.03154.x

Sota, T., Yamamoto, S., Cooley, J. R., Hill, K. B. R., Simon, C., and Yoshimura, J. (2013) Independent divergence of 13-and 17-y life cycles among three periodical cicada lineages *Proc. Natl. Acad. Sci. U S A.* 110, 6919–6924. doi: 10.1073/pnas.1220060110

Spear, L. B., and Ainley, D. G. (2008). Flight speed of seabirds in relation to wind speed and direction. *Ibis* 139, 234–251. doi: 10.1111/j.1474-919X.1997.tb04621.x

Stramma, L., and Schott, F. (1999). The mean flow field of the tropical Atlantic ocean. *Deep Sea Res. Part II: Topic. Stud. Oceanogr* 46, 279–303. doi: 10.1016/S0967-0645(98)00109-X

Tang, J., Körner, C., Muraoka, H., Piao, S., Shen, M., Thackeray, S. J., et al. (2016). Emerging opportunities and challenges in phenology: a review. *Ecosphere* 7, e01436. doi: 10.1002/ECS2.1436

Taylor, R. S., Bailie, A., Gulavita, P., Birt, T., Aarvak, T., Anker-Nilssen, T., et al. (2018). Sympatric population divergence within a highly pelagic seabird species complex (*Hydrobates* spp.). *J. Avian Biol* 49, 1–14. doi: 10.1111/jav.01515

Taylor, R. S., Bolton, M., Beard, A., Birt, T., Deane-Coe, P., Raine, A. F., et al. (2019). Cryptic species and independent origins of allochronic populations within a seabird species complex (*Hydrobates* spp.). *Mol. Phylogenet. Evol* 139, 1–15. doi: 10.1016/j.ympev.2019.106552

Taylor, R. S., and Friesen, V. L. (2017). The role of allochrony in speciation. *Mol. Ecol.* 26, 3330–3342. doi: 10.1111/mec.14126

Thiebot, J. B., Cherel, Y., Trathan, P. N., and Bost, C. A. (2012). Coexistence of oceanic predators on wintering areas explained by population-scale foraging segregation in space or time. *Ecology* 93, 122–130. doi: 10.1890/11-0385.1

Thomé, M. T. C., Carstens, B. C., Rodrigues, M. T., Galetti, P. M.Jr., Alexandrino, J., and Haddad, C. F. B. (2021). A role of asynchrony of seasons in explaining genetic differentiation in a Neotropical toad. *Heredity* 2021, 1–10. doi: 10.1038/s41437-021-00460-7

Ventura, F., Catry, P., Dias, M. P., Breed, G. A., Folch, A., and Granadeiro, J. P. (2022). A central place foraging seabird flies at right angles to the wind to jointly optimize locomotor and olfactory search efficiency. *Proc. Roy. Soc. B.* 289, 1–10. doi: 10.1098/RSPB.2022.0895

Warham, J. (1992). *The petrels: Their ecology and breeding systems* (London: Academic Press).

Watanuki, Y. (2002). Moonlight and activity of breeders and non-breeders of leach's storm-petrels. *J. Yam. Inst. Orn.* 34, 245–249. doi: 10.3312/JYIO1952.34.245

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis* (New York: Springer-Verlag).

Wilczek, A. M., Roe, J. L., Knapp, M. C., Cooper, M. D., Lopez-Gallego, C., Martin, L. J., et al. (2009). Effects of genetic perturbation on seasonal life history plasticity. *Science* 1979) 323, 930–934. doi: 10.1126/SCIENCE.1165826

Wood, S. N. (2001). *Mgcv: GAMs and generalized ridge regression for R. R News.* 1, 20–25.

Zuur, A. F., Ieno, E. N., and Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* 1, 3–14. doi: 10.1111/J.2041-210X.2009.00001.X

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EDITED BY
Nuno Queiroz,
Centro de Investigacao em Biodiversidade e Recursos Geneticos (CIBIO-InBIO), Portugal

REVIEWED BY
Ana Filipa Sobral,
University of the Azores, Portugal
Abigail Mary Moore,
Hasanuddin University, Indonesia

*CORRESPONDENCE
Edy Setyawan
edy.setyawan@auckland.ac.nz

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Population estimates of photo-identified individuals using a modified POPAN model reveal that Raja Ampat's reef manta rays are thriving

Edy Setyawan[1]*, Ben C. Stevenson[2], Mark V. Erdmann[3], Abdi W. Hasan[4], Abraham B. Sianipar[5], Imanuel Mofu[6], Mochamad I. H. Putra[7], Muhamad Izuan[4], Orgenes Ambafen[6], Rachel M. Fewster[2], Robin Aldridge-Sutton[2], Ronald Mambrasar[4] and Rochelle Constantine[1,8]

[1]Institute of Marine Science, The University of Auckland, Auckland, New Zealand, [2]Department of Statistics, The University of Auckland, Auckland, New Zealand, [3]Conservation International Aotearoa, The University of Auckland, Auckland, New Zealand, [4]West Papua Program, Konservasi Indonesia, Sorong, Papua Barat, Indonesia, [5]School of Veterinary and Life Sciences, Murdoch University, Perth, WA, Australia, [6]Jaga Laut, Badan Layanan Umum Daerah Unit Pelaksana Teknis Daerah (BLUD UPTD) Pengelolaan Kawasan Konservasi Perairan (KKP) Kepulauan Raja Ampat, Waisai, Papua Barat, Indonesia, [7]Elasmobranch and Charismatic Species Program, Konservasi Indonesia, Jakarta, Indonesia, [8]School of Biological Sciences, The University of Auckland, Auckland, New Zealand

The 6.7-million-hectare Raja Ampat archipelago is home to Indonesia's largest reef manta ray (*Mobula alfredi*) population and a representative network of nine marine protected areas (MPAs). However, the population dynamics of *M. alfredi* in the region are still largely unknown. Using our photo-identification database, we fitted modified POPAN mark-recapture models with transience and per capita recruitment parameters to estimate key demographic characteristics of *M. alfredi* from two of Raja Ampat's largest MPAs: Dampier Strait and South East (SE) Misool. A total of 1,041 unique individuals were photo-identified over an 11-year period (2009–2019) from Dampier Strait ($n = 515$) and SE Misool ($n = 536$). In our models, apparent survival probabilities and per capita recruitment rates were strongly linked with El Niño–Southern Oscillation (ENSO) events. Our models also estimated high apparent survival probabilities and significant increases in (sub)population sizes in both MPAs over a decade. In Dampier Strait, the estimated population size increased significantly ($p = 0.018$) from 226 (95% CI: 161, 283) to 317 (280, 355) individuals. Likewise, the estimated population size in SE Misool increased significantly ($p = 0.008$) from 210 (137, 308) to 511 (393, 618) individuals. Regardless of variation in the percentage change in population size between years throughout the study, the estimated overall population change shows a compound growth of 3.9% (0.7, 8.6) per annum in Dampier Strait and 10.7% (4.3, 16.1) per annum in SE Misool. Despite the global decline in oceanic sharks and rays due to fishing pressure in the last five decades, our study demonstrates the positive impact of a suite of long-term conservation efforts, coupled with the influence of ENSO events, on increasing *M. alfredi* abundance in Raja Ampat MPAs. Our study also underscores the importance of long-term monitoring to evaluate the effectiveness of conservation management measures on manta ray populations. Our modification of the standard POPAN model by incorporating per capita recruitment and transience parameters represents an important advance in mark-recapture modelling that should prove useful when examining other manta ray populations and other highly migratory species that are likely to have a substantial percentage of transient individuals.

KEYWORDS

marine protected areas (MPA), marine megafauna, mark-recapture, citizen science, Indonesia, conservation, abundance estimation, population dynamics

Introduction

Understanding population dynamics, particularly abundance and growth, through demographic modelling is crucial in evaluating the effectiveness of management strategies for threatened marine species in marine protected areas (MPAs) (Beissinger and Westphal, 1998; Norris, 2004). MPAs have long been known to provide protection to sessile benthos (e.g., hard corals) and to increase the abundance and biomass of relatively sedentary fish and invertebrate species (e.g., snappers, groupers and lobsters) both within and outside their boundaries (Gell and Roberts, 2003; PISCO, 2007). Recently, MPAs have also been shown to promote the recovery of populations of large mobile species (e.g., reef sharks) particularly when the MPAs themselves are large (Knip et al., 2012; Edgar et al., 2014; Jaiteh et al., 2016; Speed et al., 2018). Nonetheless, in large and remote MPAs, where enforcement is costly and difficult, the populations of those species with large home ranges are potentially more exposed to illegal fishing activities (Graham et al., 2010; Jacoby et al., 2020).

Estimating the abundance of highly mobile and migratory marine megafauna can be challenging, as individuals are capable of traveling vast distances, often remain submerged, and commonly use different habitats on a seasonal basis (Carroll et al., 2013; Couturier et al., 2014; Armstrong et al., 2019). Given these challenges, investigating predictable aggregation sites regularly occupied by these species provides an excellent opportunity to estimate demographic parameters such as population abundance through mark-recapture studies (Dudgeon et al., 2008; Williams et al., 2011).

The reef manta ray *Mobula alfredi*, listed as Vulnerable (VU) (Marshall et al., 2019) on the IUCN Red List, is distributed throughout the Indo-Pacific around nearshore areas in tropical and subtropical regions (Marshall et al., 2009). At a regional scale, *M. alfredi* frequently demonstrates seasonal movement patterns (Jaine et al., 2014; Setyawan et al., 2018; Armstrong et al., 2020; Harris et al., 2020). At a local scale, this philopatric species shows high site fidelity to key aggregation sites such as cleaning sites and feeding grounds (Dewar et al., 2008; Couturier et al., 2011; Setyawan et al., 2018; Peel et al., 2019). The predictable presence of *M. alfredi* at known and accessible aggregation sites facilitates the compilation of photographic identification (photo-ID) databases (Marshall and Pierce, 2012; Stevens, 2016), similar to those used extensively for population studies of whale sharks (*Rhincodon typus*) and white sharks (*Carcharodon carcharias*) (Graham and Roberts, 2007; Towner et al., 2013; McKinney et al., 2017).

Photo-ID techniques have been used to study the population demographics of manta rays in many regions. This non-invasive technique uses the patterns of natural ventral markings that are unique to each individual (Marshall et al., 2011). These markings remain unchanged throughout the individual's life, or at least for periods of 30 years or more (Couturier et al., 2014). These characteristics have enabled long-term photo-ID data to be used extensively to examine life history traits and reproductive strategies, and determine the fecundity and age at maturity of *M. alfredi* (Stevens, 2016). Long-term photo-ID datasets have also been used to estimate *M. alfredi* population size and survival probabilities using mark-recapture models in several countries (Deakos et al., 2011; Kitchen-Wheeler et al., 2011; Marshall et al., 2011; Couturier et al., 2014; Peel, 2019; Venables, 2020).

The Raja Ampat archipelago in West Papua, Indonesia, harbours large populations of both *M. alfredi* and oceanic manta rays *M. birostris* (Setyawan et al., 2020). Although manta rays have been subject to targeted fisheries in several regions of Indonesia (Heinrichs et al., 2011; Lewis et al., 2015), historically, they have not been systematically targeted by local fisheries in Raja Ampat waters (Beale et al., 2019). Nonetheless, there are anecdotal reports of sporadic targeting of manta ray aggregations in the early 2000s by shark fishers in northern Raja

Ampat (Varkey et al., 2010). Local fishers also reported that manta rays were frequently observed as bycatch when outsider fishing boats using large drift nets occasionally operated in Raja Ampat in the 1990s and early 2000s (Setyawan et al., 2022a). Importantly, Raja Ampat's manta rays have been protected since 2007, when the Raja Ampat local government and local stakeholders started to implement a series of conservation measures in the region that began with the implementation of a network of MPAs, progressed to the declaration of all of Raja Ampat's regency waters as Southeast Asia's first shark and ray sanctuary in 2012, and culminated with the Indonesian government granting full national-level protection to both species of manta ray in 2014 (Setyawan et al., 2022a). As a result, Raja Ampat's manta rays have enjoyed increasingly strict protections for over a decade. However, the impact of these management measures on *M. alfredi* in one of Indonesia's most popular manta diving tourism destinations (O'Malley et al., 2013) has not yet been formally assessed. Setyawan et al. (2020) provided a broad overview of the natural history and basic demographic features of the *M. alfredi* population in Raja Ampat; however, no analysis of population dynamics was conducted. The only study to date on manta ray population dynamics in Raja Ampat was focused on *M. birostris*. Using mark-recapture models, Beale et al. (2019) estimated high survival probabilities for both females and males in annual population surveys from 2011–2016. This research highlighted the impact of the 2015–2016 major El Niño-Southern Oscillation (ENSO) event in significantly increasing *M. birostris* sightings in southern Raja Ampat at the time.

In a recent assessment, Pacoureau et al. (2021) reported the global abundance of 31 species of oceanic sharks and rays (including *M. alfredi* and *M. birostris*) declined by 71% over the past five decades, primarily due to an 18-fold increase in relative fishing pressure. Similarly, Rohner et al. (2013; 2017) reported dramatic declines in *M. alfredi* sightings in southern Mozambique (with a 98% decrease between 2003 and 2016), while numerous authors have noted that the life history characteristics of manta rays (including late maturation and extremely low fecundity) make them highly vulnerable to population decline (Ward-Paige et al., 2013; Dulvy et al., 2014; Croll et al., 2015). While anecdotal evidence and testimonies by local communities and marine tourism operators suggest that Raja Ampat's *M. alfredi* population has been spared such a fate (Setyawan et al., 2022a), the aim of this paper is to examine manta ray population trends in Raja Ampat in a quantitative manner. Here, we used open population mark-recapture models based on photo-ID sighting data of *M. alfredi* sourced from citizen science and active surveys by the authors to explicitly examine the potential impacts of manta ray conservation and management efforts in the extensive Raja Ampat MPA network. The use of sightings data contributed by the public through citizen science, integrated with those collected by researchers, has been shown to be accurate and robust in mark-recapture studies (Davies et al., 2012; Robinson et al., 2018), and have been used in studies involving a range of different species including whale sharks (Meekan et al., 2006; Holmberg et al., 2009; Magson et al., 2022), manta rays (Beale et al., 2019), and sperm whales (*Physeter macrocephalus*) (Boys et al., 2019).

Using a modified version of the POPAN model (Schwarz and Arnason, 1996), we aimed to estimate the annual population sizes, survival probabilities, sighting probabilities, and per capita recruitment rates of *M. alfredi* (sub)populations using 11 years of sightings data from the two MPAs in Raja Ampat with the highest manta ray survey effort: Dampier Strait and South East (SE) Misool. Importantly, Raja Ampat's *M. alfredi* population is best described as a metapopulation consisting of at least four (and up to seven) local subpopulations, including those in the Dampier Strait and SE Misool (Setyawan et al., 2020). While individuals have been recorded moving between Dampier Strait and SE Misool MPAs using both photo-ID and acoustic telemetry, such movements are rare (only 10 recorded in fifteen years' of survey effort (Setyawan et al., 2020)), leading us to fit separate POPAN models for these two subpopulations. In general, the subpopulation in SE Misool MPA is relatively isolated (over 160 km between the closest known manta ray aggregation sites in SE Misool and Dampier Strait and with deep water to the south of the SE Misool MPA). By comparison, the Dampier Strait subpopulation shows the strongest connections to other subpopulations in Raja Ampat based upon evidence of movement of individuals from photo-ID and acoustic telemetry data (Setyawan et al., 2018; Setyawan et al., 2020). Given the proximity of the Dampier Strait to other hypothesised subpopulations (12-20 km to the West Waigeo and Fam subpopulations, respectively) and the frequent observation in Dampier Strait of large seasonal feeding aggregations of up to 112 individuals (Setyawan et al., 2020), we expected a significant number of "transient" individuals pass through Dampier Strait and might not be recorded there again – a situation that violates one of the key assumptions of the standard POPAN model. Based upon this concern, we have also incorporated a transience parameter in modelling the Dampier Strait subpopulation (described further below in the POPAN methods section).

2 Material and methods

2.1 Study area

The Raja Ampat Archipelago covers an area of ~6.7 million hectares and is situated on the northwestern tip of West Papua Province in eastern Indonesia (Figure 1). The region is protected by a network of nine MPAs (including Dampier Strait and SE Misool) that cover nearly two million hectares; this network is

FIGURE 1
Map of the Raja Ampat Archipelago in West Papua, Indonesia, denoting both the network of nine MPAs (shaded green polygons) and the 51 sites from which *M. alfredi* photo-ID data have been collected (red dots with white outline).

part of a larger network of 26 MPAs covering 5.2 million hectares of a region commonly referred to as the Bird's Head Seascape of West Papua (Mangubhai et al., 2012; Setyawan et al., 2022a). In Raja Ampat, *M. alfredi* sightings have been documented from at least 101 different sites within the archipelago (Setyawan et al., 2020), while ventral photo-IDs of *M. alfredi* were captured from 51 sites (Figure 1).

2.2 Data collection

2.2.1 Photo-ID

We collected *M. alfredi* ventral identification photos or videos (Stevens, 2016; Stevens et al., 2018) from three primary sources (active surveys by the authors, submissions from collaborating dive resorts and liveaboard vessels, and contributions from citizen scientists) and entered into the Raja Ampat *M. alfredi* photo-ID database using the protocols developed by Stevens (2016). We determined the sex of individual manta rays from the presence (male) or absence (female) of claspers. We further used the length and extent of calcification of the claspers and development of clasper glands to estimate maturity in males (Marshall and Bennett, 2010). We recorded the presence of mating scars or visible signs of pregnancy and used these as indicators of sexual maturity in females (Marshall and Bennett, 2010; Stevens, 2016).

As detailed in Setyawan et al. (2020), each *M. alfredi* sighting in the Raja Ampat database included photographs of the ventral surface of the individual and associated metadata including date, time, location, estimated size (wingspan), sex, notes on maturity, and a number of other variables not pertinent to the present study. Sightings data contributed by citizen scientists consisted of photo-ID images, date and time, and location. We (ES and MI) manually matched all photo-ID images from each *M. alfredi* sighting, including those from collaborators and citizen scientists, to the Raja Ampat *M. alfredi* identification catalogue. We then recorded either as a resighted individual or assigned a new unique identification code if sighted for the first time.

Here we used *M. alfredi* sightings data from only two MPAs (SE Misool and Dampier Strait) (Figure 1), where the collection of photo-ID data was the most consistent and where the most *M. alfredi* sightings data were recorded (Setyawan et al., 2020). Furthermore, we restricted our modelling to sightings data collected only from 2009–2019, due to the small amount of data available before 2009 (Supplementary Figure 1). These 2009–2019 data from SE Misool and Dampier Strait MPAs were from 27 of the 51 sites in Raja Ampat from which *M. alfredi* ventral ID photos were recorded. Here we used the same *M. alfredi* sightings data reported in Setyawan et al. (2020), together with additional historical sightings data collected subsequently from professional underwater photographers.

2.3 POPAN models for Dampier Strait and SE Misool

2.3.1 Overview

First described by Schwarz and Arnason (1996), POPAN is an open population capture-recapture model capable of estimating population size, and how it changes, over a number of sampling occasions. The parameters directly estimated by a POPAN model are M, the superpopulation size of individuals available for sighting on at least one occasion; p, sighting probability; ϕ, apparent survival probability; and p_e, the entry probability (i.e., the expected proportion of the M individuals that are first available for sighting on any given occasion). Estimates of these parameters are used to derive estimates of the expected population size for each occasion, denoted $E(N_t)$ for occasion t. See Supplementary Materials for further details.

Under the simplest POPAN model, sighting probabilities, survival probabilities, and entry probabilities are assumed to be constant over time. Alternatively, POPAN models allow us to estimate how these demographic parameters change between occasions, either by modelling how they relate to occasion-level covariates or by estimating a separate parameter for each occasion. They also allow us to estimate separate parameters and expected population sizes for males and females, choosing to either share parameters across sexes or estimate them separately. We denote p_t, ϕ_t, and $p_{e,t}$ as the parameters for occasion t, noting that we require one fewer ϕ parameter than the number of occasions, because ϕ_t denotes the probability of survival between one occasion and the next, and the number of intervals between occasions is one fewer than the number of occasions.

Standard POPAN models require us to assume that sighting and survival probabilities are the same for all individuals within the same occasion. Because survey effort varied between Dampier Strait and SE Misool, we expected sighting probabilities for individuals typically resident at each location to be different. Differing environmental conditions may also induce spatial variation in survival. We therefore analyzed sighting data from Dampier Strait and SE Misool separately, allowing us to estimate different model parameters (including population size) at each location. We considered each year to be an occasion, and so the data required by our model is a capture history for each detected individual, indicating the years in which each individual was detected.

2.3.2 Goodness-of-fit

We assessed goodness-of-fit for standard POPAN models using the suite of tests implemented in the R package R2ucare (Gimenez et al., 2018). Tests applied included an overall test for goodness-of-fit and TEST 3.SR that is often interpreted as a test for transience.

2.3.3 POPAN models with transience

As mentioned above, we considered transience is a likely scenario in the Dampier Strait *M. alfredi* subpopulation. The presence of transient individuals violates the assumption of constant survival probability required by standard POPAN models: transient individuals are only available for a single occasion before they permanently emigrate, thus, upon recruitment, they have apparent survival probabilities of zero. See Pradel et al. (1997) and Genovart and Pradel (2019) for the treatment of transience effects in capture-recapture models, although their focus is on models that estimate survival and recruitment only; here we focused on models that additionally estimate abundance.

We developed an extension to the standard POPAN model to accommodate transient individuals. Technical details of our new model are available in the Supplementary Materials. We used a two-component discrete mixture to model survival probabilities (similar to "Parameterisation B" proposed by Genovart and Pradel (2019)), which introduces a new parameter, γ_t, the probability that an individual recruited on occasion t is a transient. Newly-recruited individuals have apparent survival probabilities of zero with probability γ_t, and the usual apparent survival probability of ϕ_t with probability 1-γ_t. By considering transience a latent state, our model does not require us to determine which individuals are transients and which are not.

2.3.4 POPAN models with per capita recruitment

We made one further modification to the standard POPAN model. Typically, recruitment is estimated using the parameter p_e, t, the expected proportion of the M individuals in the superpopulation that are recruited on occasion t. Under a null-model specification for recruitment, the same number of individuals is expected to be recruited each year, regardless of the underlying population size.

However, it is common for population dynamics models to link recruitment to the size of the population, because larger populations have the capacity to recruit more individuals (Snider and Brimlow, 2013). We included this feature by reparametrizing the POPAN model to directly estimate per capita recruitment, denoted ψt for occasion t, rather than the probabilities of entry, p_e, t, so that the expected number of new recruits in year t+1 is given by $\psi_t N_t$. One advantage of our specification over the standard POPAN model is that per capita recruitment rates are more easily interpreted and are more biologically relevant than probabilities of entry. See Supplementary Materials for further details, including how to calculate the usual probabilities of entry from our model as derived parameters.

2.3.5 Incorporating covariates

We considered the effects of an environmental covariate, the bimonthly Multivariate ENSO Index (MEI), on apparent survival, per capita recruitment, and sighting probabilities. We used the bimonthly MEI obtained from the NOAA Physical Sciences Laboratory (https://psl.noaa.gov/enso/mei/) to represent environmental conditions in the region. High positive values (>0.5) of the bimonthly MEI denote El Niño events, while low negative values (<-0.5) denote La Niña events (Supplementary Figure 2). We then averaged the bimonthly MEI into annual indices to be consistent with the annual values of demographic parameters.

2.3.6 Candidate models

We first fitted models without transience and considered eight different model specifications (Table 1) for the sighting probabilities, survival probabilities, and per capita recruitment rates. We used a log link function to model per capita recruitment rates, and logit link functions for sighting and survival probabilities. With eight possible specifications for each of the three parameters, we obtained a total of 512 total candidate models. We did not consider models including effects of both time and MEI, because the parameters of such a model are not identifiable.

In the event that goodness-of-fit tests provided evidence for lack-of-fit, and in particular indicated the presence of transient individuals, we then additionally considered the same 512 model specifications, but also accommodated the effects of transience using our new model. We considered models that have a different transience probability for the first year of the study,

TABLE 1 Description of model specifications for the sighting probabilities, survival probabilities, and per capita recruitment rates of *M. alfredi* subpopulations in Dampier Strait and SE Misool MPAs.

No.	Model specification	Description
1	Intercept only	The parameter was constant for all years and the same for both sexes.
2	MEI only	After applying a link function, the parameter varied over time according to a linear relationship with MEI.
3	Time only	The parameter varied freely for each occasion but was the same for both sexes. This specification required estimating a separate sighting probability parameter for each occasion
4	Sex only	The parameter was constant over time, but different for each sex.
5	MEI and sex (additive)	After applying a link function, the parameter varied over time according to a linear relationship with MEI, and also with a constant difference between sexes.
6	MEI and sex (interaction)	After applying a link function, the parameter varied over time according to a linear relationship with MEI, with a different linear effect of MEI for each sex
7	Time and sex (additive)	The parameter varied freely for each occasion with a constant difference between sexes, so that the effect of time was the same for both sexes.
8	Time and sex (interaction)	The parameter varied freely for each occasion, with separate effects of time estimated for each sex.

then a constant transience probability for the remaining years. In the first year of our study, all individuals present are considered newly available for sighting, including those that were recruited that year (a mixture of transients and non-transients) and those that were recruited in previous years (all of which must be non-transients, because transients do not survive from one year to the next). On later occasions, only the mixture of transients and non-transients recruited that year are newly available for sighting, thus we expected a higher proportion of these new individuals to be transients compared to the first occasion.

2.3.7 Model selection and model averaging

We used AIC to assess the degree to which each model is supported by the data, or QAIC if goodness-of-fit tests indicated the presence of overdispersion (Cooch and White, 2001). In the event that (Q)AIC did not identify a single model with considerably more support than all others, we calculated model-averaged estimates using the bootstrap approach recommended by Buckland et al. (2001).

Under this procedure, we selected a final candidate set of models within 10 (Q)AIC units of the model with the highest support (i.e., lowest (Q)AIC value). For each of 1,000 bootstrap iterations, we resampled *n* capture histories with replacement, where *n* is the number of capture histories in the original data. To each new data set, we fitted all the final candidate models. We retained estimates from the model with highest (Q)AIC support from each iteration. We then calculated the model-averaged point estimates by taking the mean of these retained estimates across the bootstrap resamples. Furthermore, we obtained 95% confidence interval (CI) limits from the 2.5th (lower CI limit) and 97.5th percentiles (upper CI limit) of these retained point estimates.

We also used the bootstrap procedure for hypothesis testing. We conducted hypothesis tests comparing males and females in terms of population size, survival probability, per capita recruitment rate, and sighting probability. For each, the null hypothesis was no difference between the sexes. We also tested for changes in these parameters over time. Again, each null hypothesis tested was for no difference between two specified occasions. To calculate a *p*-value, we obtained the proportion of estimates retained across the 1,000 bootstrap iterations that were in the tail of the distribution beyond the hypothesised value and multiplied this proportion by 2 for a two-sided test.

We conducted all analyses of goodness-of-fit, model fitting, model selection, model averaging, and hypothesis testing using custom code written in R version 4.1.2 (R Core Team, 2021), available in GitHub (https://github.com/b-steve/manta-popan).

2.3.8 Environmental variables

We examined two environmental variables, sea surface temperature (SST) and chlorophyll-*a* (chl-*a*) concentration to characterize the occurrence of El Niño events in the study area, as ENSO is a known contributor to the interannual variability of surface chl-*a* concentration and SST (Setiawan et al., 2020). We obtained annual SST Level 3 data between 2009 and 2019 from Moderate Resolution Imaging Spectroradiometer (MODIS) (https://oceancolor.gsfc.nasa.gov/) and plotted these using QGIS 3.22.3 (QGIS.org, 2021). Similarly, we used seasonal SST and chl-*a* distribution to examine the distribution changes of these variables every quarter between 2014 and 2016. The spatial resolution of both SST and chl-*a* was 4 km x 4 km.

3 Results

3.1 Population demographics and pregnancy rates

A total of 1,041 unique *M. alfredi* individuals were identified from 3,759 sightings recorded over 11 years of observations (2009–2019) in both Dampier Strait and SE Misool MPAs. Of these, more sightings were recorded in Dampier Strait (n = 2,580 sightings) than in SE Misool (n = 1,179 sightings). Despite this, the number of unique individuals identified was slightly higher in SE Misool (n = 536) than in Dampier Strait (n = 515), with 10 individuals recorded in both MPAs. Of these, 256 individuals (47.8%) in SE Misool and 332 individuals (64.5%) in Dampier Strait were resighted at least once.

The proportion of pregnant *M. alfredi* that were sighted and resighted in Dampier Strait, SE Misool, and both MPAs combined fluctuated over time from 2009–2019 (Figure 2). In Dampier Strait, the percentage of pregnant *M. alfredi* ranged from 0–26.9% (mean ± SD = 12.8 ± 8.7%). In SE Misool, the percentage of pregnant *M. alfredi* ranged from 3.2–41.4% (mean ± SD = 23.9 ± 12.9%) with high pregnancy rates in 2011 and 2015–2016. The lowest percentage of pregnancies were recorded in 2016 (Dampier Strait) and 2017 (SE Misool). Combining pregnancy rates in both MPAs, the rate declined after a peak in 2011 before rising sharply to the highest rate (35.1%) in 2016.

3.2 Goodness-of-fit (GOF) tests

The GOF tests on capture history data showed contrasting results between SE Misool and Dampier Strait. The overall test was not significant (χ^2_{70}= 65.462, p = 0.631) for SE Misool, but was significant (χ^2_{69}= 187.003, p < 0.001) for Dampier Strait. Further tests for Dampier Strait showed that TEST 3.SR for females was significant (χ^2_{9}= 46.682, p < 0.001, z = 5.339), and likewise TEST 3.SR for males was significant (χ^2_{9}= 30.482, p < 0.001, z = 3.357), which can be explained by the presence of transient individuals (Genovart and Pradel, 2019). This provided evidence of lack-of-fit for a standard POPAN model, which is

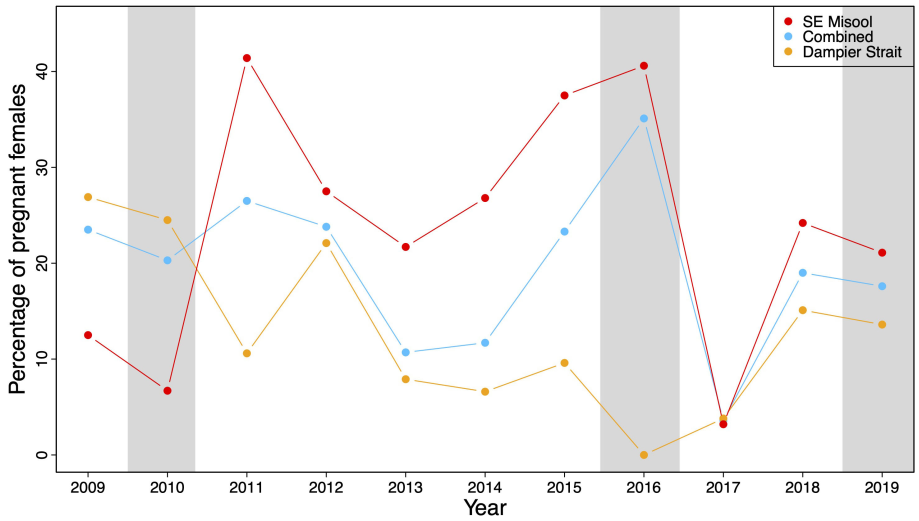

FIGURE 2
The percentage of pregnant *M. alfredi* relative to the total number of females in South East (SE) Misool (in red), Dampier Strait (in orange), and both MPAs (in blue) combined in 2009–2019. Grey shading represents three different El Niño events based on MEI.

unsurprising given that we expected the presence of transient individuals in Dampier Strait.

3.3 Population modelling

We considered models that accommodate transients for Dampier Strait MPA because the GOF tests indicated that the standard POPAN models did not fit well. Model selection did not clearly identify a single combination of covariates that was best supported by the data. For each location, we retained models with an AIC/QAIC value within 10 units of the model with the highest AIC/QAIC support, resulting a total of 33 best-fitting models for Dampier Strait and 32 best-fitting models for SE Misool. Nevertheless, all retained models estimated similar increasing population trajectories for both MPAs, with variations in several years over the study period (Supplementary Figures 3, 4).

In Dampier Strait, the annual estimated population sizes varied slightly amongst all best models (Supplementary Figure 3). Several models showed a steady increase during the study period; some showed a considerable increase in 2010–2012 followed by a slight drop in 2016. Several other models showed two declines in the estimated population size in 2011, before a sharp increase in 2012–2014, despite an overall increasing trend over time. In comparison, the population sizes in SE Misool were relatively stable or increased steadily over the study period (Supplementary Figure 4). Most models demonstrated substantial increases in 2016–2017 following the relatively stable rise in 2010–2015. Because the data did not clearly support one model over the others, we used a model-averaging procedure to calculate final estimates (Buckland et al., 2001). In the following three subsections, we report estimates obtained from the model averaging procedure described in subsection 2.3.7 (Model selection and model averaging) using the following format: point estimate (lower 95% CI limit, upper 95% CI limit).

3.4 Estimated population size

The total estimated population of females and males showed an increasing trend throughout the survey both in Dampier Strait (Figures 3A, B) and SE Misool (Figures 4A, B). In Dampier Strait, due to high uncertainty in the estimated population size in 2009 (which was likely caused by the low survey effort in that year), we did not include the estimates from 2009 when examining the population changes over time. Over the period 2010–2019, the estimated total population size increased significantly ($p = 0.018$) from 226 (161, 283) to 317 (280, 355), with a difference of 90 (18, 179) individuals over the decade. Although the percentage change in population size between years varied throughout the study, the estimated overall increase between 2010 and 2019 is the same as we would observe from a population with a compound growth of 3.9% (0.7, 8.6) per annum. A particularly steep rise occurred between 2011 and 2014, with a significant ($p = 0.012$) increase of 58 (7, 135) individuals and a compound annual growth of 8.1% (0.9, 20.5). The highest rate of change was estimated between 2013 and 2014, during which the population increased significantly ($p = 0.006$) at a rate of 11.8% (0.94, 39.3) in one year. Between sexes, there was no significant difference ($p = 0.968$) in the compound annual growth between males (4.0%; 0.7, 8.7) and females (3.9%; 0.2, 8.8) in 2010–

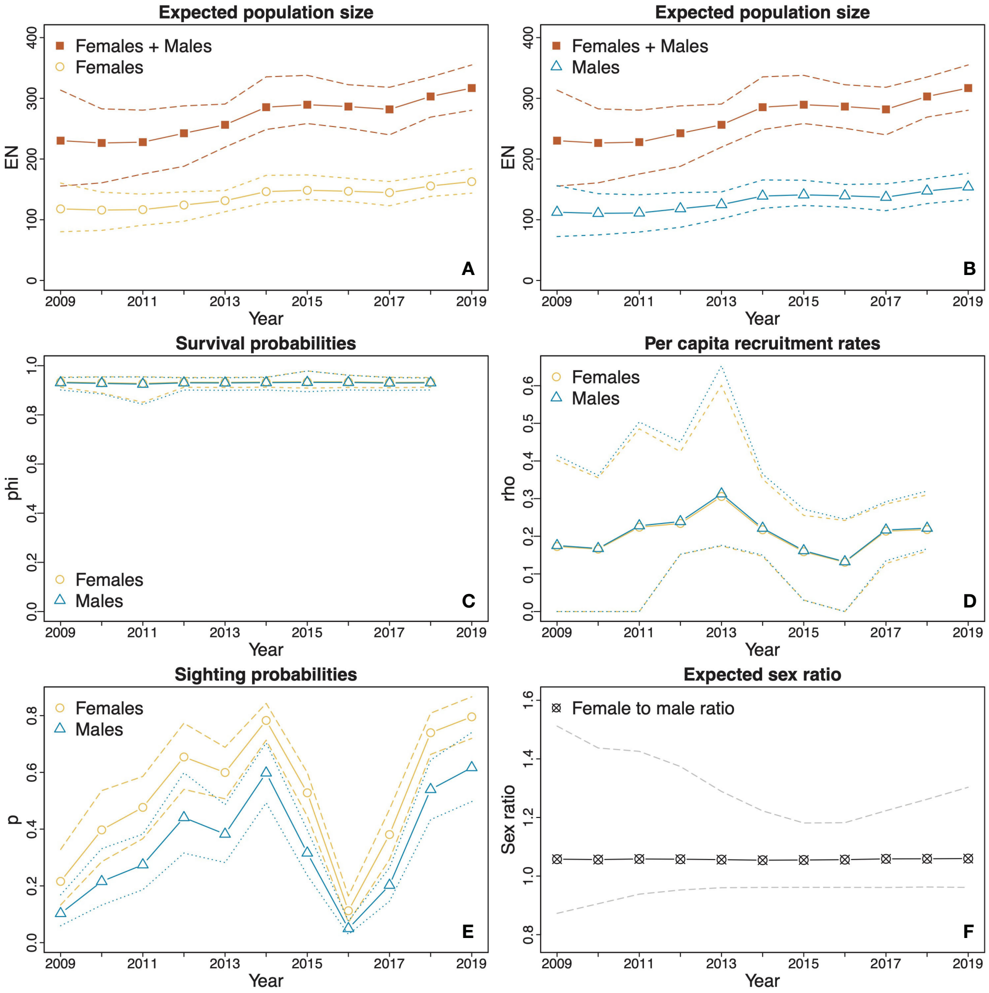

FIGURE 3
Estimates (solid lines) and CIs (dotted and dashed lines) derived from model averaging procedures for the *M. alfredi* subpopulation in the Dampier Strait MPA. (A and B) The estimated expected population sizes of females and males relative to the estimated expected overall population sizes of both sexes combined; **(C)** Survival probabilities of females and males; **(D)** Per capita recruitment rates of males and females; **(E)** Sighting probabilities of females and males; and **(F)** Expected female to male ratio. The orange lines represent female estimates, blue lines represent male estimates, and red lines represent total estimates of females and males. Black and grey lines represent sex ratio estimates (female to male). Dotted lines represent upper and lower confidence intervals.

2019. Furthermore, the mean population size of females (137 individuals; 125, 151) was not significantly ($p = 0.264$) larger than that of males (130 individuals; 114, 148), with a mean expected female to male ratio of 1.06:1 (0.96:1, 1.24:1) (Figure 3F).

In SE Misool, due to high uncertainty in the estimated population size in 2019, we did not include the estimates from 2019 when examining the population changes over time. Over the period 2009–2018, the estimated total (female and male) population size increased significantly ($p = 0.008$) from 210 (137, 308) to 511 (393, 618), with an estimated difference of 300 (139, 427) individuals over a decade. Despite variation in the percentage change in population size between years throughout the study, the estimated overall change during this period is the same as we would observe from a population with a compound annual growth of 10.7% (4.3, 16.1). A steep rise occurred between 2015 and 2017, during which the estimated population size increased significantly ($p = 0.034$) from 327 (253, 418) to 474 (390, 575) in just two years, with an estimated difference of 147 (5, 277) individuals and a compound annual growth of 21.1% (0.6, 41.8). In 2015–2017, the compound annual growth of females (30.8%, 13.7, 47.4) was higher than that of males (5.7%, -26.3, 62.4). In 2016, in particular, the estimated female population size increased at the highest rate (41.5%; 15.0, 71.7). Additionally, the estimated mean population size of females was significantly ($p < 0.001$) larger than that of males, with a difference of 111 (70, 149) individuals and a mean

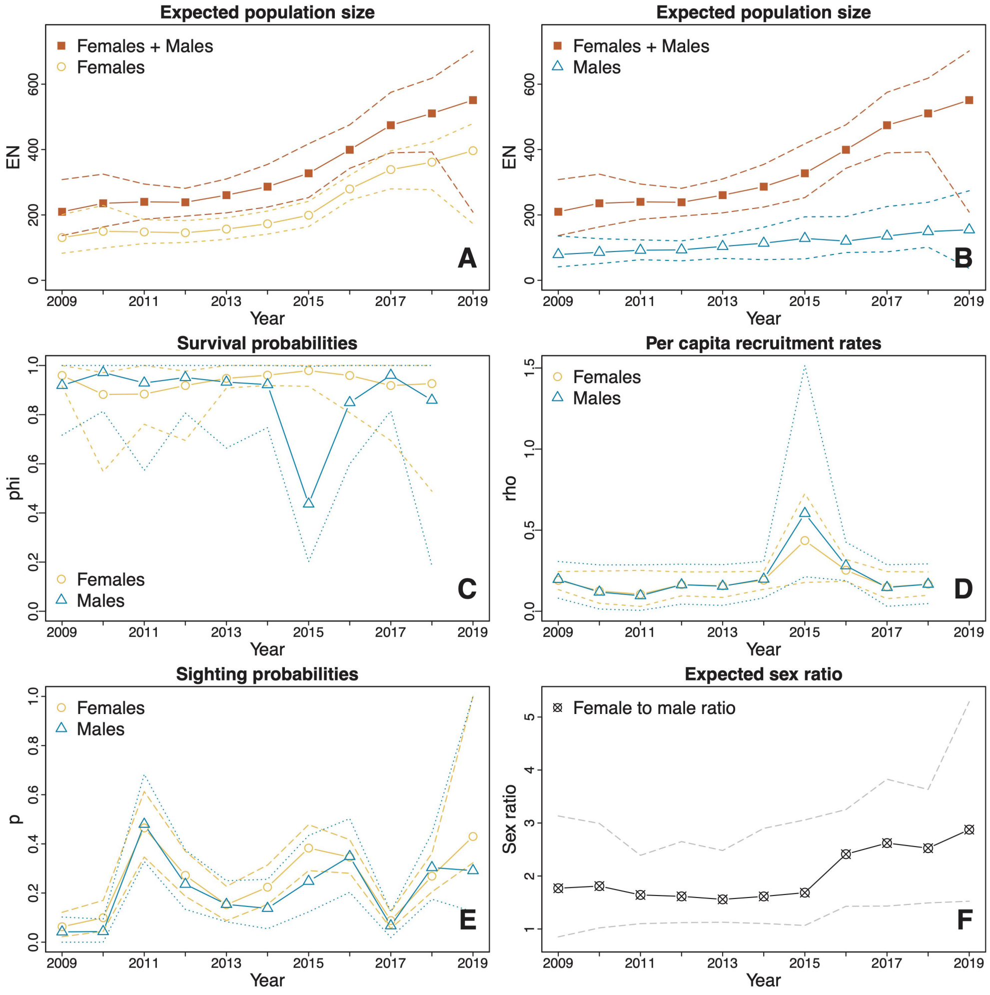

FIGURE 4
Estimates (solid lines) and CIs (dotted and dashed lines) derived from model averaging procedures for the *M. alfredi* subpopulation in the SE Misool MPA. **(A, B)** The estimated expected population sizes of females and males relative to the estimated expected overall population sizes of both sexes combined; **(C)** Survival probabilities of females and males; **(D)** Per capita recruitment rates of males and females; **(E)** Sighting probabilities of females and males; and **(F)** Expected female to male ratio. The orange lines represent female estimates, blue lines represent male estimates, and red lines represent total estimates of females and males. Black and grey lines represent sex ratio estimates (female to male). Dotted lines represent upper and lower confidence intervals.

expected female to male ratio of 2.01:1 (1:48:1, 2.59:1) (Figure 4F).

3.5 Survival probabilities and per capita recruitment rates

The estimated apparent survival probabilities in both MPAs showed no significant differences between years or sexes. In Dampier Strait, the estimated survival probabilities were similar across all years and the difference between sexes was not significant (Figure 3C). The estimated mean apparent survival probability was 0.93 (0.91, 0.95) for females and 0.93 (0.90, 0.95) for males with no significant difference between the sexes (p = 0.940). In SE Misool, the estimated mean apparent survival probability for females (0.93; 0.87, 0.97) was higher than that of males (0.87; 0.76, 0.94), however, the difference was also not significant (p = 0.216) (Figure 4C). The estimated apparent survival probability for males decreased to 0.44 (0.20, 1.00) in 2015, however, the drop was not significant as seen from the wide CI.

The estimated per capita recruitment rates in both MPAs were typically around 0.20 for both sexes (Figures 3D and 4D). There were no significant differences between years or sexes. In Dampier Strait, the estimated mean per capita recruitment rate for females was slightly higher than that of males, but the difference was not significant ($p = 0.959$). In SE Misool, the sharp increases in per capita recruitment rates in 2015 were not significant given the wide CIs.

3.6 Sighting and transient probabilities

The estimates of sighting probabilities in Dampier Strait (Figure 3E) overall were higher than those in SE Misool (Figure 4E). For both MPAs, the estimated sighting probabilities varied depending on sex and years. In Dampier Strait, the estimated mean sighting probabilities of females $\hat{p}^f = 0.52$ (0.47, 0.57) was significantly ($p < 0.001$) higher than that of males $\hat{p}^m = 0.34$ (0.28, 0.38). The sighting probabilities showed a similar trend over time, with general increase from 2009 to 2014, reaching the lowest probability in 2016 and rising again in the following years. In SE Misool, the estimated mean sighting probability of females $\hat{p}^f = 0.25$ (0.21, 0.31) was slightly higher than that of males $\hat{p}^m = 0.21$ (0.16, 0.30), but the difference was not significant ($p = 0.294$). A significant dip was estimated in 2017 for both sexes.

Transient probabilities were only estimated for Dampier Strait MPA following the GOF test results. As per the Methods subsection *POPAN models with transience*, we estimated a constant transience probability across all occasions, aside from the first occasion (2009), for which we estimated a separate probability. The estimated transience probability for the first occasion was 0.10 (0.00, 0.30) and was 0.49 (0.32, 0.63) for the remaining occasions.

4 Discussion

Over a decade during the study period, the estimates of the population size of *M. alfredi* in both the Dampier Strait and SE Misool MPAs showed increasing trends, with slightly different growth patterns between populations. In Dampier Strait, the population exhibited a significant growth in size, particularly between 2011 and 2014. In comparison, the population in SE Misool was estimated to have increased substantially after 2015. The increased estimated population size in both MPAs over a decade suggests that these are robust findings. Setyawan et al. (2020) reported a higher proportion of pregnant females in Raja Ampat than in other studied populations of *M. alfredi* across the Indo-Pacific. Despite several studies reporting biennial or longer reproductive periodicities (Marshall and Bennett, 2010; Deakos et al., 2011; Stevens, 2016), a total of 16 female *M. alfredi* in Raja Ampat were recorded with annual reproductive periodicity, including one exceptional individual which had four consecutive-year pregnancies and a total of five pregnancies confirmed in seven years. Setyawan et al. (2020; 2022b) reported four *M. alfredi* nurseries in Raja Ampat, and 65 young-of-the-year (YoY) were identified between 2011 and 2019, a number that surpasses other published studies (Marshall and Bennett, 2010; Couturier et al., 2014; Stevens, 2016; Germanov et al., 2019; Germanov et al., 2022). These findings all support the suggestions of our models that *M. alfredi* (sub)populations are growing in both Raja Ampat MPAs studied here, with high fecundity and per capita recruitment rates. Importantly, the overall rates of annual population increase estimated in our study (3.9% in Dampier Strait and 10.7% in SE Misool) match well with the theoretical rates of increase calculated by previous authors. Dulvy et al. (2014) calculated the maximum intrinsic rate of population increase (r_{max}) of manta rays, with the median r_{max} of 0.116 per year (notably, one of the lowest r_{max} of 106 species of sharks and rays examined), while Ward-Paige et al. (2013) estimated an intrinsic rate of population increase of *M. alfredi* of 5% per year.

The 2016–2017 increase in estimated population size in SE Misool, which was largely driven by females, is likely associated with favorable environmental conditions in Raja Ampat, particularly in the southern region. This coincides with the occurrence of an intense El Niño event between May 2015 and May 2016, as indicated by high positive MEI values (Supplementary Figure 2). Beale et al. (2019) showed that El Niño conditions lead to a drop in SST and an increase in wind-driven vertical mixing in SE Misool, which in turn leads to a shallowing of the thermocline and apparent increases in plankton density. With this in mind, we posit that the intense El Niño in 2016–2017 likely enhanced the environmental conditions for feeding for *M. alfredi* and therefore attracted migrants into the study area from neighboring regions or unmonitored areas in SE Misool. This can be seen from the spikes in the per capita recruitment rates estimated for both females and males in SE Misool in 2015 (Figure 4D). Among all 32 best models in SE Misool, the per capita recruitment rates in 29 models and survival probabilities in 18 models varied depending on MEI (Supplementary Table 2). Similarly, among the 33 best models in Dampier Strait, the per capita recruitment rates in 14 models and the survival probabilities in 19 models varied depending on MEI (Supplementary Table 1). Given the small number of YoY and juveniles observed in the study area, it is possible that the high per capita recruitment rates in this period may not reflect YoY individuals entering the existing study populations but are rather indicative of the immigration of adult or subadult individuals, as observed for *M. birostris* during the extreme El Niño event in 2015–2016 (Beale et al., 2019). The sharp spike of estimated per capita recruitment rates in 2015 led to the substantial increase in the estimated population size in 2016. This increase, however, only occurred with female *M. alfredi* mainly due to the drop in male survival probability regardless of the high per capita recruitment rates. One possibility is that in 2015 several males in the population left the SE Misool study area, but at the same time males immigrated from neighboring regions outside the study area. However, our estimates of per capita recruitment rate and survival probability for males in 2015 are imprecise, as indicated by their wide CIs, and so care should be taken when interpreting patterns in these estimates.

The 2015–2016 El Niño also likely led to the increase in sighting probabilities in SE Misool (Figure 4E). This extreme El Niño, combined with the southeast monsoon at a regional scale, generated upwelling-induced cooler SSTs, and high chl-*a* concentrations. These were indicative of higher-than-normal productivity (Gordon, 2005; Setiawan et al., 2020), especially in the third and last quarter of 2015 (Supplementary Figures 6, 7). Chl-*a* concentrations were positively correlated with the number of *M. alfredi* sighted (Jaine et al., 2012; Harris et al., 2020) and the high number of sightings is most likely due to increases in zooplankton density, attracting foraging aggregations (Weeks et al., 2015).

In comparison to the SE Misool population, the extreme 2015–2016 El Niño likely affected the *M. alfredi* in Dampier Strait differently. In this region, the sighting probabilities for both females and males were estimated to drop significantly in 2015 and were lowest in 2016 (Figure 3E), despite the high and stable apparent survival probabilities for both sexes. Moreover, the per capita recruitment was also estimated to be declining after reaching a peak in 2013 and was lowest in 2016 for both sexes. In 2015–2016, the relatively low sighting probabilities and per capita recruitment rates in Dampier Strait were likely driven by fewer individuals sighted due to temporary emigration to areas of high productivity to maximize foraging activities, possibly to west Waigeo Island. Setyawan et al. (2018) found that *M. alfredi* tracked using passive acoustic telemetry moved seasonally between Dampier Strait and areas in the west of Waigeo. During the second half of 2015, the west Waigeo region and southwestern Raja Ampat waters were substantially cooler than in the Dampier Strait (Figure 1; Supplementary Figure 6). During this time period, which coincided with the southeast monsoon and the extreme El Niño event, considerably fewer acoustic tagged *M. alfredi* were detected by the receiver at Manta Ridge in Dampier Strait compared to the same period in the previous year, and there were more detections on receivers located at Yefnabi Kecil and Eagle Rock in west Waigeo region, situated less than 70 km from Manta Ridge (Setyawan et al., 2018) (Figure 1).

The cooler waters and higher productivity measured in SE Misool during El Niño events likely resulted in highly abundant prey for *M. alfredi* during these periods. Based on our field observations, these periods of increased prey availability also seem to have caused more frequent and larger *M. alfredi* aggregations, leading to increases in the opportunities for mating (Setyawan et al., 2020). We hypothesize that increased pregnancy rates, in particular those in SE Misool in 2011 and 2015–2016, were likely caused by the El Niño events leading to greater foraging opportunities, better body condition and more mating opportunities in the cooler waters (Supplementary Figures 5, 6). This is supported by per capita recruitment rates and apparent survival probabilities in SE Misool that are strongly linked with MEI (Supplementary Table 2). In the same region and period, Beale et al. (2019) reported a significant increase in *M. birostris* sightings as a result of the favorable feeding conditions created by the ENSO event.

The high pregnancy rates occurred during and/or shortly after the El Niño events, with an elevated number of YoY individuals expected to enter the population approximately 1–2 years thereafter. However, only small numbers of juveniles were observed in the Dampier Strait and SE Misool, the majority of which were newly identified sub-adults or adults >2.4 m disc width (DW) (Setyawan et al., 2020). This apparent lack of YoY individuals in the study areas following periods of high pregnancy rates is perhaps not surprising. As observed in other countries (Couturier et al., 2014; Stevens, 2016; Peel, 2019), primary *M. alfredi* feeding and cleaning sites such as those in Dampier Strait and SE Misool tend to be dominated by adults, while YoY and juvenile individuals are generally believed to occupy nursery areas, where they are assumed to have a reduced risk of predation, until they are large enough to join adult aggregations (Marshall and Bennett, 2010; Heupel et al., 2019). With this in mind, we hypothesize that the expected high number of YoY manta rays following these periods of high pregnancy rates were most probably born and remained in nursery areas adjacent to Dampier Strait and SE Misool. For example, many juveniles <2.4 m DW have been observed in Yefnabi Kecil (Figure 1) in West Waigeo (Setyawan et al., 2022c), while three other nursery habitats have been identified in areas adjacent to the Dampier Strait, with juvenile residency periods up to 28 months (Setyawan et al., 2020). Despite being further away from Dampier Strait and SE Misool, the best studied manta ray nursery in Raja Ampat, the Wayag lagoon nursery (Setyawan et al., 2022b), may also have hosted a number of the YoY expected after the high pregnancy rates seen during El Niño events. Indeed, Setyawan et al. (2020) also documented the movement of a YoY first identified in the Wayag lagoon nursery as a 1.8 m DW male and then resighted six years later as a 2.6 m DW young adult male in SE Misool, 296 km south of the nursery.

As the 2015–2016 El Niño event ceased, the environmental conditions changed and a La Niña event ensued from mid 2016 until early 2018, indicated by negative MEI values in that time period. This may be associated with decreases in the sighting probabilities in 2017 and gradual declines in per capita recruitment rates between 2016 and 2017 in SE Misool, slightly slowing the rate of increase of the population towards the end of the study period. In Dampier Strait, the situation was reversed, where the per capita recruitment rates and also the sighting probabilities increased in 2017 and 2018. During the La Niña event, the surface waters in southern (around Misool) and western Raja Ampat (West Waigeo) were relatively warmer and less productive (Setiawan et al., 2020), and hence less favorable to manta ray feeding. A decrease in the amount of food might lead to two different possible scenarios. First, fewer individuals immigrated to the study area in SE Misool from neighboring regions, therefore the per capita recruitment rates declined. At the same period, more individuals immigrated into the study area in the Dampier Strait from neighboring regions in western Raja Ampat. Second, Chapman et al. (2012) highlights that partial migration is extremely common in fishes, in which some individuals in the population are residents and some are migratory. Andrzejaczek et al. (2020) suggested that *M. alfredi* may be partial migrants, from which we might conclude that resident individuals in SE Misool and West Waigeo stayed and exploited deeper water to forage, while migratory individuals left these areas to forage in more productive areas around Raja Ampat, including the Dampier Strait.

The high apparent survival probabilities of non-transient female and male *M. alfredi* in both MPAs implies a relatively low rate of individual mortality, or a low rate of permanent emigration from the core study areas, or likely a combination of both. The low rates of mortality and permanent emigration are reflected in the high frequency of resighting, with several individuals sighted regularly over periods of more than ten years. Setyawan et al. (2020) reported that 46% of the *M. alfredi* identified were resighted at least once after they were first sighted, with some individuals resighted up to 13 years later. High apparent survival was also reported from eastern Australia (Couturier et al., 2014) and Hawaii (Deakos et al., 2011), where *M. alfredi* showed strong site fidelity to aggregation sites and targeted fisheries were absent. By comparison, *M. alfredi* in Mozambique were targeted in subsistence fisheries (O'Malley et al., 2017), and the population showed a decreasing trend in annual estimated apparent survival from 0.76 to 0.65 over 15 years (2003–2018), suggesting high mortality associated with continuing pressure from targeted fisheries and insufficient conservation efforts to protect the population (Rohner et al., 2013; Venables, 2020). Increasing fishing pressure is responsible for major global declines in oceanic shark and ray populations in the last five decades (Dulvy et al., 2021; Pacoureau et al., 2021). *M. alfredi* is a long-lived and late-maturing species that only becomes sexually mature at 11 (males) and 15 years (females) of age (Stevens, 2016); therefore, a high survival probability over a long period of time is required to ensure that populations persist and continue to thrive (Kanive et al., 2015).

Overall, the estimated sighting probabilities were higher in Dampier Strait than in SE Misool, which likely reflects the higher survey effort and substantially larger amount of sightings data collected in Dampier Strait than in SE Misool. The estimated sighting probabilities for females were in general higher than those for males, in particular in Dampier Strait. This is likely because most *M. alfredi* sightings collected in both MPAs were from cleaning sites, and females, especially adults, visit cleaning sites more frequently than males (Couturier et al., 2014; Stevens, 2016; Perryman et al., 2019). Indeed, the majority of the 20 most-sighted individuals in Raja Ampat were females (Setyawan et al., 2020).

Using TEST 3.SR, we found evidence to suggest that new individuals sighted for the first time had a lower probability of being resighted in comparison with individuals that had been sighted previously, and the presence of transient individuals is one explanation for this effect (Genovart and Pradel, 2019). Using our model, we estimated that approximately half of individuals (0.49; 95% CI: 0.32, 0.63) recruited to the population in Dampier Strait were transients. Transience might be higher in wide-ranging species capable of travelling long distances (Armstrong et al., 2019) and in large aggregations (Setyawan et al., 2020), thereby increasing the challenge of photo-identifying all individuals. Future studies using long-term photo-ID and incorporating photos from other regions may reveal the transient individuals as permanent or temporary migrants (Hupman et al., 2018). Our modification of the standard POPAN model by incorporating per capita recruitment and transience parameters represents an important advance in mark-recapture modelling that should prove useful when examining other manta ray populations and other highly migratory species that are likely to have a significant percentage of transient individuals.

Science-based management, MPA enforcement, and protection of aggregation sites and critical habitats (e.g., nursery areas) are each considered critical to ensure the recovery of elasmobranch populations (Ward-Paige et al., 2013). The adoption of each of these components in a holistic approach to manta ray conservation and management by the Raja Ampat MPA Management Authority likely helps explain the significant population increase reported in our study (Setyawan et al., 2022a). These management measures were responsible for effectively forcing shark fishers to relocate to areas outside Raja Ampat or change their livelihoods (Jaiteh et al., 2016). While limited shark fishing (and the resulting potential for manta ray bycatch) undoubtedly still occurs in the more remote and unpatrolled areas outside of Raja Ampat's MPA boundaries, almost all known manta ray aggregation sites and all known nurseries are located within the actively-patrolled MPA network – suggesting that Raja Ampat's *M. alfredi* are indeed well-protected (Setyawan et al., 2020). By contrast, the reef regions in closest proximity to Raja Ampat (including Halmahera to the west and Seram to the south) both host local populations of manta rays, but they are currently not protected by MPAs. *M. alfredi* in Raja Ampat exhibit a strong pattern of residency, likely due to the year-round presence of reliable and abundant food sources precluding any need to risk crossing the deep-water barriers to these adjacent islands and reef systems (Setyawan et al., 2018; Setyawan et al., 2020). As such, while occasional movements to unprotected reef areas are certainly possible, we suggest that the current MPA network and associated manta ray protection measures in Raja Ampat (Setyawan et al., 2022a) are seemingly sufficient to ensure this population is both protected and in fact actively growing. Viewed in the context of the Pacoureau et al. (2021) report of a major global decline in oceanic shark and ray populations (including *M. alfredi*) over the last five decades, primarily due to increasing fishing pressure, the reverse situation in Raja Ampat provides a reason for optimism when a holistic approach is adopted for elasmobranch conservation initiatives. This study also underlines the importance of long-term monitoring to evaluate the effectiveness of conservation management measures on *M. alfredi* populations.

5 Conclusions

We found strong evidence that the populations of *M. alfredi* in both the Dampier Strait and SE Misool MPAs in the Raja Ampat archipelago have increased significantly over our decade-long study period. Our results suggest that the series of conservation and management measures implemented in Raja Ampat since 2007 (Setyawan et al., 2022a), including the creation and enforcement of a large-scale network of nine MPAs, the designation of Southeast Asia's first shark and ray sanctuary, a national manta ray protection regulation, and the formulation of gear restrictions and manta tourism regulations in Raja Ampat MPAs, have substantially reduced fisheries-related pressures on the *M. alfredi* populations there. Coupled with El Niño–Southern Oscillation events that are strongly associated with increased per capita recruitment rates and high apparent survival probabilities, all these factors have enabled the *M. alfredi* (sub)populations in the Dampier Strait and SE Misool MPAs to thrive. Finally, we made substantial advances in the use of POPAN models to estimate the population size of large migratory species like manta rays by incorporating transience and per capita recruitment parameters.

Data availability statement

The datasets presented in this study can be found in the https://github.com/b-steve/manta-popan]. Further inquiries can be directed to the corresponding author.

Ethics statement

The animal study was reviewed and approved by The University of Auckland Animal Ethics Committee.

Author contributions

ES, BS, RC, ME conceived the ideas and conceptualization. ES, RM, AH, AS, IM, OA, MI, and MP collected the data. ES curated the data. ES, BS, RF, and RA-S performed the statistical analysis. ES created figures, tables, and map with guidance from BS. ES, BS, RC, ME drafted the manuscript. ME, RC, and BS provided guidance and supervision, reviewed, and edited drafts 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.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.1014791/full#supplementary-material

References

Andrzejaczek, S., Chapple, T. K., Curnick, D. J., Carlisle, A. B., Castleton, M., Jacoby, D. M., et al. (2020). Individual variation in residency and regional movements of reef manta rays *Mobula alfredi* in a large marine protected area. *Mar. Ecol. Prog. Ser.* 639. doi: 10.3389/fmars.2020.00558

Armstrong, A. O., Armstrong, A. J., Bennett, M. B., Richardson, A. J., Townsend, K. A., and Dudgeon, C. L. (2019). Photographic identification and citizen science combine to reveal long distance movements of individual reef manta rays *Mobula alfredi* along Australia's east coast. *Mar. Biodivers. Rec.* 12 (1), 14. doi: 10.1186/s41200-019-0173-6

Armstrong, A. J., Armstrong, A. O., McGregor, F., Richardson, A. J., Bennett, M. B., Townsend, K. A., et al. (2020). Satellite tagging and photographic identification reveal connectivity between two UNESCO world heritage areas for reef manta rays. *Front. Mar. Sci.* 7. doi: 10.3389/fmars.2020.00725

Beale, C. S., Stewart, J. D., Setyawan, E., Sianipar, A. B., and Erdmann, M. V. (2019). Population dynamics of oceanic manta rays (*Mobula birostris*) in the Raja Ampat archipelago, West Papua, Indonesia, and the impacts of the El Niño-Southern Oscillation on their movement ecology. *Divers. Distrib.* 25, 1472–1487. doi: 10.1111/ddi.12962

Beissinger, S. R., and Westphal, M. I. (1998). On the use of demographic models of population viability in endangered species management. *J. Wildl. Manage.* 62, 821–841. doi: 10.2307/3802534

Boys, R. M., Oliveira, C., Pérez-Jorge, S., Prieto, R., Steiner, L., and Silva, M. A. (2019). Multi-state open robust design applied to opportunistic data reveals dynamics of wide-ranging taxa: the sperm whale case. *Ecosphere* 10 (3), e02610. doi: 10.1002/ecs2.2610

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L., and Thomas, L. (2001). *Introduction to distance sampling: estimating abundance of biological populations* (United Kingdom: Oxford University Press).

Carroll, E., Childerhouse, S., Fewster, R., Patenaude, N., Steel, D., Dunshea, G., et al. (2013). Accounting for female reproductive cycles in a superpopulation capture–recapture framework. *Ecol. Appl.* 23 (7), 1677–1690. doi: 10.1890/12-1657.1

Chapman, B., Skov, C., Hulthén, K., Brodersen, J., Nilsson, P. A., Hansson, L. A., et al. (2012). Partial migration in fishes: definitions, methodologies and taxonomic distribution. *J. Fish Biol.* 81 (2), 479–499. doi: 10.1111/j.1095-8649.2012.03349.x

Cooch, E., and White, G. (2001). “"Goodness of fit testing…",” in *Program MARK: A gentle introduction*, 1–36. (Colorado, USA: Colorado State University).

Couturier, L. I. E., Dudgeon, C. L., Pollock, K. H., Jaine, F. R. A., Bennett, M. B., Townsend, K. A., et al. (2014). Population dynamics of the reef manta ray *Manta alfredi* in eastern Australia. *Coral Reefs* 33 (2), 329–342. doi: 10.1007/s00338-014-1126-5

Couturier, L. I. E., Jaine, F. R. A., Townsend, K. A., Weeks, S. J., Richardson, A. J., and Bennett, M. B. (2011). Distribution, site affinity and regional movements of the manta ray, *Manta alfredi* (Krefft, 1868), along the east coast of Australia. *Mar. Freshwat. Res.* 62 (6), 628–637. doi: 10.1071/MF10148

Croll, D. A., Dewar, H., Dulvy, N. K., Fernando, D., Francis, M. P., Galván-Magaña, F., et al. (2015). Vulnerabilities and fisheries impacts: the uncertain future of manta and devil rays. *Aquat. Conserv.: Mar. Freshwat. Ecosyst.* 26 (3), 562–575. doi: 10.1002/aqc.2591

Davies, T. K., Stevens, G., Meekan, M. G., Struve, J., and Rowcliffe, J. M. (2012). Can citizen science monitor whale-shark aggregations? investigating bias in mark–recapture modelling using identification photographs sourced from the public. *Wildlife Res.* 39 (8), 696–704. doi: 10.1071/WR12092

Deakos, M. H., Baker, J. D., and Bejder, L. (2011). Characteristics of a manta ray *Manta alfredi* population off Maui, Hawaii, and implications for management. *Mar. Ecol. Prog. Ser.* 429, 245–260. doi: 10.3354/MEPS09085

Dewar, H., Mous, P., Domeier, M., Muljadi, A., Pet, J., and Whitty, J. (2008). Movements and site fidelity of the giant manta ray, *Manta birostris*, in the Komodo Marine Park, Indonesia. *Mar. Biol.* 155 (2), 121–133. doi: 10.1007/s00227-008-0988-x

Dudgeon, C. L., Noad, M. J., and Lanyon, J. M. (2008). Abundance and demography of a seasonal aggregation of zebra sharks stegostoma fasciatum. *Mar. Ecol. Prog. Ser.* 368, 269–281. doi: 10.3354/meps07581

Dulvy, N. K., Pacoureau, N., Rigby, C. L., Pollom, R. A., Jabado, R. W., Ebert, D. A., et al. (2021). Overfishing drives over one-third of all sharks and rays toward a global extinction crisis. *Curr. Biol.* 31, 4773–4787. doi: 10.1016/j.cub.2021.08.062

Dulvy, N. K., Pardo, S. A., Simpfendorfer, C. A., and Carlson, J. K. (2014). Diagnosing the dangerous demography of manta rays using life history theory. *PeerJ* 2, e400. doi: 10.7717/peerj.400

Edgar, G. J., Stuart-Smith, R. D., Willis, T. J., Kininmonth, S., Baker, S. C., Banks, S., et al. (2014). Global conservation outcomes depend on marine protected areas with five key features. *Nature* 506 (7487), 216–220. doi: 10.1038/nature13022

Gell, F. R., and Roberts, C. M. (2003). Benefits beyond boundaries: the fishery effects of marine reserves. *Trends Ecol. Evol.* 18 (9), 448–455. doi: 10.1016/S0169-5347(03)00189-7

Genovart, M., and Pradel, R. (2019). Transience effect in capture-recapture studies: The importance of its biological meaning. *PloS One* 14 (9), e0222241. doi: 10.1371/journal.pone.0222241

Germanov, E. S., Bejder, L., Chabanne, D. B., Dharmadi, D., Hendrawan, I. G., Marshall, A. D., et al. (2019). Contrasting habitat use and population dynamics of reef manta rays within the Nusa Penida marine protected area, Indonesia. *Front. Mar. Sci.* 6. doi: 10.3389/fmars.2019.00215

Germanov, E. S., Pierce, S. J., Marshall, A. D., Hendrawan, I. G., Kefi, A., Bejder, L., et al. (2022). Residency, movement patterns, behavior and demographics of reef manta rays in Komodo National Park. *PeerJ* 10, e13302. doi: 10.7717/peerj.13302

Gimenez, O., Lebreton, J.-D., Choquet, R., and Pradel, R. (2018). R2ucare: An R package to perform goodness-of-fit tests for capture-recapture models. *Methods Ecol. Evol* 9, 1749–54. doi: 10.1111/2041-210X.13014

Gordon, A. L. (2005). Oceanography of the Indonesian seas and their throughflow. *Oceanography* 18 (4), 14–27. doi: 10.5670/oceanog.2005.01

Graham, R. T., and Roberts, C. M. (2007). Assessing the size, growth rate and structure of a seasonal population of whale sharks (*Rhincodon typus* Smith 1828) using conventional tagging and photo identification. *Fish. Res.* 84 (1), 71–80. doi: 10.1016/j.fishres.2006.11.026

Graham, N. A., Spalding, M. D., and Sheppard, C. R. (2010). Reef shark declines in remote atolls highlight the need for multi-faceted conservation action. *Aquat. Conserv.: Mar. Freshwat. Ecosyst.* 20 (5), 543–548. doi: 10.1002/aqc.1116

Harris, J. L., McGregor, P. K., Oates, Y., and Stevens, G. M. (2020). Gone with the wind: Seasonal distribution and habitat use by the reef manta ray (*Mobula alfredi*) in the Maldives, implications for conservation. *Aquat. Conserv.: Mar. Freshwat. Ecosyst*. doi: 10.1002/aqc.3350

Heinrichs, S., O'Malley, M., Medd, H., and Hilton, P. (2011). *The Global Threat to Manta and Mobula Rays.* (USA: Manta Ray of Hope).

Heupel, M. R., Kanno, S., Martins, A. P., and Simpfendorfer, C. A. (2019). Advances in understanding the roles and benefits of nursery areas for elasmobranch populations. *Mar. Freshwat. Res.* 70 (7), 897–907. doi: 10.1071/MF18081

Holmberg, J., Norman, B., and Arzoumanian, Z. (2009). Estimating population size, structure, and residency time for whale sharks *Rhincodon typus* through collaborative photo-identification. *Endanger. Species Res.* 7 (1), 39–53. doi: 10.3354/esr00186

Hupman, K., Stockin, K. A., Pollock, K., Pawley, M. D. M., Dwyer, S. L., Lea, C., et al. (2018). Challenges of implementing mark-recapture studies on poorly marked gregarious delphinids. *PloS One* 13 (7), e0198167. doi: 10.1371/journal.pone.0198167

Jacoby, D. M., Ferretti, F., Freeman, R., Carlisle, A. B., Chapple, T. K., Curnick, D. J., et al. (2020). Shark movement strategies influence poaching risk and can guide enforcement decisions in a large, remote marine protected area. *J. Appl. Ecol.* 57 (9), 1782–1792. doi: 10.1111/1365-2664.13654

Jaine, F. R., Couturier, L. I., Weeks, S. J., Townsend, K. A., Bennett, M. B., Fiora, K., et al. (2012). When giants turn up: sighting trends, environmental influences and habitat use of the manta ray *Manta alfredi* at a coral reef. *PloS One* 7 (10), e46170. doi: 10.1371/journal.pone.0046170

Jaine, F., Rohner, C., Weeks, S., Couturier, L., Bennett, M., Townsend, K., et al. (2014). Movements and habitat use of reef manta rays off eastern Australia: Offshore excursions, deep diving and eddy affinity revealed by satellite telemetry. *Mar. Ecol. Prog. Ser.* 510, 73–86. doi: 10.3354/meps10910

Jaiteh, V. F., Lindfield, S. J., Mangubhai, S., Warren, C., Fitzpatrick, B., and Loneragan, N. R. (2016). Higher abundance of marine predators and changes in fishers' behavior following spatial protection within the world's biggest shark fishery. *Front. Mar. Sci.* 3. doi: 10.3389/fmars.2016.00043

Kanive, P. E., Rotella, J. J., Jorgensen, S. J., Chapple, T. K., Anderson, S. D., Klimley, A. P., et al. (2015). Estimating apparent survival of sub-adult and adult white sharks (*Carcharodon carcharias*) in central California using mark-recapture methods. *Front. Mar. Sci* 2 (19). doi: 10.3389/fmars.2015.00019

Kitchen-Wheeler, A., Ari, C., and Edwards, A. J. (2011). Population estimates of Alfred mantas (*Manta alfredi*) in central Maldives atolls: North Male, Ari and Baa. *Environ. Biol. Fishes* 93 (4), 557–575. doi: 10.1007/s10641-011-9950-8

Knip, D. M., Heupel, M. R., and Simpfendorfer, C. A. (2012). Evaluating marine protected areas for the conservation of tropical coastal sharks. *Biol. Conserv.* 148 (1), 200–209. doi: 10.1016/j.biocon.2012.01.008

Lewis, S. A., Setiasih, N., Dharmadi, D., O'Malley, M. P., Campbell, S. J., Yusuf, M., et al. (2015). Assessing Indonesian manta and devil ray populations through historical landings and fishing community interviews. *PeerJ Preprints* 6, e1334v1. doi: 10.7287/peerj.preprints.1334v1

Magson, K., Monacella, E., Scott, C., Buffat, N., Arunrugstichai, S., Chuangcharoendee, M., et al. (2022). Citizen science reveals the population structure and seasonal presence of whale sharks in the Gulf of Thailand. *J. Fish Biol* 3, 540–549. doi: 10.1111/jfb.15121

Mangubhai, S., Erdmann, M. V., Wilson, J. R., Huffard, C. L., Ballamu, F., Hidayat, N. I., et al. (2012). Papuan Bird's Head Seascape: Emerging threats and challenges in the global center of marine biodiversity. *Mar. pollut. Bull.* 64 (11), 2279–2295. doi: 10.1016/j.marpolbul.2012.07.024

Marshall, A., Barreto, R., Carlson, J., Fernando, D., Fordham, S., Francis, M. P., et al. (2019) *Mobula alfredi. the IUCN red list of threatened species 2019: e.T195459A68632178*. Available at: https://dx.doi.org/10.2305/IUCN.UK.2019-3.RLTS.T195459A68632178.en (Accessed 09 April 2021).

Marshall, A. D., and Bennett, M. B. (2010). Reproductive ecology of the reef manta ray *Manta alfredi* in southern Mozambique. *J. Fish Biol.* 77 (1), 169–190. doi: 10.1111/j.1095-8649.2010.02669.x

Marshall, A. D., Compagno, L. J., and Bennett, M. B. (2009). Redescription of the *Genus manta* with resurrection of *Manta alfredi* (Krefft 1868) (Chondrichthyes; Myliobatoidei; Mobulidae). *Zootaxa* 2301, 1–28. doi: 10.11646/ZOOTAXA.2301.1.1

Marshall, A. D., Dudgeon, C., and Bennett, M. (2011). Size and structure of a photographically identified population of manta rays *Manta alfredi* in southern Mozambique. *Mar. Biol.* 158 (5), 1111–1124. doi: 10.1007/s00227-011-1634-6

Marshall, A. D., and Pierce, S. J. (2012). The use and abuse of photographic identification in sharks and rays. *J. Fish Biol.* 80 (5), 1361–1379. doi: 10.1111/j.1095-8649.2012.03244.x

McKinney, J. A., Hoffmayer, E. R., Holmberg, J., Graham, R. T., Driggers, W. B.III, de la Parra-Venegas, R., et al. (2017). Long-term assessment of whale shark population demography and connectivity using photo-identification in the Western Atlantic ocean. *PloS One* 12 (8), e0180495. doi: 10.1371/journal.pone.0180495

Meekan, M. G., Bradshaw, C. J., Press, M., McLean, C., Richards, A., Quasnichka, S., et al. (2006). Population size and structure of whale sharks *Rhincodon typus* at ningaloo reef, Western Australia. *Mar. Ecol. Prog. Ser.* 319, 275–285. doi: 10.3354/meps319275

Norris, K. (2004). Managing threatened species: the ecological toolbox, evolutionary theory and declining-population paradigm. *J. Appl. Ecol.* 41 (3), 413–426. doi: 10.1111/j.0021-8901.2004.00910.x

O'Malley, M. P., Townsend, K. A., Hilton, P., Heinrichs, S., and Stewart, J. D. (2017). Characterization of the trade in manta and devil ray gill plates in China and South-east Asia through trader surveys. *Aquat. Conserv.: Mar. Freshwat. Ecosyst.* 27 (2), 394–413. doi: 10.1002/aqc.2670

O'Malley, M. P., Lee-Brooks, K., and Medd, H. B. (2013). The global economic impact of manta ray watching tourism. *PloS One* 8 (5), e65051. doi: 10.1371/journal.pone.0065051

Pacoureau, N., Rigby, C. L., Kyne, P. M., Sherley, R. B., Winker, H., Carlson, J. K., et al. (2021). Half a century of global decline in oceanic sharks and rays. *Nature* 589 (7843), 567–571. doi: 10.1038/s41586-020-03173-9

Peel, L. R. (2019). *Movement patterns and feeding ecology of the reef manta ray (*Mobula alfredi*) in Seychelles* (University of Western Australia, Perth, Australia: PhD Dissertation).

Peel, L. R., Stevens, G. M. W., Daly, R., Daly, C. A. K., Lea, J. S. E., Clarke, C. R., et al. (2019). Movement and residency patterns of reef manta rays *Mobula alfredi* in the Amirante Islands, Seychelles. *Mar. Ecol. Prog. Ser.* 621, 169–184. doi: 10.3354/meps12995

Perryman, R. J., Venables, S. K., Tapilatu, R. F., Marshall, A. D., Brown, C., and Franks, D. W. (2019). Social preferences and network structure in a population of reef manta rays. *Behav. Ecol. Sociobiol.* 73 (8), 114. doi: 10.1007/s00265-019-2720-x

PISCO (2007). *The science of marine reserves, 2nd Edition.*(California and Oregon, USA: Oregon State University; University of California Santa Barbara; University of California Santa Cruz; and Stanford University).

Pradel, R., Hines, J. E., Lebreton, J.-D., and Nichols, J. D. (1997). Capture-recapture survival models taking account of transients. *Biometrics* 53, 60–72. doi: 10.2307/2533097

QGIS.org (2021)QGIS geographic information system. QGIS association. In: . Available at: https://www.qgis.org/.

R Core Team (2021). "*R: A language and environment for statistical computing*," (Vienna, Austria: R Foundation for Statistical Computing). Available at: http://www.R-project.org/.

Robinson, O. J., Ruiz-Gutierrez, V., Fink, D., Meese, R. J., Holyoak, M., and Cooch, E. G. (2018). Using citizen science data in integrated population models to inform conservation. *Biol. Conserv.* 227, 361–368. doi: 10.1016/j.biocon.2018.10.002

Rohner, C. A., Flam, A. L., Pierce, S. J., and Marshall, A. D. (2017). Steep declines in sightings of manta rays and devilrays (Mobulidae) in southern Mozambique. *PeerJ PrePrints* doi: 10.7287/peerj.preprints.3051v1

Rohner, C., Pierce, S., Marshall, A., Weeks, S., Bennett, M., and Richardson, A. (2013). Trends in sightings and environmental influences on a coastal aggregation of manta rays and whale sharks. *Mar. Ecol. Prog. Ser.* 482, 153–168. doi: 10.3354/meps10290

Schwarz, C. J., and Arnason, A. N. (1996). A general methodology for the analysis of capture-recapture experiments in open populations. *Biometrics* 52, 860–873. doi: 10.2307/2533048

Setiawan, R., Wirasatriya, A., Hernawan, U., Leung, S., and Iskandar, I. (2020). Spatio-temporal variability of surface chlorophyll-a in the halmahera Sea and its relation to ENSO and the Indian ocean dipole. *Int. J. Remote Sens.* 41 (1), 284–299. doi: 10.1080/01431161.2019.1641244

Setyawan, E., Erdmann, M. V., Gunadharma, N., Gunawan, T., Hasan, A. W., Izuan, M., et al. (2022a). A holistic approach to manta ray conservation in the Papuan Bird's Head Seascape: Resounding success, ongoing challenges. *Mar. Policy* 137, 104953. doi: 10.1016/j.marpol.2021.104953

Setyawan, E., Erdmann, M. V., Lewis, S. A., Mambrasar, R., Hasan, A. W., Templeton, S., et al. (2020). Natural history of manta rays in the bird's head seascape, Indonesia, with an analysis of the demography and spatial ecology of *Mobula alfredi* (Elasmobranchii: Mobulidae). *J. Ocean Sci. Found.* 36, 49–83. doi: 10.5281/zenodo.4396260

Setyawan, E., Erdmann, M. V., Mambrasar, R., Hasan, A. W., Sianipar, A. B., Constantine, R., et al. (2022b). Residency and use of an important nursery habitat, Raja Ampat's Wayag Lagoon, by juvenile reef manta rays (*Mobula alfredi*). *Front. Mar. Sci.* 9. doi: 10.3389/fmars.2022.815094

Setyawan, E., Sianipar, A. B., Erdmann, M. V., Fischer, A. M., Haddy, J. A., Beale, C. S., et al. (2018). Site fidelity and movement patterns of reef manta rays (*Mobula alfredi*: Mobulidae) using passive acoustic telemetry in northern Raja Ampat, Indonesia. *Nat. Conserv. Res.* 3 (4), 17–31. doi: 10.24189/ncr.2018.043

Setyawan, E., Stevenson, B. C., Izuan, M., Constantine, R., and Erdmann, M. V. (2022c). How big is that Manta ray? A novel and non-invasive method for measuring reef manta rays using small drones. *Drones* 6 (3), 63. doi: 10.3390/drones6030063

Snider, S., and Brimlow, J. (2013). An introduction to population growth. *Nat. Educ. Knowledge* 4 (4), 3.

Speed, C. W., Cappo, M., and Meekan, M. G. (2018). Evidence for rapid recovery of shark populations within a coral reef marine protected area. *Biol. Conserv.* 220, 308–319. doi: 10.1016/j.biocon.2018.01.010

Stevens, G. M. W. (2016). *Conservation and population ecology of manta rays in the Maldives* (University of York: PhD Dissertation).

Stevens, G. M. W., Hawkins, J. P., and Roberts, C. M. (2018). Courtship and mating behaviour of manta rays *Mobula alfredi* and *M. birostris* in the Maldives. *J. Fish Biol.* 93 (2), 344–359. doi: 10.1111/jfb.13768

Towner, A. V., Wcisel, M. A., Reisinger, R. R., Edwards, D., and Jewell, O. J. (2013). Gauging the threat: the first population estimate for white sharks in South Africa using photo identification and automated software. *PloS One* 8 (6), e66035. doi: 10.1371/journal.pone.0066035

Varkey, D. A., Ainsworth, C. H., Pitcher, T. J., Goram, Y., and Sumaila, R. (2010). Illegal, unreported and unregulated fisheries catch in Raja Ampat Regency, Eastern Indonesia. *Mar. Policy* 34 (2), 228–236. doi: 10.1016/j.marpol.2009.06.009

Venables, S. K. (2020). *Ecology and conservation of a threatened reef manta ray (*Mobula alfredi*) population in southern Mozambique* (The University of Western Australia, Perth, Australia: PhD Dissertation).

Ward-Paige, C. A., Davis, B., and Worm, B. (2013). Global population trends and human use patterns of *Manta* and *Mobula* rays. *PloS One* 8 (9), e74835. doi: 10.1371/journal.pone.0074835

Weeks, S. J., Magno-Canto, M. M., Jaine, F. R. A., Brodie, J., and Richardson, A. J. (2015). Unique sequence of events triggers manta ray feeding frenzy in the Southern Great Barrier Reef, Australia. *Remote Sens.* 7 (3), 3138–3152. doi: 10.3390/rs70303138

Williams, K. A., Frederick, P. C., and Nichols, J. D. (2011). Use of the superpopulation approach to estimate breeding population size: an example in asynchronously breeding birds. *Ecology* 92 (4), 821–828. doi: 10.1890/10-0137.1

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EDITED BY
Lars Bejder,
University of Hawaii at Manoa,
United States

REVIEWED BY
Massimiliano Rosso,
CIMA Research Foundation, Italy
Bruno Díaz López,
Bottlenose Dolphin Research Institute
(BDRI), Spain

*CORRESPONDENCE
Rita Ferreira
rita.ferreira@mare-centre.pt

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Unraveling site fidelity and residency patterns of sperm whales in the insular oceanic waters of Macaronesia

Rita Ferreira[1,2*], Lisa Steiner[3], Vidal Martín[4], Francesca Fusar Poli[4], Ana Dinis[1], Manfred Kaufmann[2,5], Marc Fernandez[1,6] and Filipe Alves[1]

[1]MARE – Marine and Environmental Sciences Centre/ARNET - Aquatic Research Network, Agência Regional para o Desenvolvimento da Investigação Tecnologia e Inovação (ARDITI), Funchal, Madeira, Portugal, [2]Marine Biology Station of Funchal, Faculty of Life Sciences, University of Madeira, Madeira, Portugal, [3]Whale Watch Azores, Horta, Azores, Portugal, [4]Canary Islands Cetaceans Research Centre, Society for the Study of Cetaceans in the Canary Archipelago (SECAC), Lanzarote, Canary Islands, Spain, [5]CIIMAR-Interdisciplinary Centre of Marine and Environmental Research of the University of Porto, Matosinhos, Portugal, [6]cE3c/Azorean Biodiversity Group, Departamento de Biologia, Faculdade de Ciências e Tecnologia, Universidade dos Açores, Ponta Delgada, Portugal

Knowledge of the distribution and residency of pelagic marine megafauna, particularly deep-diving species, is scarce due to their high mobility over difficult-to-access oceanic areas and long periods underwater. However, the threatened status of many of these species, such as the sperm whale *Physeter macrocephalus*, increases the need to obtain quantitative data to support conservation measures. In the warm temperate waters of Macaronesia (Eastern North Atlantic), sperm whales occur year-round in a set of island systems (the Azores, Madeira, and the Canaries), mainly in social groups of females and juveniles with the occasional visits of mature males. Although it is known that they perform inter-archipelago movements, information on site fidelity and residency times is still scarce. Here, based on photographic-identification data, site fidelity and residency times of sperm whales were estimated for subareas of the Azores and the Madeira archipelagos, with a preliminary assessment for a subarea of the Canaries. The Azores and Madeira subareas presented similar proportions of individuals with recaptures (~25%), mainly inter-annual, while in the subarea of the Canaries, only <10% of the individuals were recaptured. Standardized Site Fidelity Indexes showed very low values (<0.01) for both the Azores and Madeira subareas. Lagged identification rates based on models including emigration and reimmigration estimated that an average of 44.8 individuals (SE=4.9) spent 12.9 days (SE=1.5) in the Azores before leaving for 99.1 days (SE=12.5), while 8.4 individuals (SE=16.1) spent 0.8 day (SE=6.6) in Madeira before leaving for 8.6 days (SE=6.9), with a very low mortality rate. This study i) indicates a degree of residency of about ¼ of the identified individuals for the Azores and Madeira subareas and ii) supports that these oceanic archipelagos constitute an important habitat for a Vulnerable species in the Atlantic. Moreover, it also highlights the importance of combining data from opportunistic and dedicated surveys and joint national and international efforts toward the conservation of marine megafauna.

KEYWORDS

marine megafauna, philopatry, transnational conservation, Atlantic, photographic-identification, capture-recapture, habitat use

Introduction

Research and conservation of top oceanic predators present unique challenges due to their high mobility over difficult-to-access areas, with costly and logistically complex data collection. Most pelagic marine megafauna is not easily seen and has large ranges extending to offshore areas (Tittensor et al., 2010; Kaschner et al., 2011). In the case of deep-diving species, there are increased difficulties associated with their long submersion periods (Aoki et al., 2012; Li & Rosso, 2021; Badenas et al., 2022). Moreover, many of these species are of significant conservation concern and represent an ecologically and functionally important part of marine biodiversity (Katona & Whitehead, 1988; Schipper et al., 2008; Pimiento et al., 2020; Alves et al., 2022; Braun et al., 2022). Thus, information on the distribution and movements of these species is valuable for planning practical conservation efforts.

The sperm whale *Physeter macrocephalus*, the largest deep-diver and toothed animal, is distributed worldwide. It ranges from the ice edge in both hemispheres to tropical waters (Whitehead, 2018). Its distribution is highly connected to social structure and sex, with social groups of females and immatures inhabiting low and mid-latitudes. On the other hand, males leave their maternal groups and aggregate in bachelors groups for a few years before living mainly solitary in high latitudes, returning to tropical and subtropical waters to mate (Cantor et al., 2019).

Sperm whales are globally classified as Vulnerable by the International Union for Conservation of Nature, with an unknown worldwide population trend (Taylor et al., 2019), with recent studies indicating a global population of 844 761 individuals (Whitehead & Shin, 2022). This species was extensively hunted worldwide since the 18th century, growing from a shore-based enterprise to industrial whaling that only ceased in the 1980s. This caused a decrease of 68% in the global population, with males being more heavily targeted (Whitehead, 2002; Whitehead, 2018). Due to the low reproduction rates of these long-lived mammals, the populations of sperm whales are still recovering. However, presently, they still face several threats, such as entanglement in fishing gear, ingestion of plastics, chemical pollution, or ship strikes (Schipper et al., 2008; Savery et al., 2013; Notarbartolo-Di-Sciara, 2014; Fais et al., 2016; Whitehead, 2018; Arregui et al., 2019).

The Macaronesian archipelagos of the Azores, Madeira, and Canaries (Eastern North Atlantic) are some of the most isolated oceanic habitats of the North Atlantic, surrounded by steep submarine canyons and deep waters due to their volcanic origin and lack of continental shelf (Carracedo & Troll, 2021), which offer easy access to study deep-divers and oceanic species. Here, social groups of females and immature sperm whales are present year-round, with the occasional presence of visiting males (André, 1997; Silva et al., 2014; Fernandez et al., 2021). This biogeographic region is known to be used by sperm whales for reproduction, besides feeding and calving (Clarke, 1956; André, 1997; Steiner et al., 2012; Correia-Fagundes & Romano, 2013; Silva et al., 2014; Alves et al., 2018; Mullin et al., 2022). The sperm whale was the target species of a whaling activity that killed around 26 000 individuals in the Azores and Madeira, while in the Canaries it was a residual activity. This resulted in a reduction of 55% of the population in this region (Cabral et al., 2005; Brito, 2008; Perez, 2011). Currently, these three archipelagos are important destinations for whale-watching, with as many as 30 cetacean species identified so far, where the sperm whale is one of the target species in the Azores and, to a lesser extent, in Madeira (Freitas et al., 2012; Silva et al., 2014; Ferreira et al., 2017; Alves et al., 2018; Cartagena-Matos et al., 2021; Herrera et al., 2021; McIvor et al., 2022). In Macaronesia, and specifically in the Canaries, collision with ships is nowadays a relevant threat to the population of sperm whales, presenting one of the world's highest rates of ship strikes, with an annual average of two stranded whales from ship-strikes (Fais et al., 2016). Due to the oceanic habits of sperm whales, many more events may go unreported in offshore waters, creating a high level of conservation concern. Therefore, the sperm whale is still vulnerable to human-induced disturbances in these remote archipelagos.

To understand population movement patterns and life history, it is essential to evaluate site fidelity and residency (Baird et al., 2008; Tschopp et al., 2018). Site fidelity, defined as the tendency of an animal to return to a previously occupied place, is a well-documented behavior in many taxonomic groups (e.g., birds, Hoover, 2003; Iverson & Esler, 2006; seals, Lunn & Boyd, 1991; Pomeroy et al., 2001; insects, Switzer, 1997). It is known to provide evolutionary benefits and may increase survival (Greenwood, 1980; Switzer, 1993; Bose et al., 2017). Sperm whales, like other mammalian species (e.g., deers, Bose et al., 2017; elephants, Archie et al., 2006), demonstrate female philopatry and male dispersal due to the higher dependency of females on local resources (Greenwood, 1980). Male sperm whales show limited site fidelity to their feeding grounds, with few possible resident individuals (Jaquet et al., 2000; Lettevall et al., 2002; Rødland & Bjørge, 2015; Somerford et al., 2021). On the other hand, females exhibit site fidelity across years in several locations (e.g., Caribbean, Gero et al., 2014; Mediterranean Sea, Drouot-Dulau & Gannier, 2007), which may lead to genetic differentiation of specific populations (Engelhaupt et al., 2009).

Studies exploring site fidelity and residency of sperm whales in the oceanic environment of the Eastern North Atlantic are limited to the archipelago of the Azores, where both photographic-identification and genetic studies indicate some degree of site fidelity in females, although there are no permanent resident individuals (Matthews et al., 2001; Silva et al., 2006; Pinela et al., 2009; van der Linde & Eriksson, 2020). The more than 40 individual photographic-identification matches within the Macaronesian archipelagos of the Azores, Madeira, and Canaries (Steiner et al., 2015; Steiner, 2022) indicate that these animals carry out inter-archipelago movements and support the existence of a single population in this region of the Atlantic. Nevertheless, quantitative information on site fidelity and residency times is limited (to one archipelago) or unavailable for Macaronesia.

Here, photographic data of sperm whales from three subareas of Macaronesian archipelagos were used to investigate and quantify this species' habitat use, with a main focus on Azores and Madeira. More specifically, composite indexes and likelihood techniques were applied to i) calculate the site fidelity of sperm whales in subareas of the Azores and Madeira, and ii) estimate residency times to inform on the movements in and out of these areas. Filling these knowledge gaps regarding population habitat use will provide novel insights into future coordinated efforts between the countries involved (i.e., Portugal and Spain) to establish transborder conservation measures.

Material and methods

Study area

This study was conducted in subareas of three oceanic archipelagos of Macaronesia: around Pico and Faial islands in the Azores (approximately 3 500 km^2), south and southeast of Madeira island (approximately 800 km^2), and along the eastern coast of Lanzarote and Fuerteventura in the Canaries (approximately 6 500 km^2) (Figure 1). The biogeographical unit of Macaronesia, by definition, also includes Cabo Verde islands; however, recent studies support the exclusion of the latter due to considerable differences, specifically regarding marine biodiversity, and aggregates the three remaining archipelagos in one province within the Lusitanian ecoregion (Spalding et al., 2007; Freitas et al., 2019). These warm-temperate archipelagos are located in the Eastern North Atlantic Ocean, between latitudes 28 and 39°N, and share natural, geological, oceanographic, and biogeographical features (Freitas et al., 2019). The Azores archipelago is located approximately 1 800 km west of Lisbon (Portugal), around the Mid-Atlantic Ridge, and is surrounded by very narrow shelves and steep slopes, with the frequent presence of seamounts, and a mean depth of about 3 000 m (Morato et al., 2008). The Madeira archipelago is located approximately 1 000 km off the European continent and 500 km off the African coast, being also surrounded by steep submarine canyons and deep waters (approximately 1 500 m in depth) very close to the coast, due to the lack of a continental shelf (Geldmacher et al., 2000). The Canaries archipelago is located 100 km off the African coastline and is formed by seven main islands, that extend over 500 km. The average depth increases towards the west, from depths of 1 200 m in Lanzarote and Fuerteventura (the most eastern islands) to 4 000 m in La Palma and Hierro (the most western islands) (Valdés & Déniz-González, 2015).

Data collection and photographic analysis

Photographic-identification (hereafter, photo-id) data from sperm whales were collected in the three subareas. In the Azores, data was collected from April to October, from 2014 to 2019, during dedicated research and opportunistic surveys (whale-watching trips). In Madeira, data was collected year-round from 2007 to 2019 during dedicated research and opportunistic surveys (whale-watching trips). In the Canaries, data was collected year-round in 2009, 2011 and 2012 during dedicated research surveys.

In each subarea, photographs were collected and classified into a catalogue following standard photo-id procedures (Arnbom, 1987; Würsig & Jefferson, 1990). Sperm whale individuals were identified using photographs of the ventral or dorsal side of the fluke based on natural or acquired markings on the trailing edge. Scars and pigmentation patterns on the fluke and peduncle were used to confirm matches. Each photograph was graded for quality (from 1=poor to 4=excellent) and distinctiveness (from 1=non-distinctive to 4=very distinctive) (Alves et al., 2013). To maximize the reliability of each of the three catalogues (one per subarea), the analysis was limited to photographic quality and distinctiveness ratings from 2 to 4. Each catalogue was compiled visually by a single researcher and verified whenever needed by experienced secondary researchers.

For the three subareas, catalogues were analyzed to determine the number of individuals captured only once and of individuals that presented recaptures. Recaptured individuals were then classified taking into consideration if the recaptures were intra-annual (i.e. all the recaptures of the individual occurred within the same year) or inter-annual (i.e. at least one of the recaptures occurred in a different year). Percentages of the individuals captured once and with intra and inter-annual recaptures were then calculated, and the capture frequency histograms were plotted. Discovery curves were created by plotting the cumulative number of identifications against the number of identified individuals throughout the study period. When the population is fully

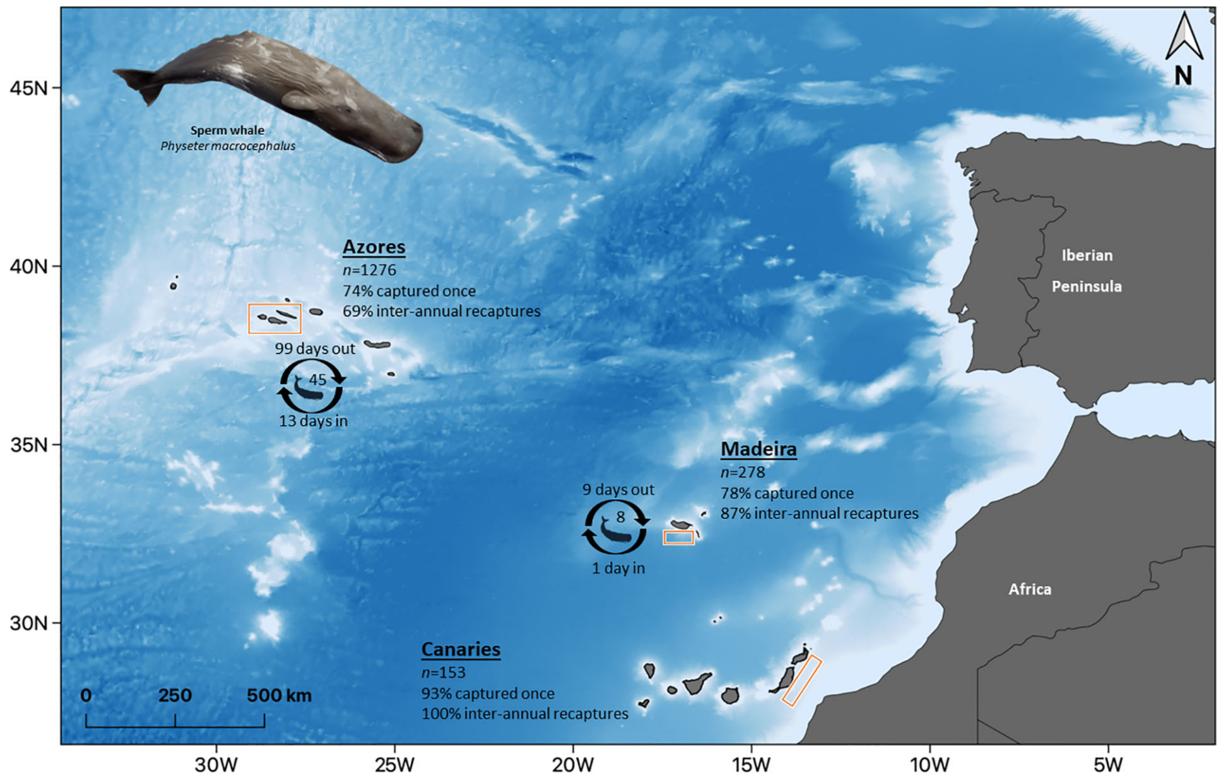

FIGURE 1
Location of the study area in the Eastern North Atlantic, Macaronesia, formed by the archipelagos of the Azores, Madeira, and the Canaries. Bathymetry ranging from approximately 1 000 to 4000 m, from white to blue, respectively. *n* indicates the number of identified individuals in each archipelago. Percentages refer to the proportion of individuals captured once and of individuals recaptured inter-annually. Number of individuals and time spent in and out of the area refer to the estimates of the best model of lagged identification rates (Table 2). Illustration by E. Berninsone © ARDITI.

identified, the curve reaches a plateau; but if the curve is continuously growing and no stabilization occurs, it means that there are still new individuals being added to the catalogue. This analysis was performed with Socprog 2.9 (Whitehead, 2009).

Site fidelity and residency analysis

Evaluation of site fidelity and residency were only conducted for the Azores and Madeira datasets, since the dataset from the Canaries presented very few recaptures, which did not allow further analysis. A truncated dataset was used for Madeira to homogenize the effort, restricting to the years with the highest effort, i.e. from 2014 to 2019.

Site fidelity of sperm whales was assessed using the Standardized Site Fidelity Index (SSFI), a composite site fidelity index developed by Tschopp et al. (2018). Definition and quantification of site fidelity varies greatly among research studies and is largely dependent on species behaviour, life cycle and research objectives, among others (Tschopp et al., 2018). Also, is usually done at an individual level. Therefore, the development of a standardized index that provided information of site fidelity at a populational level and allowed for comparison between studies was needed. SSFI was the index that had the best performance in all of the evaluated scenarios (both theoretical and with real data) and was calculated based on the indicators of permanence and periodicity.

Permanence (*IT*) is the proportion of time in the study area given by the time between the capture and last recapture (F_i), over the sampling period (F):

$$IT_i = \frac{F_i}{F}$$

Periodicity (*It*) is the recurrence of an individual, determined by the inverse of the average time between successive recaptures:

$$It_i = \left(\frac{F_i}{\sum_{j=1}^{T} c_{ij} - 1} \right)^{-1}$$

where c_{ij} indicates a capture (one) or an absence to capture (zero) of an individual i on the sampling occasion j, and T is the number of sampling occasions.

SSFI is therefore defined as:

$$SSFI = \frac{2}{\frac{1}{IT} + \frac{1}{It}}$$

SSFI quantifies site fidelity at a populational level using capture-recapture data and varies between zero (population without site fidelity) and one (resident population). This index works when effort is not constant and when the detection of the subject presents difficulties. This is the case with cetaceans in general and sperm whales in particular, due to their long diving periods associated with feeding (Cantor et al., 2019).

Likelihood techniques were used to estimate parameters of residency models (Whitehead, 2001). These techniques use datasets where animals are identified individually, but the identifications are distributed neither randomly nor systematically in space or time, and where the identifications themselves are used as a measure of effort. To estimate residency times, we applied the models developed by Whitehead (2001), that evaluate the estimated population size in the study area, the amount of time an individual spends within an area and the movements into and out of that area. Lagged identification rates (LIR) were calculated, which estimate the probability that an individual identified in the study area at any given time will be identified again in the study area some time lag after (Whitehead, 2001). Due to overdispersion (when the variance inflation factor >3, which may represent fundamental problems with the data; Lebreton et al., 1992), data from the Azores was limited to the months with the most homogeneous number of identifications (June to September). Since overdispersion for the Madeira dataset <3, the entire year was used in the analysis. The sampling period was defined as day for both archipelagos. Estimated LIRs were compared to expected LIRs from exponential mathematical models of residency established by Whitehead (2001) and fitted using maximum-likelihood methods. The model with the lowest quasi-Akaike information criterion (QAIC) was selected as providing the best fit to the data (Whitehead, 2009). Precision (SE) was estimated using a bootstrap method. The analysis was performed with Socprog 2.9 (Whitehead, 2009).

Results

Photographic analysis

Information on the photographic analysis for the three archipelagos is presented in Table 1. The number of individuals identified in the Azores is higher than in Madeira and the Canaries. However, Azores and Madeira showed similarities in the percentages of individuals captured only once (74.3 and 77.7%, respectively) and, consenquently, of individuals with recaptures (25.7 and 22.3%, respectively). These two archipelagos also presented a higher prevalence of individuals recaptured in more than one year (68.9% for the Azores and 87.1% for Madeira). In the Canaries, only 11 individuals presented recaptures (maximum two recaptures), all captured on the same two dates in 2009 and 2011. In Madeira, there was a maximum of 14 inter-annual recaptures, while in the Azores, the maximum was 27 (Figure 2A). The discovery curves indicated that, for all archipelagos, the number of individuals identified has not stabilized, and therefore the whole population is yet to be sampled (Figure 2B). Nevertheless, the curves for the Azores and Madeira were very similar in shape, despite the differences in the number of identified individuals, and presented an initial tendency for stabilization. The Canaries curve was still in linear growth with no signs of stabilization.

Site fidelity and residency analysis

For the subarea of the Azores, the SSFI showed a median of 0.0067 (SD=0.0093, range 0.0056-0.0078; IT median=0.3207,

TABLE 1 Total number and *percentages* of catalogued individuals for the three archipelagos.

Area		Total number of catalogued individuals	Individuals captured once	Individuals with recaptures		
				Total	Intra-annual	Inter-annual
Azores						
	Number	1276	948	328	102	226
	%		*74.3*	*25.7*	*31.1*	*68.9*
Madeira						
	Number	278	216	62	8	54
	%		*77.7*	*22.3*	*12.9*	*87.1*
Canaries						
	Number	153	142	11	0	11
	%		*92.8*	*7.2*	*0*	*100*

Individuals were classified into animals presenting one capture and more than one recapture, whether the recaptures were within the same year (intra-annual) or in different years (inter-annual).

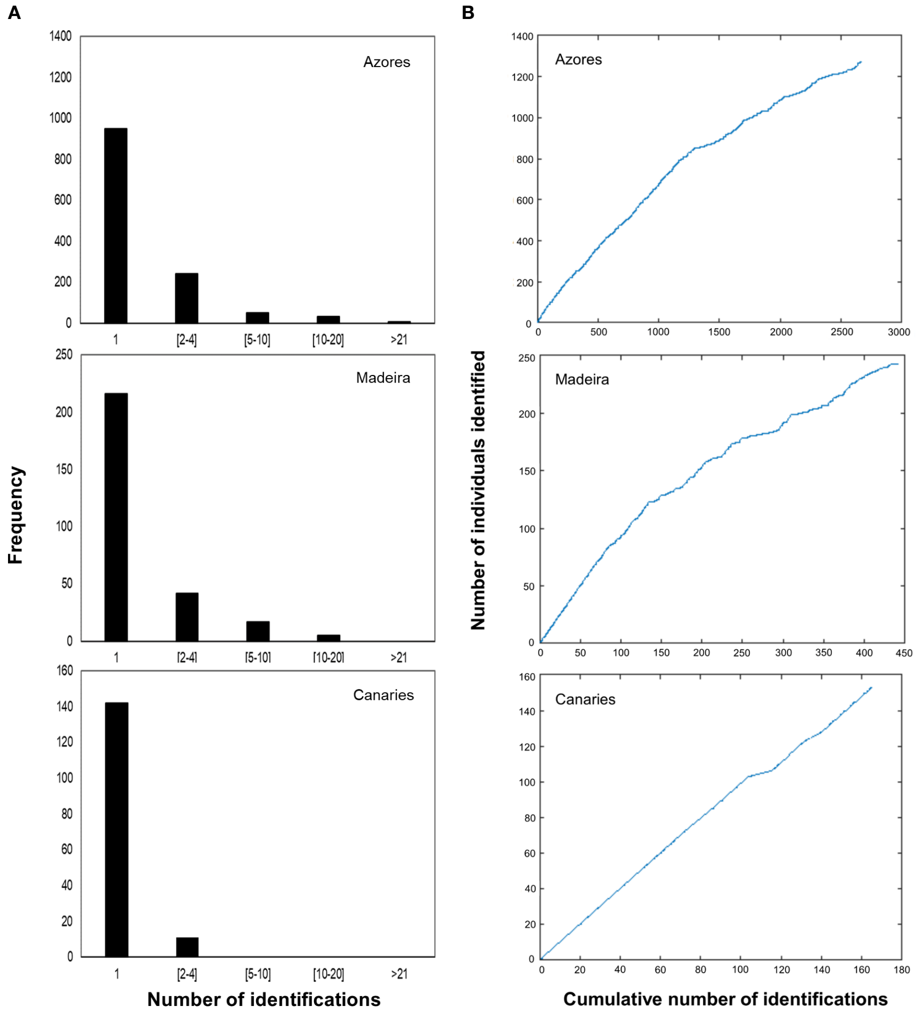

FIGURE 2
(A) Capture frequency histograms for individual sperm whales for the three subareas of the Azores, Madeira and the Canaries. Most of the individuals of the three subareas were captured only once. Captures were aggregated in categories to facilitate visualization. **(B)** Discovery curves for individual sperm whales in the three subareas, based on the cumulative number of identifications concerning the number of identified individuals throughout the study period.

SD=0.2818; It median = 0.0045, SD=0.1946). For the subarea of Madeira, SSFI presented a median of 0.0094 (SD=0.0069, range 0.0076-0.0112; IT median=0.3713, SD=0.2388; It median=0.0056; SD=0.1928) (Figure 3).

Four residency models were fitted to the lagged identification rate: "closed" (no changes in the individuals present in the area), "emigration/mortality" (individuals leave the area and never return), "emigration + reimmigration" (individuals leave the area and may return), and "emigration + reimmigration + mortality" (individuals leave the area and may or not return due to emigration or mortality) (Table 2). The model that best fitted the LIR for the Azores subarea was Emigration + reimmigration and for Madeira subarea was Emigration + reimmigration + mortality (Table 2, Figure 4). For the Azores subarea, from June to September, there was an average of 44.8 individuals (SE = 4.9) at any given time and individuals resided in the area for 12.9 days (SE = 1.5), before leaving for 99.1 days (SE = 12.5); goodness of fit x^2 = 1643.563, df = 455, P = 0. For the Madeira subarea, there was an average of 8.4 individuals (SE = 16.1) at any given time and individuals resided in the area for 0.8 days (SE = 6.6) before leaving for 8.6 days (SE = 6.9), with a very low mortality rate of 0.0008 (SE = 0.0002); goodness of fit x^2 = 91.534, df = 58, P = 0.0033.

Discussion

This study provides the first assessment of site fidelity and residency of sperm whales in a remote oceanic environment in

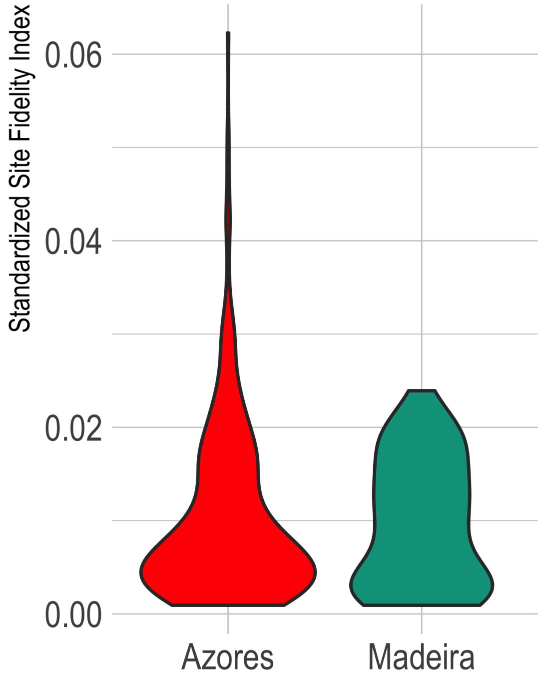

FIGURE 3
Violin chart for the Standardized Site Fidelity Index (SSFI) for the archipelagos of Azores and Madeira. SSFI varies between 0 and 1, with zero being a population without site fidelity and one for a resident population.

the Eastern North Atlantic. It brings forth valuable insights for a threatened species population whose offshore habitat and deep-diving behavior impair data collection. Through the collaborative effort from national and international teams, it was possible to identify areas in Macaronesia as important habitats for a portion of the population of sperm whales inhabiting the North Atlantic. Moreover, it is shown that individuals used this region intra- and inter-annually. Although this study brings forth important scientific knowledge, it is nonetheless a preliminary approach due to, among other factors, its geographic limitation that impairs the extrapolation of these conclusions to the whole Macaronesia. This first characterization allows to identify existing data gaps in Macaronesia and highlights the increasing need to obtain reliable quantitative data from more extended areas to obtain a solid assessment of sperm whales in this area of the Eastern North Atlantic. For the Canaries, the dataset did not allow for more than preliminary results, and therefore the main core of this study was conducted in subareas of the Azores and Madeira archipelagos. This study also highlighted the importance of using both opportunistic and dedicated effort when working with species displaying pelagic habits, such as the sperm whale. This contributed to a more profound knowledge that will allow implementing appropriate conservation measures.

The findings of this study are inferred from a combination of different analyses that support three broad main results. First, there is heterogeneity in capture probability, given that approximately ¼ of the identified individuals of the Azores and the Madeira subareas (25.7% and 22.3%, respectively) were captured more than once, with most of these (68.9% for the Azores and 87.1% for Madeira) presenting inter-annual recaptures. This result strongly indicates the importance of these subareas for a portion (¼) of the population that uses it on a regular basis, supporting previous studies (Silva et al., 2006; Boys et al., 2019; van der Linde & Eriksson, 2020). The Canaries dataset presents individuals captured mainly once (92.8%), which, together with the linear growth demonstrated by the discovery curve, indicates that the entire population is still far from being captured. This is most likely due to two reasons: i) low sampling effort, with the dataset covering only three years with homogenous effort and with a relative low number of identified individuals, and ii) geographic limitation (already a limitation for this study in general), with previous studies

TABLE 2 **Models fitted to lagged identification rates (LIRs) for sperm whales in the archipelagos of the Azores and Madeira from 2014 to 2019.**

Area Model	No. of parameters	QAIC	Summed log likelihood
Azores			
Emigration + reimmigration	3	**20244.6**	-37804.1
Emigration + reimmigration + mortality	4	20281.9	-37869.9
Emigration/mortality	2	20646.0	-38557.4
Closed	1	20763.7	-38781.1
Madeira			
Emigration + reimmigration + mortality	4	**5080.9**	-4004.5
Emigration/mortality	2	5085.8	-4011.6
Emigration + reimmigration	3	5127.3	-4042.7
Closed	1	5141.8	-4057.3

For the Azores, only data from the peak season (June to September) were used, while for Madeira was year-round. Models used following Whitehead, 2001.
Models ranked by the quasi-Akaike information criterion (QAIC); the lowest QAIC (in bold) indicates the best-fitting model.

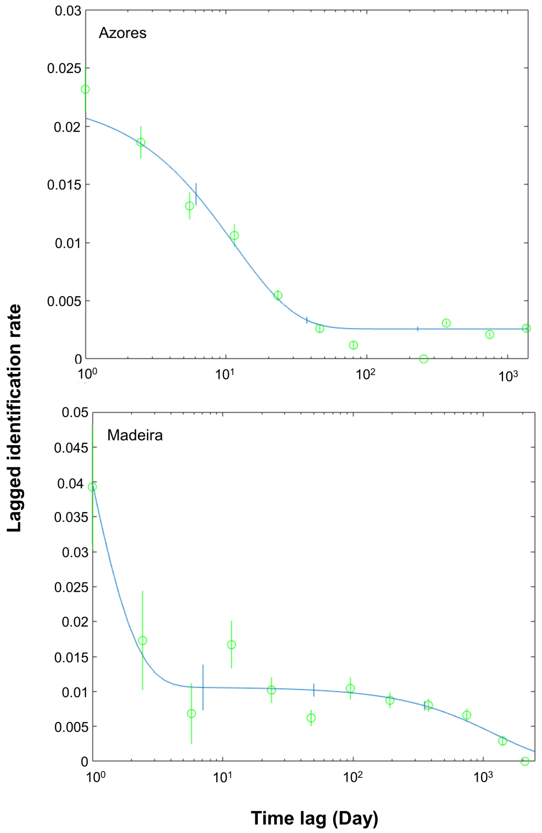

FIGURE 4
Lagged identification rates (LIRs) for sperm whales in the archipelagos the Azores (Silva et al., 2013; Prieto et al., 2014; González-Garcia et al., 2022) and Madeira from 2014 to 2019. For the Azores, analysis was restricted to the peak season, from June to September, while for Madeira was year-round. The figures show the probability that an individual identified in the study area at any time will be identified again in the study area some time lag after. The line represents the best-fitting model according to Table 2, and the vertical bars indicate standard errors calculated using the bootstrap method.

reporting a higher presence of sperm whales in other areas of the Canaries archipelago unsampled in this study (André, 1997; Fais et al., 2016; Correia et al., 2020; Herrera et al., 2021). Broader and more systematic research on sperm whales is needed for the Canaries, especially considering that this area could work as an sink habitat due to the high mortality associated with ship strikes (Fais et al., 2016). Taking into consideration the existing connection between Macaronesian archipelagos already demonstrated by photo-id and genetics (Pinela et al., 2009; Steiner et al., 2015; Steiner, 2022), this could be causing a decrease in the Macaronesian population (as demonstrated with the stranding in the Canaries in 2019 of an individual already sighted in the Azores, with signs of ship strike; Vidal Martín and Lisa Steiner own data). This impact could include the whole North Atlantic population if we consider the movement of males between Macaronesia, Norway, and the Bahamas (Steiner et al., 2012; Mullin et al., 2022).

Second, the site fidelity index values for the Azores and Madeira subareas are similarly low (0.0067 ± 0.0093 and 0.0094 ± 0.0069, respectively; SSFI varies between 0 and 1). This follows the results of the photo-id analysis and supports that only a minor part of the population presents site fidelity to these subareas, while the majority uses them as passage. Studies focusing on site fidelity of sperm whales in this area of the Atlantic are limited to the Azores archipelago and indicate a lack of geographical and genetic structure, providing indirect evidence of site fidelity over short periods as well as between years from part of a larger oceanic population (Matthews et al., 2001; Pinela et al., 2009). Sperm whales are known as ocean nomads, with both solitary males and social groups of females and juveniles traveling thousands of kilometers regularly (Cantor et al., 2019), although recent studies have identified populations with solid site fidelity (e.g., Gero et al., 2014; Vachon et al., 2022). The complex social structure and the large spatial and temporal scales in which sperm whales occur are challenging for understanding their populations and ecology (Kaschner et al., 2012). Differences arise not only between populations but also between oceans, with the North Atlantic populations of sperm whales being more geographically and genetically structured than the Pacific, demonstrating shorter range movements and smaller group sizes, together with a higher number of calves (Whitehead et al., 2012). Therefore, extrapolating results across geographical areas without corroborating them with regional observations could provide incorrect conclusions (Kaschner et al., 2011; Vachon et al., 2022).

Third, the LIR estimates for the Azores and Madeira subareas support the previous results, with individuals spending more extended periods out of the sampled areas than within. For each area, the best model presented differences in QAIC that vastly surpassed the minimum value of two required for the model choice, reinforcing the selection of the best-fitting model as the most appropriate one (Burnham & Anderson, 2002). This is also in agreement with the model selected from an ecological viewpoint, given the high levels of emigration and reimmigration expected from highly mobile species inhabiting vast oceanic areas, as also shown by other cetaceans in the region (Silva et al., 2013; Prieto et al., 2014; Dinis et al., 2016; Alves et al., 2019; Ferreira et al., 2021; Badenas et al., 2022; González-Garcia et al., 2022). Moreover, previous studies on the target species for the Azores Archipelago support these results (Silva et al., 2006; Boys et al., 2019; van der Linde & Eriksson, 2020), while for Madeira, this is the first study to conduct such analysis.

This study presents inevitable limitations associated with data collection, by joining information from multiple platforms across several areas, that covered only a small part of each archipelago. This invalidates the comparison between archipelagos, providing instead a characterization for each of the surveyed subareas: Pico and Faial islands in the Azores, south and southeast of Madeira island, and the eastern coast of Lanzarote and Fuerteventura in the

Canaries. Also, while in Madeira and the Canaries the surveys took place year-round, in the Azores the weather conditions in the Winter invalidated such temporal scale, and data does not cover the entire year. However, the extended data collection period, together with the use of only good quality pictures and distinctive individuals, helped minimizing biases. In the Canaries, the smaller dataset hindered part of the analysis, and therefore more effort is needed for conclusions to be made regarding this area. This is already taking place with an ongoing project dedicated to the sperm whales in the Canaries. Opportunistic data is increasingly being used in cetacean research (e.g., Moura et al., 2012; Hupman et al., 2015; Alves et al., 2018; Fernandez et al., 2021). Although it presents limitations, those can be surpassed with adequate data analysis. The chosen index for this study, SSFI (Tschopp et al., 2018), is appropriate for situations where detection is not perfect, and the effort is heterogeneous, as in our study, thus providing robust quantifications of site fidelity at a populational level. This index accounts for the behavioral aspects of the target species and the characteristics of the sampling effort, which significantly improved the reliability of these results. Moreover, the use of likelihood techniques for residency parameters takes into consideration heterogeneous effort (Whitehead, 2001; Vachon et al., 2022).

Knowledge of biogeographical movement patterns is still limited for most pelagic species. Nevertheless, it is pivotal since many animals may encompass large geographical ranges within and beyond national waters (Dunn et al., 2019). The sperm whale is a cosmopolitan species with a complex differentiated behavior between sexes and populations. Yet, although having been the target of several studies worldwide (e.g., Drouot-Dulau & Gannier, 2007; Engelhaupt et al., 2009; Whitehead et al., 2012; Boys et al., 2019; Cantor et al., 2019), information on movements at the individual level is scarce for many populations. Its global threatened statuses require dedicated effort to establish conservation measures; however, its oceanic habitat hinders data collection and the coordination between stakeholders and governments. Conservation measures should include not only the core-used areas where social groups spend most of their time, exhibiting higher degrees of philopatry, but also the corridors used by males during their migrations between feeding and breeding grounds (Gero et al., 2014; Sahri et al., 2022). Remote islands such as the ones in Macaronesia provide an excellent location for studying this marine predator and/or the effects of anthropogenic threats, but surveillance of the open ocean is paramount since only a small part of the population approaches the islands regularly. For example, recent assessments of the cetaceans' vulnerability to climate change in the biogeographic region of Macaronesia showed that the sperm whale presented a moderate to high vulnerability score (Sousa et al., 2019; Sousa et al., 2021). All combined, identifying the critical habitats for sperm whales, both offshore and closer to islands, as well as quantifying parameters of fidelity and residency at the individual level, is a crucial issue in the conservation of populations that may show considerable variability in their habitat use (Vachon et al., 2022).

Data availability statement

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

Author contributions

RF, FA conceived the study design. RF, MF analyzed the data. RF wrote the original draft of the manuscript. RF, LS, VM, FFP, AD, FA supported the data collection and organized the databases. MK, FA supervised the work. 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.

Publisher's note

References

Alves, F., Alessandrini, A., Servidio, A., Mendonça, A. S., Hartman, K. L., Prieto, R., et al. (2019). Complex biogeographical patterns support an ecological connectivity network of a large marine predator in the northeast Atlantic. *Divers. Distrib.* 25 (2), 269–284. doi: 10.1111/ddi.12848

Alves, F., Ferreira, R., Fernandes, M., Halicka, Z., Dias, L., and Dinis, A. (2018). Analysis of occurrence patterns and biological factors of cetaceans based on long-term and fine-scale data from platforms of opportunity: Madeira island as a case study. *Mar. Ecol.* 39 (2), e12499. doi: 10.1111/maec.12499

Alves, F., Quérouil, S., Dinis, A., Nicolau, C., Ribeiro, C., Freitas, L., et al. (2013). Population tructure of short-finned pilot whales in the oceanic archipelago of Madeira based on photo-identificationcation and genetic analyses: Implications for conservation. *Aquat. Conserv.: Mar. Freshw. Ecosyst.* 23 (5), 758–776. doi: 10.1002/aqc.2332

Alves, F., Rosso, M., Li, S., and Nowacek, D. P. (2022). A sea of possibilities for marine megafauna. *Science* 375 (6579), 391–392. doi: 10.1126/science.abn6022

André, M. (1997). *Distribución y conservación del cachalote (Physeter macrocephalus) en las islas canarias. PhD thesis* (Gran Canaria, Canaries, Spain: University of Las Palmas de Gran Canaria).

Aoki, K., Amano, M., Mori, K., Kourogi, A., Kubodera, T., and Miyazaki, N. (2012). Active hunting by deep-diving sperm whales: 3D dive profiles and maneuvers during bursts of speed. *Mar. Ecol. Prog. Ser.* 444, 289–301. doi: 10.3354/meps09371

Archie, E. A., Moss, C., and Alberts, S. C. (2006). The ties that bind: genetic relatedness predicts the fission and fusion of social groups in wild African elephants. *Proc. R. Soc B* 273, 513e522. doi: 10.1098/rspb.2005.3361

Arnbom, T. (1987). Individual identification of sperm whales. *Rep. Int. Whal. Comm* 37 (SC/38/Sp4), 201–204.

Arregui, M., Quirós, Y., Saavedra, P., Sierra, E., Suárez-Santana, C., Arbelo, M., et al. (2019). Fat embolism and sperm whale ship strikes. *Front. Mar. Sci.* 6. doi: 10.3389/fmars.2019.00379

Badenas, A., Dinis, A., Ferreira, R., Sambolino, A., Hamard, E., Berninsone, L., et al. (2022). Behavioural ecology traits of elusive deep-diver whales unravel a complex social structure influenced by female philopatry and defence polygyny. *Front. Mar. Sci.* 9. doi: 10.3389/fmars.2022.809902

Baird, R., Webster, D., Mahaffy, S., McSweeney, D., Schorr, G., and Ligon, A. (2008). Site fidelity and association patterns in a deep-water dolphin: Rough-toothed dolphins (*Steno bredanensis*) in the Hawaiian archipelago. *Mar. Mamm. Sci.* 24 (3), 535–553. doi: 10.1111/j.1748-7692.2008.00201.x

Bose, S., Forrester, T., Brazeal, J., Sacks, B., Casady, D., and Wittmer, H. (2017). Implications of fidelity and philopatry for the population structure of female black-tailed deer. *Behav. Ecol.* 28 (4), 983–990. doi: 10.1093/beheco/arx047

Boys, R., Oliveira, C., Pérez-Jorge, S., Prieto, R., Steiner, L., and Silva, M. (2019). Multi-state open robust design applied to opportunistic data reveals dynamics of wide-ranging taxa: The sperm whale case. *Ecosphere* 10 (3), e02610. doi: 10.1002/ecs2.2610

Braun, C., Arostegui, M., Thorrold, S., Papastamatiou, Y., Gaube, P., Fontes, J., et al. (2022). The functional and ecological significance of deep diving by large marine predators. *Ann. Rev. Mar. Sci.* 14 (1), 129–159. doi: 10.1146/annurev-marine-032521-103517

Brito, C. (2008). Assessment of catch statistics during the land-based whaling in Portugal. *Mar. Biodiver. Rec.* 1, e92. doi: 10.1017/S175526720700930X

Burnham, K. P., and Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information theoretic approach* (New York: Springer Verlag).

Cabral, M. J., Almeida, J., Almeida, P. R., Dellinger, T., Almeida, N. F., Oliveira, M. E., et al. (2005). *Livro vermelho dos vertebrados de Portugal* (Lisboa: Instituto de Conservação da Natureza).

Cantor, M., Gero, S., Whitehead, H., and Rendell, L. (2019). "Sperm Whale: The Largest Toothed Creature on Earth", in Ethology and Behavioral Ecology of Odontocetes. Eds. B. Würsig. *Ethology and behavioral ecology of odontocetes* (Springer, Cham). doi: 10.1007/978-3-030-16663-2_12

Carracedo, J., and Troll, V. (2021). "North-East Atlantic islands: The macaronesian archipelagos," in *Encyclopedia of geology, 2nd Edition*. Eds. D. Alderton and S. A. Elias (Academic Press), 674–699. doi: 10.1016/B978-0-08-102908-4.00027-8

Cartagena-Matos, B., Lugué, K., Fonseca, P., Marques, T., Prieto, R., and Alves, F. (2021). Trends in cetacean research in the Eastern north Atlantic. *Mamm. Rev.* 51 (3), 436–453. doi: 10.1111/mam.12238

Clarke, R. (1956). Sperm whales of the Azores. *Discovery Rep.* 28, 237–298.

Correia-Fagundes, C., and Romano, H. (2013). Observation of a birth of a sperm whale *Physeter macrocephalus* at Madeira (NE Atlantic). *Bocagiana* 236, 1–3.

Correia, M., Gil, A., Valente, R., Rosso, M., Sousa-Pinto, I., and Pierce, G. (2020). Distribution of cetacean species at a large scale - connecting continents with the macaronesian archipelagos in the Eastern north Atlantic. *Divers. Distrib.* 26 (10), 1234–1247. doi: 10.1111/ddi.13127

Dinis, A., Alves, F., Nicolau, C., Ribeiro, C., Kaufmann, M., Cañadas, A., et al. (2016). Bottlenose dolphins *Tursiops truncatus* group dynamics, site fidelity, residency and movement patterns in the Madeira archipelago (North-East Atlantic). *Afr. J. Mar. Sci.* 38 (2), 151–160. doi: 10.2989/1814232X.2016.1167780

Drouot-Dulau, V., and Gannier, A. (2007). Movements of sperm whale in the Western Mediterranean Sea: Preliminary photo-identification results. *J. Mar. Biolog. Assoc. U.K.* 87 (1), 195–200. doi: 10.1017/S0025315407054860

Dunn, D., Harrison, A., Curtice, C., DeLand, S., Donnelly, B., Fujioka, E., et al. (2019). The importance of migratory connectivity for global ocean policy. *Proc. R. Soc B* 286 (1911), 20191472. doi: 10.1098/rspb.2019.1472

Engelhaupt, D., Hoelzel, A., Nicholson, C., Frantzis, A., Mesnick, S., Gero, S., et al. (2009). Female philopatry in coastal basins and male dispersion across the north Atlantic in a highly mobile marine pecies, the sperm whale (*Physeter macrocephalus*): Sperm whale female philopatry and male dispersal. *Mol. Ecol.* 18 (20), 4193–4205. doi: 10.1111/j.1365-294X.2009.04355.x

Fais, A., Lewis, T., Zitterbart, D., Álvarez, O., Tejedor, A., and Soto, N. A. (2016). Abundance and distribution of sperm whales in the canary islands: can sperm whales in the archipelago sustain the current level of ship-strike mortalities? *PLos One* 11 (3), e0150660. doi: 10.1371/journal.pone.0150660

Fernandez, M., Alves, F., Ferreira, R., Fischer, J. C., Thake, P., Nunes, N., et al. (2021). Modeling fine-scale cetaceans' distributions in oceanic islands: Madeira archipelago as a case study. *Front. Mar. Sci.* 8. doi: 10.3389/fmars.2021.688248

Ferreira, R., Alves, F., Gomes, C., Jardim, D., Kok, J., and Dinis, A. (2017). First confirmed record of northern bottlenose whale (*Hyperoodon ampullatus*) in Madeira archipelago, northeast Atlantic. *Aquat. Mamm.* 43 (5), 474–478. doi: 10.1578/AM.43.5.2017.474

Ferreira, R., Dinis, A., Badenas, A., Sambolino, A., Marrero-Pérez, J., Crespo, A., et al. (2021). Bryde's whales in the north-East Atlantic: New insights on site fidelity and connectivity between oceanic archipelagos. *Aquat. Conserv: Mar. Freshw. Ecosyst.* 31 (10), 2938–2950. doi: 10.1002/aqc.3665

Freitas, L., Dinis, A., Nicolau, C., Ribeiro, C., and Alves, F. (2012). New records of cetacean species for Madeira archipelago with an updated checklist. *Bol. Mus. Mun. Funchal* 62, 25–43.

Freitas, R., Romeiras, M., Silva, L., Cordeiro, R., Madeira, P., González, J., et al. (2019). Restructuring of the 'Macaronesia' biogeographic unit: a marine multi-taxon biogeographical approach. *Sci. Rep.* 9 (1), 15792. doi: 10.1038/s41598-019-51786-6

Geldmacher, J., Van Den Bogaard, P., Hoernle, K., and Schmincke, H. U. (2020). The 40Ar/39Ar age dating of the Madeira Archipelago and hotspot track (eastern North Atlantic). *Geochemistry, Geophysics, Geosystems* 1 (2), 1999GC000018. doi: 10.1029/1999GC000018

Gero, S., Milligan, M., Rinaldi, C., Francis, P., Gordon, J., Carlson, C., et al. (2014). Behavior and social structure of the sperm whales of Dominica, West indies. *Mar. Mamm. Sci.* 30 (3), 905–922. doi: 10.1111/mms.12086

González Garcia, L., Pierce, G. J., and Autret, Palenzuela, J. M. T. (2022). Alongside but separate: Sympatric baleen whales choose different habitat conditions in São Miguel, Azores. *Deep Sea Res.* 184, 103766. doi: 10.1016/j.dsr.2022.103766

Greenwood, P. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* 28, 1140–1162. doi: 10.1016/S0003-3472(80)80103-5

Herrera, I., Carrillo, M., Esteban, M. C., and Haroun, R. (2021). Distribution of cetaceans in the canary islands (Northeast Atlantic ocean): implications for the natura 2000 network and future conservation measures. *Front. Mar. Sci.* 8. doi: 10.3389/fmars.2021.669790

Hoover, J. (2003). Decision rules for site fidelity in a migratory bird, the prohonotary warbler. *Ecology* 84 (3), 416–430. doi: 10.1890/0012-9658(2003)084[0416:DRFSFI]2.0.CO;2

Hupman, K., Visser, F., Martinez, E., and Stockin, K. (2015). Using platforms of opportunity to determine the occurrence and group characteristics of orca (*Orcinus orca*) in the hauraki gulf, new Zealand. *N. Z. J. Mar. Freshw. Res.* 49 (1), 132–149. doi: 10.1080/00288330.2014.980278

Iverson, S., and Esler, D. (2006). Site fidelity and the demographic implications of winter movements by a migratory bird, the harlequin duck *Histrionicus histrionicus*. *J. Avian Biol.* 37 (3), 219–228. doi: 10.1111/j.2006.0908-8857.03616.x

Jaquet, N., Dawson, S., and Slooten, E. (2000). Seasonal distribution and diving behaviour of male sperm whales off kaikoura: foraging implications. *Can. J. Zool.* 78 (3), 407–419. doi: 10.1139/z99-208

Kaschner, K., Quick, N., Jewell, R., Williams, R., and Harris, C. (2012). Global coverage of cetacean line-transect surveys: status quo, data gaps and future challenges. *PLos One* 7 (9), e44075. doi: 10.1371/journal.pone.0044075

Kaschner, K., Tittensor, D., Ready, J., Gerrodette, T., and Worm, B. (2011). Current and future patterns of global marine mammal biodiversity. *PLos One* 6 (5), e19653. doi: 10.1371/journal.pone.0019653

Katona, S., and Whitehead, H. (1988). Are cetacea ecologically important? *Oceanogr. Mar. Biol.* 26, 553–568.

Lebreton, J. D., Burnham, K. P., Clobert, J., and Anderson, D. R. (1992). Modelling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecol. Monog.* 62, 67–118. doi: 10.2307/2937171

Lettevall, E., Richter, C., Jaquet, N., Slooten, E., Dawson, S., Whitehead, H., et al. (2002). Social structure and residency in aggregations of male sperm whales. *Can. J. Zool.* 80 (7), 1189–1196. doi: 10.1139/z02-102

Li, S., and Rosso, M. (2021). Lack of knowledge threatens beaked whales. *Science* 371 (6531), 791. doi: 10.1126/science.abg892

Lunn, N., and Boyd, I. (1991). Pupping-site fidelity of Antarctic fur seals at bird island, south Georgia. *J. Mammal.* 72 (1), 202–206. doi: 10.2307/1381999

Matthews, J. N., Steiner, L., and Gordon, J. (2001). Mark-recapture analysis of sperm whale (*Physeter macrocephalus*) photo-id data from the azores, (1987–1995). *J. Cetacean Res. Manage.* 3 (3), 219–226.

McIvor, A., Williams, C., Alves, F., Dinis, A., Pais, M., and Canning-Clode, J. (2022). The status of marine megafauna research in macaronesia: a systematic review. *Front. Mar. Sci.* 9. doi: 10.3389/fmars.2022.819581

Morato, T., Machete, M., Kitchingman, A., Tempera, F., Lai, S., Menezes, G., et al. (2008). Abundance and distribution of seamounts in the Azores. *Mar. Ecol. Prog. Ser.* 357, 17–21. doi: 10.3354/meps07268

Moura, A., Sillero, N., and Rodrigues, A. (2012). Common dolphin (*Delphinus delphis*) habitat preferences using data from two platforms of opportunity. *Acta Oecol.* 38, 24–32. doi: 10.1016/j.actao.2011.08.006

Mullin, K., Steiner, L., Dunn, C., Claridge, D., González, L., Gordon, J., et al. (2022). Long-range longitudinal movements of sperm whales (*Physeter macrocephalus*) in the north Atlantic ocean revealed by photo-identification. *Aquat. Mamm.* 48 (1), 3–8. doi: 10.1578/AM.48.1.2022.3

Notarbartolo-Di-Sciara, G. (2014). Sperm whales, *Physeter macrocephalus*, in the Mediterranean Sea: a summary of status, threats, and conservation recommendations. *Aquat. Conserv: Mar. Freshw. Ecosyst.* 24 (S1), 4–10. doi: 10.1002/aqc.2409

Perez, J. (2011). The cetacean fishing in the canary islands. *Anuario Estudos Atlânticos* 57, 277–300.

Pimiento, C., Leprieur, F., Silvestro, D., Lefcheck, J. S., Albouy, C., Rasher, D. B., et al. (2020). Functional diversity of marine megafauna in the anthropocene. *Sci. Adv.* 6 (16), eaay7650. doi: 10.1126/sciadv.aay7650

Pinela, A., Quérouil, S., Magalhães, S., Silva, M., Prieto, R., Matos, J. A., et al. (2009). Population genetics and social organization of the sperm whale (*Physeter macrocephalus*) in the Azores inferred by microsatellite analyses. *Can. J. Zool.* 87 (9), 802–813. doi: 10.1139/Z09-066

Pomeroy, P., Twiss, S., and Redman, P. (2001). Philopatry, site fidelity and local kin associations within grey seals breeding colonies. *Ethology* 106 (10), 899–919. doi: 10.1046/j.1439-0310.2000.00610.x

Prieto, R., Silva, M. A., Waring, G. T., and Gonçalves, J. M. A. (2014). Sei whale movements and behaviour in the North Atlantic inferred from satellite telemetry. *Endang. Species Res.* 26, 103–113. doi: 10.3354/esr00630

Rødland, E., and Bjørge, A. (2015). Residency and abundance of sperm whales (*Physeter macrocephalus*) in the bleik canyon, Norway. *Mar. Biol. Res.* 11 (9), 974–982. doi: 10.1080/17451000.2015.1031800

Sahri, A., Jak, C., Putra, M., Murk, A., Andrews-Goff, V., Double, M., et al. (2022). Telemetry-based home range and habitat modelling reveals that the majority of areas important for pygmy blue whales are currently unprotected. *Biol. Conserv.* 272, 109594. doi: 10.1016/j.biocon.2022.109594

Savery, L., Evers, D., Wise, S., Falank, C., Wise, J., Gianios, C., et al. (2013). Global mercury and selenium concentrations in skin from free-ranging sperm whales (*Physeter macrocephalus*). *Sci. Total Environ.* 450–451, 59–71. doi: 10.1016/j.scitotenv.2013.01.070

Schipper, J., Chanson, J., Chiozza, F., Cox, N., Hoffmann, M., Katariya, V., et al. (2008). The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science* 322 (5899), 225–230. doi: 10.1126/science.1165115

Silva, M., Magalhães, S., Prieto, R., Quérouil, S., Pinela, A., Seabra, M. I., et al. (2006). Ecologia e estrutura populacional dos roazes e cachalotes nos açores: relação com as características do habitat. *Arquivos Do DOP Série Estudos* 4, 1–30.

Silva, M., Prieto, R., Jonsen, I., Baumgartner, M. F., and Santos, R. S. (2013). North Atlantic blue and fin whales suspend their spring migration to forage in middle latitudes: building up energy reserves for the journey? *Plos One* 8 (10), e76507. doi: 10.1371/journal.pone.0076507

Silva, M., Prieto, R., Cascão, I., Seabra, M., Machete, M., Baumgartner, M., et al. (2014). Spatial and temporal distribution of cetaceans in the mid-Atlantic waters around the Azores. *Mar. Biol. Res.* 10 (2), 123–137. doi: 10.1080/17451000.2013.793814

Somerford, T., Dawson, S., Slooten, E., Guerra, M., Childerhouse, S., Richter, C., et al. (2021). Long-term decline in abundance of male sperm whales visiting kaikōura, new Zealand. *Mar. Mamm. Sci.* 38 (2), 606–625. doi: 10.1111/mms.12886

Sousa, A., Alves, F., Arranz, P., Dinis, A., Fernandez, M., Gonzalez, L., et al. (2021). Climate change vulnerability of cetaceans in macaronesia: insights from a trait-based assessment. *Sci. Total Environ.* 795, 148652. doi: 10.1016/j.scitotenv.2021.148652

Sousa, A., Alves, F., Dinis, A., Bentz, J., Cruz, M. J., and Nunes, J. P. (2019). How vulnerable are cetaceans to climate change? developing and testing a new index. *Ecol. Indic.* 98, 9–18. doi: 10.1016/j.ecolind.2018.10.046

Spalding, M., Fox, H., Allen, G., Davidson, N., Ferdaña, Z., Finlayson, M., et al. (2007). Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *BioScience* 57 (7), 573–583. doi: 10.1641/B570707

Steiner, L. (2022). "Sperm whale movements around the north Atlantic and a glimpse at the new fluke matching algorithm," in *Cachalote Consortium Workshop, 24th Biennial Conference on the Biology of Marine Mammals*, Palm Beach, USA, 1-5 August.

Steiner, L., Lamoni, L., Plata, M., Jensen, S., Lettevall, E., and Gordon, J. (2012). A link between male sperm whales, *Physeter macrocephalus*, of the Azores and Norway. *J. Mar. Biolog. Assoc. U.K.* 92 (8), 1751–1756. doi: 10.1017/S0025315412000793

Steiner, L., Pérez, M., van der Linde, M., Freitas, L., Santos, R. P., Martin, V., et al. (2015). "*Long distance movements of female/immature sperm whales in the north atlantic* [Poster]," in *21st Biennial Conference of Society of Marine Mammalogy*, San Francisco, USA, 13-18 December.

Switzer, P. V. (1993). Site fidelity in predictable and unpredictable habitats. *Evol. Ecol.* 7, 533–555. doi: 10.1007/BF01237820

Switzer, P. (1997). Factors affecting site fidelity in a territorial animal, *Perithemis tenera*. *Anim. Behav.* 53 (4), 865–877. doi: 10.1006/anbe.1996.0352

Taylor, B. L., Baird, R., Barlow, J., Dawson, S. M., Ford, J., Mead, J. G., et al (2019). Physeter macrocephalus (amended version of 2008 assessment). *The IUCN Red List of Threatened Species*. 2019, e.T41755A160983555. doi: 10.2305/IUCN.UK.2008.RLTS.T41755A160983555.en. Accessed on 28 November 2022.

Tittensor, D. P., Mora, C., Jetz, W., Lotze, H., Ricard, D., Berghe, E., et al. (2010). Global patterns and predictors of marine biodiversity across taxa. *Nature* 466 (7310), 1098–1101. doi: 10.1038/nature09329

Tschopp, A., Ferrari, M., Crespo, E., and Coscarella, M. (2018). Development of a site fidelity index based on population capture-recapture data. *PeerJ* 6, e4782. doi: 10.7717/peerj.4782

Vachon, F., Hersh, T., Rendell, L., Gero, S., and Whitehead, H. (2022). Ocean nomads or island specialists? culturally driven habitat partitioning contrasts in scale between geographically isolated sperm whale populations. *R. Soc Open Sci.* 9 (5), 211737. doi: 10.1098/rsos.211737

L. Valdés and I. Déniz-González (Eds.) (2015). *Oceanographic and biological features in the canary current Large marine ecosystem* (Paris: IOC-UNESCO), 383.

van der Linde, M., and Eriksson, I. (2020). An assessment of sperm whale occurrence and social structure off são Miguel island, Azores using fluke and dorsal identification photographs. *Mar. Mamm. Sci.* 36 (1), 47–65. doi: 10.1111/mms.12617

Whitehead, H. (2001). Analysis of animal movement using opportunistic individual identifications: application to sperm whales. *Ecology* 82 (5), 1417–1432. doi: 10.2307/2679999

Whitehead, H. (2002). Current global population size, post-whaling trend and historical trajectory of sperm whales. *Sci. Rep.* 12: 19468. doi: 10.1038/s41598-022-24107-7

Whitehead, H. (2009). SOCPROG programs: analysing animal social structures. *Behav. Ecol. Sociobiol.* 63 (5), 765–778. doi: 10.1007/s00265-008-0697-y

Whitehead, H. (2018). “Sperm whale,” in *Encyclopedia of marine mammals*, *3rd Editions*. Eds. B. Würsig, J. G. M. Thewissen and K. M. Kovacs (London, UK: Academic Press), 919–924.

Whitehead, H., Antunes, R., Gero, S., Wong, S., Engelhaupt, D., and Rendell, L. (2012). Multilevel societies of female sperm whales (*Physeter macrocephalus*) in the Atlantic and pacific: why are they so different? *Int. J. Primatol.* 33 (5), 1142–1164. doi: 10.1007/s10764-012-9598-z

Whitehead, H., and Shin, M. (2022). Current global population size, post-whaling trend and historical trajectory of sperm whales. *Sci. Rep*. 12, 19468. doi: 10.1038/s41598-022-24107-7

Würsig, B., and Jefferson, T. A. (1990). Methods of photo-identification for small cetaceans. *Rep. Internat. Whal. Commun. Special issue* 12, 43–52.

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EDITED BY
Filipe Alves,
Center for Marine and Environmental Sciences (MARE), Portugal

REVIEWED BY
Aldo S. Pacheco,
National University of San Marcos, Peru
Guido J. Parra,
Flinders University, Australia

*CORRESPONDENCE
Daniel M. Palacios
✉ daniel.palacios@oregonstate.edu

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Priorities for ecological research on cetaceans in the Galápagos Islands

Daniel M. Palacios[1,2]* and Mauricio Cantor[1,2]

[1]Marine Mammal Institute, Oregon State University, Newport, OR, United States, [2]Department of Fisheries, Wildlife, and Conservation Sciences, Oregon State University, Newport, OR, United States

Located in the eastern tropical Pacific, the Galápagos Islands are an oceanic insular ecosystem subject to strong environmental variability driven by local and regional processes. Past research has shown that such conditions can attract and sustain at least 23 cetacean species, out of which 14 are common, including nine Delphinids, one Ziphiid, one Physeterid, and three Balaenopterids. These species occupy both coastal and oceanic habitats, most are present year-round, and a few are migratory. However, research on cetaceans in Galápagos has been sporadic and chronically underfunded and is not currently considered a priority in the research agenda for Galápagos. Based on a review of existing information and an assessment of knowledge gaps, here we identify priorities for ecological research on cetaceans in Galápagos along five topical areas: 1) spatiotemporal occurrence, 2) population assessment, 3) health assessment, 4) social ecology, and 5) trophic ecology. Addressing these knowledge gaps will also help inform actions to preserve cetacean biodiversity and to manage human activities involving or affecting cetaceans in Galápagos. Given the logistical and funding challenges of conducting cetacean research in Galápagos, we recommend optimizing data sampling and accessibility *via* integrated research protocols and open data repositories. We also recommend capitalizing on local citizen science activities, such as those conducted from cruise ships and whale-watching tours, which can serve as platforms of opportunity for obtaining basic data, thereby contributing to long-term data acquisition. Our proposed priorities should be assessed by Ecuadorian and Galápagos governmental institutions in broad and inclusive consultation with stakeholders and the scientific community prior to development and implementation of a research agenda. Collectively, these efforts will advance our understanding of the ecological role that marine megafauna, such as cetaceans, play in Galápagos and other oceanic islands, including maintaining large-scale connectivity and mitigating climate change.

KEYWORDS

cetaceans, megafauna, Galápagos Islands, eastern tropical Pacific, oceanic insular ecosystems, migratory connectivity, research priorities/questions, participatory research agenda

1 Introduction

A casual glance at oceanic islands might suggest a collection of isolated terrestrial habitats in an otherwise blue desert. A view from underwater, however, reveals that these insular ecosystems are much more than remote oases for terrestrial biota (e.g., Hasegawa et al., 2009; Gove et al., 2016). They provide habitats that attract a wealth of marine life from larval to adult stages and serve as steppingstones for migratory species (e.g., Pinheiro et al., 2017; Fontoura et al., 2022). Due to their long life spans and wide-ranging movements, marine megafauna in particular can play a key role in linking coastal and oceanic insular ecosystems (e.g., Hindell et al., 2020; Klimley et al., 2022). Indeed, ecological connectivity *via* local, regional, and long-distance movements is increasingly recognized as an essential process in the life history of large fishes, sea turtles, and marine mammals inhabiting oceanic insular ecosystems (e.g., Ketchum et al., 2020; Rooker et al., 2019; Ferreira et al., 2021) that is worth understanding and preserving in and of themselves (Game et al., 2009; Dunn et al., 2019; Klimley et al., 2022), as well as to help preserving the ecological communities these "umbrella" species are part of (Caro and O'Doherty, 1999).

Belonging to Ecuador, the Galápagos Islands are an oceanic insular ecosystem located in the eastern tropical Pacific (ETP) 1,000 km off mainland South America (Figure 1). Despite their equatorial location, the Galápagos are subject to seasonal variability resulting from the annual intensification of the southeast trade winds and equatorial upwelling (Palacios, 2004; Sweet et al., 2007; Forryan et al., 2021), and to strong interannual variability driven by the El Niño-Southern Oscillation (Palacios et al., 2006; Fiedler and Lennert-Cody, 2019), which is intensifying with climate change (Mendelssohn et al., 2005; Dueñas et al., 2021). Variable exposure of the islands to this environmental forcing results in a marked environmental zonation (Harris, 1969; Wellington et al., 2001; Schaeffer et al., 2008), which gives rise to a distinctive biogeographic patterning across the archipelago (Edgar et al., 2004; McKinley et al., 2022). Regarding migratory connectivity, the Galápagos are a well-known stop-over for marine megafauna, including teleosts, elasmobranchs, and chelonians that regularly move among oceanic archipelagos in the ETP (e.g., Todd and Grove, 2010; Cambra et al., 2021; Silver-Gorges et al., 2020; Klimley et al., 2022).

For the equally highly mobile cetaceans, however, this regional connectivity has not been directly established, except in a few cases (Torres-Florez et al., 2015; Cantor et al., 2016; Hucke-Gaete et al., 2018; Pacheco et al., 2019). Nevertheless, the slow life history, high trophic position, and large-scale movements of cetaceans are such that their ecological roles (Bowen, 1997; Kiszka et al., 2015; Kiszka et al., 2022) could have broader implications within and beyond Galápagos waters. In their role as predators, cetaceans participate in top-down control of the marine communities they inhabit and link oceanic and coastal ecosystems (e.g., Estes et al., 1998). Further, by acting as nutrient recyclers and carbon reservoirs, cetaceans provide ecological services that are key for oceanic productivity and climate change mitigation at global scales (Martin et al., 2021; Pearson et al., 2022).

A collaboratively derived environmental research agenda was recently developed for Galápagos based on a participatory process involving governmental entities, universities, and non-governmental organizations (Izurieta et al., 2018). This process prioritized 50 research questions, including several with a marine or conservation theme, although these questions were selected for their importance for policy makers and practitioners, and the authors acknowledged the value of conducting a parallel exercise for identifying fundamental research questions (Izurieta et al., 2018). This paper is an answer to this call, by identifying research questions relevant to cetaceans in Galápagos. Toward this goal, here we summarize the existing legislative and protective framework of relevance to cetaceans in Galápagos, review the available scientific information on cetacean occurrence in Galápagos, identify knowledge gaps, and provide recommendations for advancing ecological research.

2 Legislative and protective measures

Despite having been settled by humans only relatively recently, the Galápagos Archipelago has a long history of indiscriminate human exploitation, primarily driven by extractive pressures on the rich marine resources, which has resulted in serious conservation issues that continue through today (e.g., Ruttenberg, 2001; Boersma et al., 2005; Awkerman et al., 2006; Jacquet et al., 2008; Sonnenholzner et al., 2009; Schiller et al., 2014; Ruiz et al., 2016; Usseglio et al., 2016; Alava and Paladines, 2017; Cerutti-Pereyra et al., 2020; Bonaccorso et al., 2021). Starting with 18th century whaling, the sperm whale (*Physeter macrocephalus*) was among the first species to be targeted, and by the mid 19th century the local population had become depleted (Shuster, 1983; Hope and Whitehead, 1991; Whitehead and Hope, 1991; Whitehead et al., 1997). To prevent further whaling, in 1990 the government of Ecuador declared a "whale refuge" in all its jurisdictional waters, that is, the 200-nautical-mile Exclusive Economic Zone (EEZ) (Acuerdo Ministerial No. 196, 1990; Evans, 1991; Merlen, 1992), and subsequent legislation prohibited whale hunting indefinitely in its EEZ (Registro Oficial, 2000; Registro Oficial, 2002).

In 1998, Ecuador created the Galápagos Marine Reserve (GMR; Figure 1A), extending 40 nautical miles seaward from the coastal baseline and covering an area of 138,000-km^2 (Ley Orgánica de Régimen Especial Para la Provincia de Galápagos, 1998), making it one of the largest marine protected areas in the world. In 2001, UNESCO designated the GMR as a Natural World Heritage Site, in recognition of the astonishingly rich and diverse marine communities inhabiting it (Heylings et al., 2002). The boundaries of the GMR were revised in 2022, resulting in a slightly larger area of 142,759 km^2 (Acuerdo Ministerial No. MAATE-2022-039, 2022).

Despite the protections offered by the GMR, industrial fishing pressures targeting squid, high-trophic level fish, and sharks have continued to increase just beyond the reserve—and sometimes within it due to weak enforcement—and are driving a regional conservation crisis (Edgar et al., 2011; White et al., 2020; Bonaccorso et al., 2021; Global Fishing Watch, 2021). This led the Ecuadorian government to announce in January 2022 that it would create a new marine protected area within its EEZ, named "Hermandad Marine Reserve," a 60,000-km^2 corridor adjacent to the GMR (Decreto Ejecutivo No. 319, 2022; Acuerdo Ministerial No. MAATE-2022-019, 2022; Acuerdo

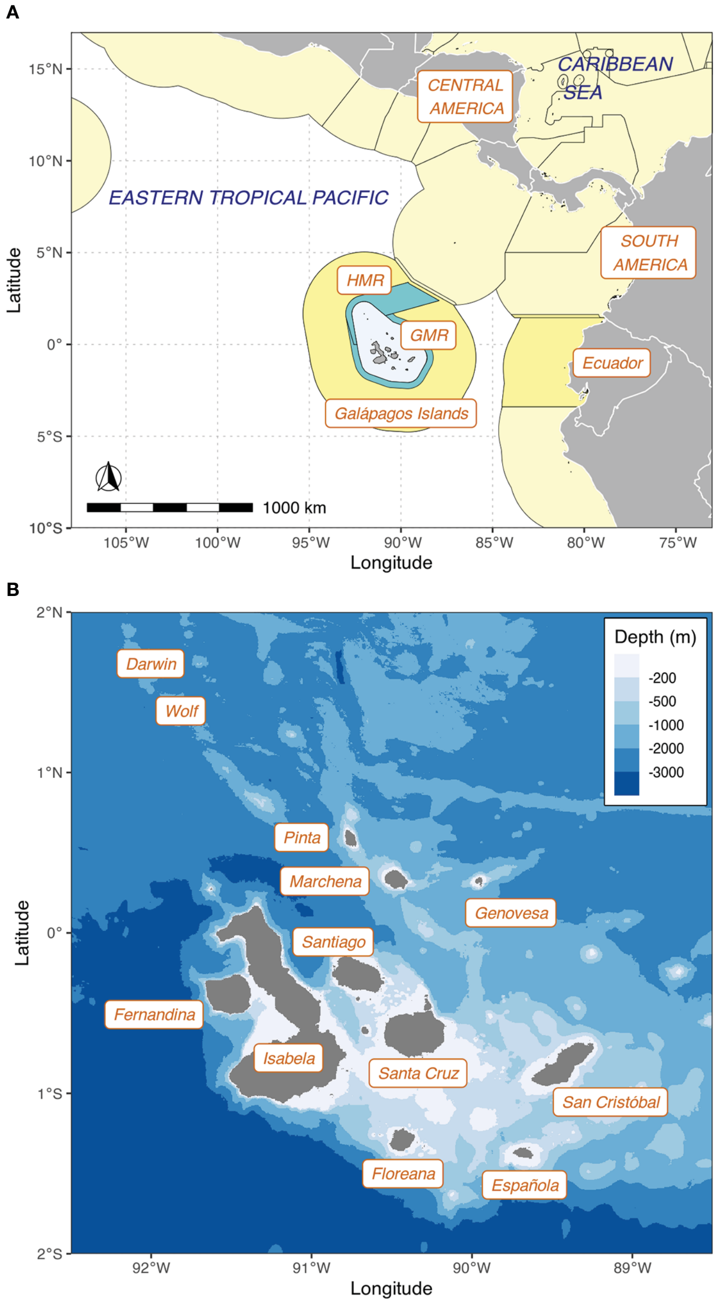

FIGURE 1
(A) Regional map showing the location of the Galápagos Islands in the eastern tropical Pacific, and the boundaries of the Galápagos Marine Reserve (GMR) and Hermandad Marine Reserve (HMR). The Exclusive Economic Zones (EEZ) of countries bordering the region are shown in yellow. **(B)** Map of the main islands of the Galápagos Archipelago (labeled) and bathymetry of the surrounding seafloor. The GMR and HMR boundaries are available from Fundación Charles Darwin's GeoData Portal at https://geodata-fcdgps.opendata.arcgis.com/. EEZ boundaries are available from Flanders Marine Institute (2019), used under Creative Commons license CC BY. Bathymetry data from SRTM15+ (Tozer et al., 2019), available from https://topex.ucsd.edu/WWW_html/srtm15_plus.html.

Ministerial No. MAATE-2022-041, 2022) (Figure 1A). The new marine reserve is part of a regional initiative that seeks to connect the insular marine protected areas of Ecuador, Costa Rica, Panama, and Colombia to achieve greater protection of their shared marine resources (Decreto Ejecutivo No. 319, 2022; Acuerdo Ministerial No. MAATE-2022-019, 2022).

Finally, in November 2022, the IUCN Marine Mammal Protected Areas Task Force announced that the Galápagos Archipelago would become one of its Important Marine Mammal Areas in the southeast temperate and tropical Pacific Ocean, recognizing that its waters harbor small and resident populations of endemic pinnipeds, provide habitat for reproductive and feeding activities of vulnerable whale species, and support aggregations of a high diversity of medium and small cetaceans (IUCN-MMPATF, 2022). These criteria provide a basis for further prioritization of conservation measures of relevance to marine mammals in Galápagos (Tetley et al., 2022).

3 A review of cetacean occurrence in Galápagos

Contemporary research on cetaceans in Galápagos waters has been largely sporadic and chronically underfunded. Collection of information on cetacean presence began in the 1970s, primarily as a casual but growing interest by local naturalist guides working aboard cruise ships touring the islands (Day, 1994; Merlen, 1995), an activity that continues through today (e.g., Palacios and Salazar, 2002; Denkinger et al., 2013; Denkinger et al., 2020). Also in the 1970s, a program to monitor dolphin mortality incidental to purse-seine tuna fishing operations in the ETP was established by the U.S.'s National Oceanic and Atmospheric Administration (NOAA) and subsequently implemented by other nations participating in the fishery (Ballance et al., 2021). These programs placed fisheries observers on tuna vessels, who collected cetacean sightings throughout the ETP, including Galápagos waters (Fiedler and Lennert-Cody, 2019). Additionally, between the mid 1980s and mid 2000s, NOAA also conducted dedicated research vessel surveys to estimate dolphin abundance and trends in the ETP, including Galápagos waters (Wade and Gerrodette, 1993; Hamilton et al., 2009).

A long-term study of sperm whales in Galápagos waters began in the mid 1980s, which has provided the basis for much of the contemporary knowledge on the species (e.g., Whitehead, 2003; Eguiguren et al., 2021). Several other research expeditions have been undertaken in Galápagos with the explicit purpose of studying cetaceans since then (Lyrholm et al., 1992; Smith and Whitehead, 1999; Palacios, 1999a; Palacios, 2000; Wise et al., 2009; Félix et al., 2011; Biggs et al., 2017; O'Hern et al., 2017). With the establishment of the GMR, since the early 2000s collaborative efforts between Galápagos-based and international scientists have continued to generate crucial knowledge about marine mammals in the area (Palacios and Salazar, 2002; Palacios et al., 2004; Denkinger et al., 2013; Biggs et al., 2017; O'Hern et al., 2017; Eguiguren et al., 2019; Denkinger et al., 2020; Eguiguren et al., 2021; Páez-Rosas et al., 2021). Finally, cetacean presence in Galápagos has also been gleaned from documentation of live-stranding events, beach-cast specimens, and osteological specimens in museums (Palacios, 1996; Palacios et al., 2004).

Several studies have attempted to characterize cetacean species diversity in Galápagos waters (Day, 1994; Merlen, 1995; Smith and Whitehead, 1999; Palacios and Salazar, 2002; Palacios, 2003; Denkinger et al., 2013). At least 23 species have been documented, although the relative sighting frequency of each species varies between studies because of differences in geographic coverage, sampling effort, and methodological approaches. To objectively assess the spatial and temporal patterns of cetacean occurrence in Galápagos waters, for purposes of this review we used the regional compilation of marine mammal sightings by Palacios (2003) and augmented it with more recent compilations of sightings for humpback whales (*Megaptera novaeangliae*) by Félix et al. (2011) and sperm whales by Cantor et al. (2017). We defined the geographic extent of our study area as a 4×4-degree box bounded by 88.5-92.5°W and 2°S-2°N (Figure 1B) and limited the marine mammal sightings data to this extent, resulting in a total of 3,227 sightings spanning the period 1973-2014 (Table 1, Figure 2A). As these sightings were collected using different methods, no standardized measure of effort was possible and instead we used the general spatiotemporal pattern in the data as a proxy for coverage (Figures 2A and 3). Out of the 20 cetacean species in our sightings compilation (Table 1), 14 were most common (i.e., species with 10 or more sightings). These included nine Delphinids (*Stenella attenuata, Stenella longirostris, Stenella coeruleoalba, Delphinus delphis delphis, Tursiops truncatus, Grampus griseus, Globicephala macrorhynchus, Pseudorca crassidens*, and *Orcinus orca*), one Ziphiid (*Ziphius cavirostris*), one Physeterid (*P. macrocephalus*), and three Balaenopterids (*Balaenoptera edeni brydei, Balaenoptera musculus*, and *M. novaeangliae*). Among the less commonly seen species, there were three Delphinids (*Peponocephala electra, Lagenodelphis hosei, Feresa attenuata*), one Balaenopterid (*Balaenoptera acutorostrata*), one Ziphiid (*Mesoplodon peruvianus*), and one Kogiid (*Kogia sima*). The relatively low sighting frequency of the Ziphiids and Kogiid is likely due to their long dive times coupled with their cryptic behavior at the surface, as the stranding record suggests that they may be more common (Palacios et al., 2004; MacLeod and Mitchell, 2006). In fact, one additional Ziphiid species, ginkgo-toothed beaked whale (*Mesoplodon ginkgodens*), is only known from strandings (Palacios, 1996; Palacios et al., 2004).

The overall spatial distribution of marine mammal sightings in our compilation indicated that the study area was covered reasonably well, although it is apparent that much of the effort has been on the deep waters (> 1500 m) of the western part of the archipelago, especially around Isabela and Fernandina islands (Figures 2A and 3). In contrast, the coastal shallow waters (< 500 m) of the central and eastern part of the archipelago have received comparatively much less effort (Figures 2A and 3). Among the commonly seen species, two had a primarily coastal (< 500 m) distribution (*T. truncatus* and *M. novaeangliae*), two occurred in both coastal and oceanic habitats (*O. orca* and *B. edeni brydei*), and the remainder were primarily found in deep (> 1000 m) waters (Figures 2 and 3).

In terms of seasonal coverage, more sightings in our compilation were collected in the first part of the year (January-May), when sea state conditions are calm, than in the second part (June-December), when sea conditions are rougher (Figure 4). Nevertheless, most species appear to use waters of the archipelago year-round, with sightings in most or all months of the year (Figure 4). Two of the Balaenopterids (*B. musculus* and *M. novaeangliae*) are seasonal migrants, being reported primarily during the second part of the year (Figure 4), coinciding with the low-latitude phase of the migratory cycle for Eastern South Pacific populations (Palacios, 1999b; Félix et al., 2011; Torres-Florez et al., 2015; Hucke-Gaete et al., 2018). Additionally, although the Bryde's whale (*B. edeni brydei*) is present year-round, a larger number of sightings during the second part of the year (Figure 4), indicates a preference for the cooler and more productive conditions characteristic of this season, as also reported by Denkinger et al. (2013). Finally, several species had more sightings in the first part of the year (*S. attenuata, S. longirostris, S. coeruleoalba, D. delphis delphis, G. griseus, G. macrorhynchus, P. macrocephalus*; Figure 4), but this pattern is likely influenced by increased sampling effort when sea conditions are calmer.

Marked fluctuations in species occurrence and distribution at interannual and long-term scales have also been described. For example, Denkinger et al. (2013) documented the apparent disappearance of Bryde's whales and short-beaked common

TABLE 1 Cetacean species reported in Galápagos, listed in decreasing frequency, based on a comprehensive compilation of marine mammal sightings (n = 3,227) in an area defined by a 4×4-degree box bounded by 88.5-92.5°W and 2°S-2°N, spanning the period 1973-2014 (see text for details and Figures 2 and 3 for graphical presentation).

Common name	Scientific name	No. sightings	Depth				
			Minimum	Maximum	Mean	Median	SD
Cetaceans							
Common bottlenose dolphin	*Tursiops truncatus*	346	70	3705	1093.8	553.0	1095.6
Short-beaked common dolphin	*Delphinus delphis delphis*	339	451	3717	2595.5	2859.0	831.2
Bryde's whale	*Balaenoptera edeni brydei*	291	22	3617	2119.9	2137.0	934.0
Sperm whale	*Physeter macrocephalus*	260	44	3783	2687.6	2990.0	756.6
Striped dolphin	*Stenella coeruleoalba*	126	201	3501	2313.5	2330.5	667.8
Risso's dolphin	*Grampus griseus*	101	423	3638	2225.6	2235.0	874.4
Short-finned pilot whale	*Globicephala macrorhynchus*	93	162	3625	2577.9	2770.0	779.8
Humpback whale	*Megaptera novaeangliae*	88	3	3595	560.5	253.0	789.0
Pantropical spotted dolphin	*Stenella attenuata*	75	724	3430	2326.7	2343.0	415.6
Pantropical spinner dolphin	*Stenella longirostris*	45	1467	3625	2395.0	2345.0	444.3
Killer whale	*Orcinus orca*	29	15	3235	1773.3	2136.0	1193.1
Blue whale	*Balaenoptera musculus*	17	2078	3604	3104.7	3220.0	477.8
Cuvier's beaked whale	*Ziphius cavirostris*	11	560	3624	2286.7	2182.0	871.8
False killer whale	*Pseudorca crassidens*	10	451	2916	2058.0	2208.0	820.2
Dwarf sperm whale	*Kogia sima*	6	2113	3636	2575.5	2258.0	610.2
Melon-headed whale	*Peponocephala electra*	4	437	1357	690.8	484.5	444.7
Minke whale	*Balaenoptera acutorostrata*	3	2047	2081	2069.7	2081.0	19.6
Fraser's dolphin	*Lagenodelphis hosei*	2	482	482	482.0	482.0	NA
Pygmy killer whale	*Feresa attenuata*	1	3007	3007	3007.0	3007.0	NA
Pygmy beaked whale	*Mesoplodon peruvianus*	1	999	999	999.0	999.0	NA
Pinnipeds							
Galápagos fur seal	*Arctocephalus galapagoensis*	104	135	3656	2808.1	3075.0	899.4
Galápagos sea lion	*Zalophus wollebaeki*	61	100	3646	927.6	340.5	1008.7
Unidentified categories							
Unidentified dolphin		812	6	3785	2342.6	2413.0	897.0
Unidentified rorqual	*Balaenoptera* sp.	155	119	3626	2139.8	2171.0	1035.8
Unidentified mesoplodont	*Mesoplodon* sp.	4	1756	2457	1985.2	1864.0	324.6
Unidentified beaked whale		30	476	3430	1892.9	1920.5	760.1
Unidentified large whale		47	122	3615	2022.9	2042.0	909.5
Unidentified small whale		16	354	3520	1996.9	1955.5	1079.0
Unidentified whale		97	91	3623	2184.9	2412.0	1074.1
Unidentified cetacean		20	49	3623	2305.2	2349.0	1032.3
Unidentified pinniped		33	88	3632	2214.2	2604.0	1196.6

While the bulk of the data came from efforts that recorded all marine mammal sightings systematically (Palacios, 2003), note that the listed order may not necessarily represent the true frequency with which these species are sighted in the study area because data for humpback whales (Félix et al., 2011) and sperm whales (Cantor et al., 2017) came in part from species-specific compilations and therefore may be overrepresented. Summary statistics for depth are given, using SRTM15+ bathymetry data (Tozer et al., 2019) available from https://topex.ucsd.edu/WWW_html/srtm15_plus.html. NA, Not Applicable.

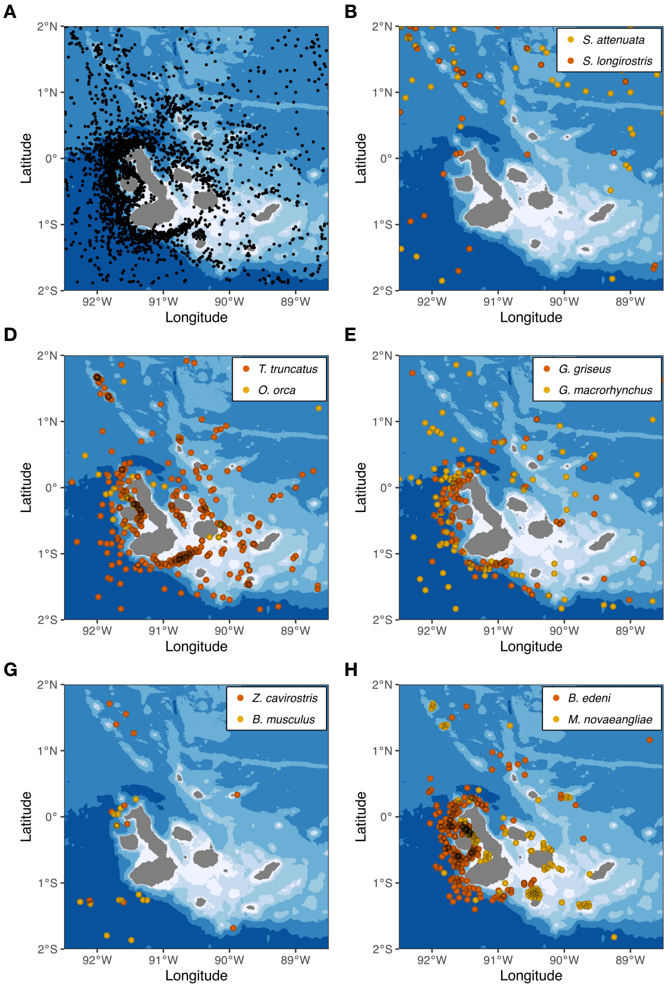

FIGURE 2

Maps depicting the distribution of 14 cetacean species commonly seen in Galápagos waters. **(A)** Locations of all marine mammal sightings (identified and unidentified) from a compilation of sightings (n = 3,227), used here as a proxy for search effort. **(B)** Sighting locations for *S. attenuata* (n = 75) and *S. longirostris* (n = 45). **(C)** Sighting locations for *D. delphis delphis* (n = 339) and *S. coeruleoalba* (n = 126). **(D)** Sighting locations for *T. truncatus* (n = 346) and *O. orca* (n = 29). **(E)** Sighting locations for *G. griseus* (n = 101) and *G. macrorhynchus* (n = 93). **(F)** Sighting locations for *P. crassidens* (n = 10) and *P. macrocephalus* (n = 260). **(G)** Sighting locations for *Z. cavirostris* (n = 11) and *B. musculus* (n = 17). **(H)** Sighting locations for *B. edeni brydei* (n = 291) and *M. novaeangliae* (n = 88). Marine mammal sighting data from Palacios (1999b), Palacios and Salazar (2002), Palacios (2003), Félix et al., (2011), and Cantor et al., (2017), used with permission or under Creative Commons licenses CC BY and CC BY-NC. Bathymetry data from SRTM15+ (Tozer et al., 2019), available from https://topex.ucsd.edu/WWW_html/srtm15_plus.html.

dolphins (*D. delphis delphis*) from the archipelago during the 1997-98 and 2010 El Niño events, when upwelling, productive conditions were suppressed. In the case of the sperm whale, a long-term study spanning the period 1985-2014 revealed large inter-decadal fluctuations in the number of animals visiting Galápagos each year (Cantor et al., 2017; Eguiguren et al., 2021), a result of the movements in and out of the archipelago undertaken by this highly social and widely roaming species (Whitehead et al., 1997; Cantor et al., 2017).

Finally, Palacios (2003) investigated the community ecology of Galápagos cetaceans in relation to oceanographic conditions through non-metric multidimensional scaling, based on nine species with sufficient occurrence data (Figure 5). The ordination provided a two-axis solution (86% and 4.2% of the information in the data, respectively), with axis 1 representing the dominant environmental gradient in the study area, contrasting upwelling conditions close to the islands at the negative end with warm and phytoplankton-poor conditions away from the islands at the positive end, and with sample units sorting out along this gradient (Figure 5A). Species showed distinct functional responses along this gradient, with pantropical spotted (*S. attenuata*) and spinner dolphin (*S. longirostris*) occurrence increasing towards the positive end; common bottlenose dolphins (*T. truncatus*), Risso's dolphins (*G. griseus*), and Bryde's whales increasing towards the negative end; and short-beaked common dolphins, short-finned pilot whales (*G. macrorhynchus*), sperm whales, and striped dolphins (*S. coeruleoalba*) peaking somewhere along these two extremes (Figure 5B). Axis 2 only explained a small amount of the information in the data and was unrelated to the environmental variables considered (Palacios, 2003). These results shed insight on how the complex oceanographic conditions around Galápagos support a diverse cetacean community with distinct habitat preferences and distribution patterns (Palacios, 2003).

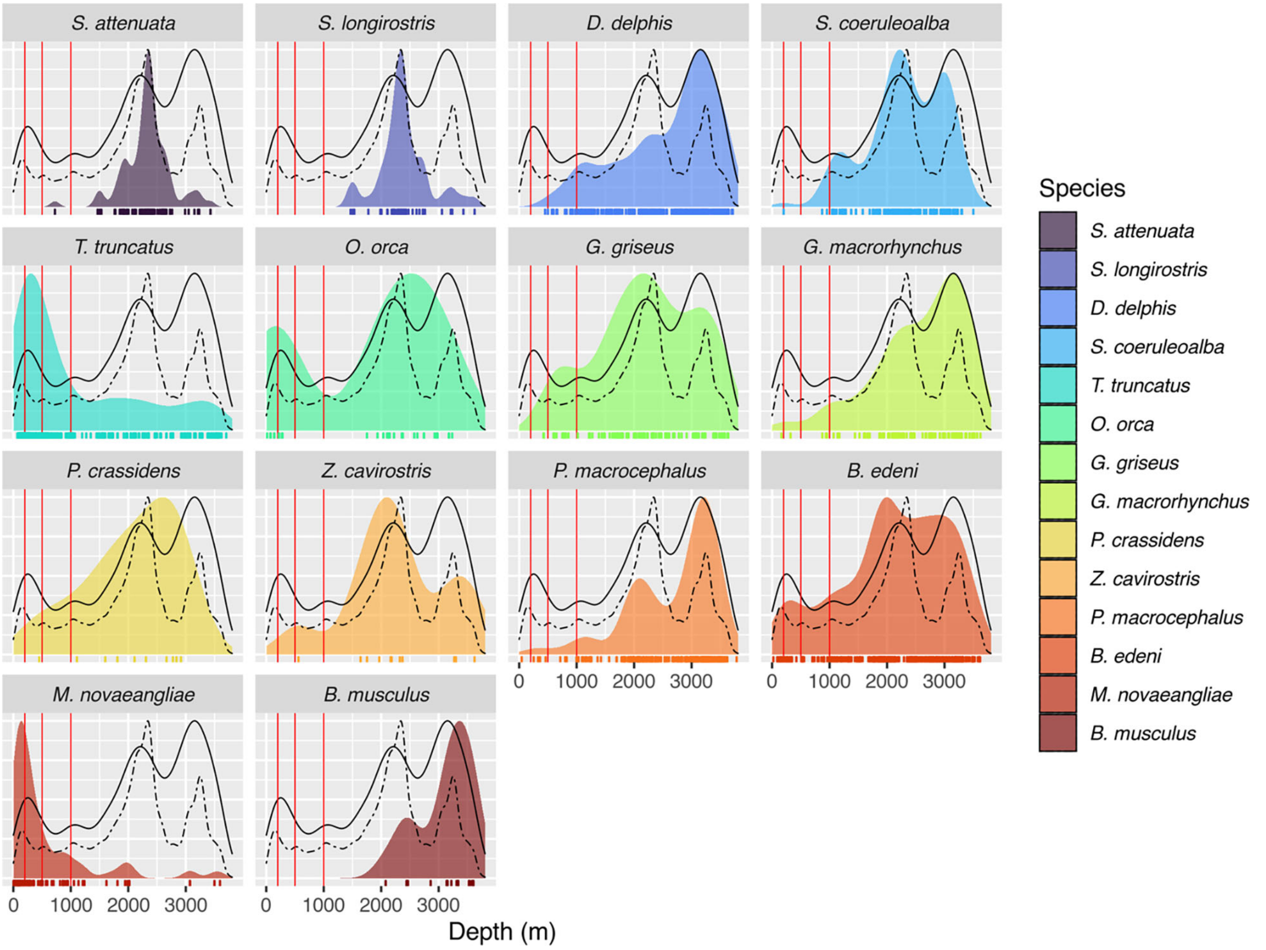

FIGURE 3
Probability density plots of the distribution of seafloor depth for sighting locations of 14 cetacean species commonly seen in Galápagos waters, as shown on the maps in Figure 2. For reference, black dashed curve is the probability density of seafloor depth for the full study area (see Figure 1B) and black solid curve is the probability density of seafloor depth for all marine mammal sightings, identified and unidentified (see Figure 2A). The three vertical red lines indicate depths of 200, 500, and 1000 m, respectively. Marine mammal sighting data from Palacios (1999b); Palacios and Salazar (2002); Palacios (2003), Félix et al., (2011), and Cantor et al. (2017), used with permission or under Creative Commons licenses CC BY and CC BY-NC. Bathymetry data from SRTM15+ (Tozer et al., 2019), available from https://topex.ucsd.edu/WWW_html/srtm15_plus.html.

4 Research priorities

The above review demonstrates that the biologically productive Galápagos Archipelago is an area that attracts and sustains an outstanding cetacean diversity. However, beyond information on spatial and temporal occurrence, little is known about the biology, ecology, and stock structure of most cetacean species in Galápagos waters or about the connectivity of their movements between the archipelago and other habitats in the ETP. This information is necessary for assessing the status of cetacean populations in Galápagos and for developing appropriate management and conservation measures. In this section, we identify 10 critical knowledge gaps along five topical priority areas for future ecological research on cetaceans in Galápagos based on feasibility and scientific merit: I) spatiotemporal occurrence, II) population assessment, III) health assessment, IV) social ecology, and V) trophic ecology. These knowledge gaps and priorities are summarized in Table 2, with consideration of relevant methodological approaches, species most amenable to these approaches, and the outcomes that may be expected from short- and long-term efforts. Although most of the knowledge gaps require long-term efforts (years to decades), short-term efforts (months to years) will be crucial for generating the necessary baseline information. We emphasize that these priorities are based on our combined experiences and perceptions as international academic scientists conducting cetacean research in Galápagos, as detailed in our Positionality Statement in Section 6. By advancing these priorities, our goal is to catalyze discussion and consultation leading to setting a participative research agenda among relevant institutions, local stakeholders, and the broader scientific community interested in advancing cetacean research, management, and conservation in Galápagos.

4.1 Priority I: Spatiotemporal occurrence

4.1.1 Knowledge gap 1: Distribution

The shallow (< 500 m) and coastal waters of the central and eastern part of the archipelago have received comparatively less effort than the deep waters (> 1500 m) of the western part (Figure 2A), and

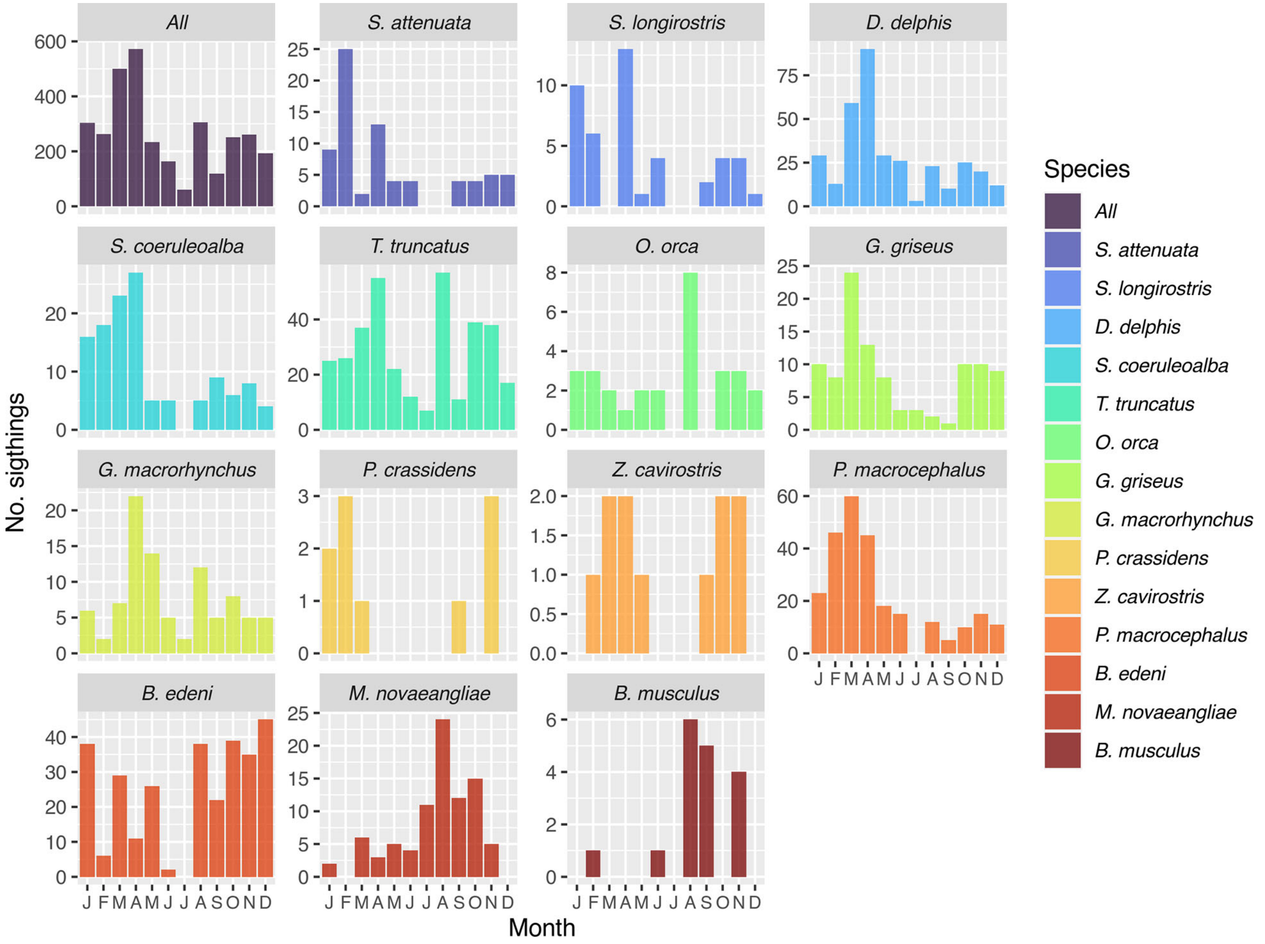

FIGURE 4
Histogram plots of number of sightings by month for 14 cetacean species commonly seen in Galápagos waters. Marine mammal sighting data from Palacios (1999b); Palacios and Salazar (2002); Palacios (2003), Félix et al. (2011), and Cantor et al. (2017), used with permission or under Creative Commons licenses CC BY and CC BY-NC.

therefore our understanding of cetacean occurrence and habitat use in neritic waters is incomplete. For example, common bottlenose dolphins appear to occur primarily in neritic waters throughout the archipelago, but sightings tend to be strongly clustered (Palacios and Salazar, 2002; Palacios, 2003; Figure 2B). Bryde's whales are common in the highly productive western part of the archipelago (Palacios and Salazar, 2002; Palacios, 2003; Figure 2G), but a temporally variable "hotspot" of occurrence has been also reported off San Cristóbal Island, on the eastern part, that appears to be driven by a localized upwelling (Denkinger et al., 2013; Biggs et al., 2017). These illustrative examples indicate that further work is needed to characterize cetacean distribution and their relationship to fine-scale oceanographic and topographic processes (Houvenaghel, 1978; Schaeffer et al., 2008; Figueroa, 2021; Neave et al., 2021).

4.1.2 Knowledge gap 2: Local and regional movements

Many studies of cetaceans around oceanic islands throughout the world have identified distinct island-associated populations (e.g., Baird et al., 2009a; Baird et al., 2013a; Oremus et al., 2012; Quérouil et al., 2013; Kiszka et al., 2014; Estrade and Dulau, 2020; Panicker et al., 2022; Sambolino et al., 2022). Further work is needed to determine whether there are island-associated cetacean populations in Galápagos, to what islands, their inter-island movements, and their differentiation with pelagic populations. Studies are also needed to characterize the movements of Bryde's whales within the archipelago and their connection to other areas where the species is seen along the mainland (Castro et al., 2017; Rasmussen and Palacios, in press[1]) and the offshore ETP (Wade and Gerrodette, 1993; Hamilton et al., 2009).

4.1.3 Methodological approaches

Future studies could combine multiple sampling approaches to advance our understanding of cetacean spatiotemporal occurrence in Galápagos (Table 2). First, for most species, this can be achieved with continued collection of sighting data (time, geographic position, species, group size, and photography for confirmation and archiving). These observational data are straightforward to record by researchers as well as by naturalists and citizen scientists aboard cruise ships (e.g., Palacios and Salazar, 2002; Denkinger et al., 2013; Alves et al., 2018; Denkinger et al., 2020). Second, photo-identification efforts will allow for the study of local and regional movements of individuals within and beyond Galápagos (e.g., Baird

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[1] Rasmussen, K., and Palacios, D. M. Bryde's whale (Balaenoptera edeni) aggregation area in the gulf of chiriqui, Panama. Rev. Biol. Trop.

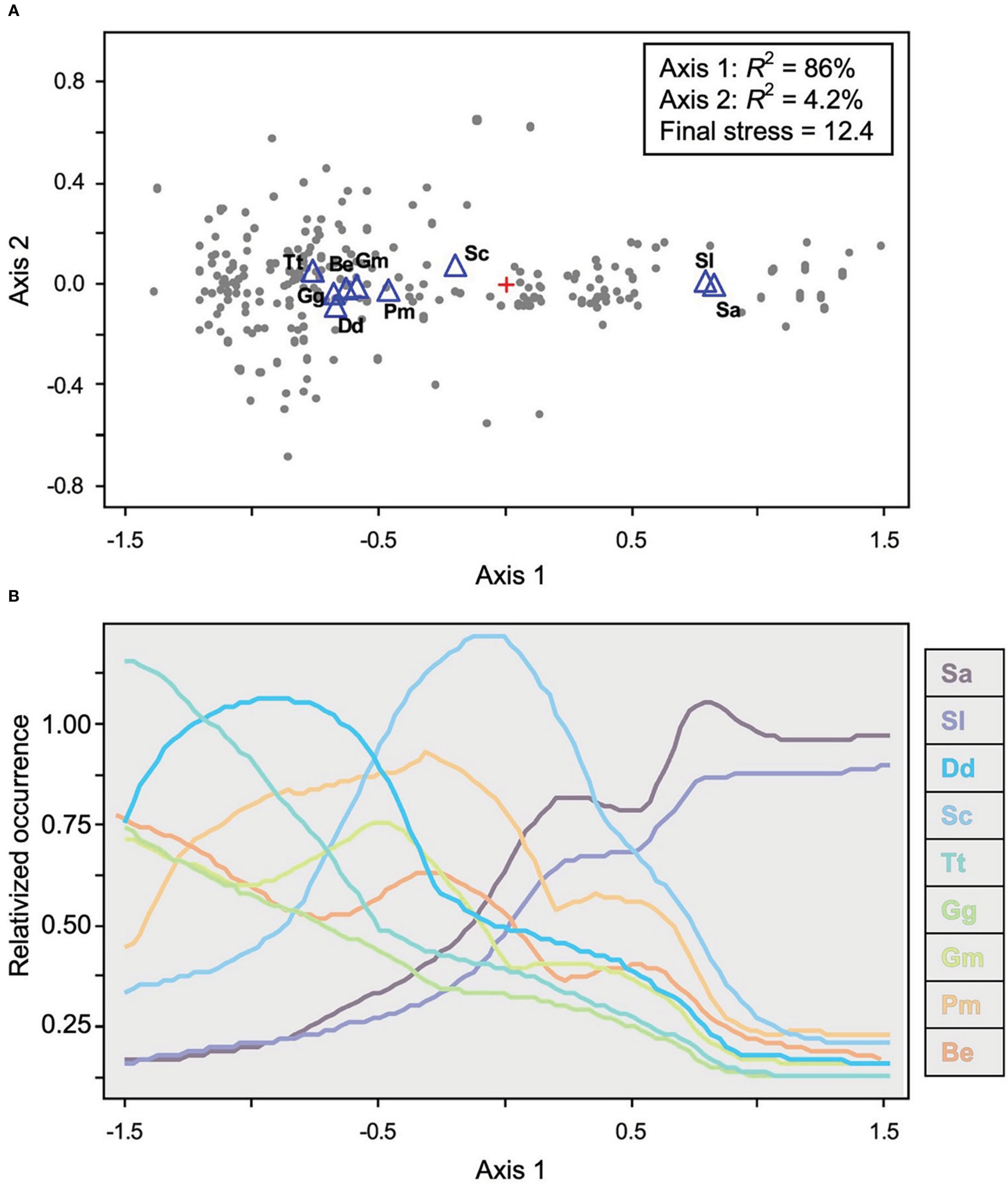

FIGURE 5
Non-metric multidimensional scaling ordination of the Galápagos cetacean community, based on nine species with acceptable sample size. **(A)** Biplot of the ordination scores on the two main axes, with gray dots corresponding to 904 sample units (0.25-degree grid cells) where species occurrence was evaluated. Open blue triangles are the average positions of the nine species, calculated by weighted averaging. **(B)** Cetacean community gradient (coenocline) for the nine species in the ordination, showing species responses (relativized occurrence) along axis 1, the dominant environmental gradient. Curves correspond to an envelope that includes points falling within two standard deviations of a running mean along the axis. Sa, *S. attenuata*; Sl, *S. longirostris*; Dd, *D delphis delphis*; Sc, *S. coeruleoalba*; Tt, *T. truncatus*; Gg, *G griseus*; Gm, *G macrorhynchus*; Pm, *P. macrocephalus*; and Be, *B edeni brydei*. Adapted from Palacios (2003).

et al., 2013a; Baird, 2016; Alves et al., 2018; Alves et al., 2019; Pacheco et al., 2019; Ferreira et al., 2021; Dinis et al., 2021), particularly for species that are easy to identify and often have distinctive markings (*T. truncatus, G. macrorhynchus, P. crassidens, O. orca, P. macrocephalus*, and *M. novaeangliae*) (e.g., Cantor et al., 2016; Denkinger et al., 2020). Third, electronic tagging will allow detailed tracking of the movements and migrations of the large whales (*B. edeni brydei, B. musculus, M. novaeangliae, P. macrocephalus*) as well as the larger-bodied Delphinids (*G. griseus, G. macrorhynchus, P. crassidens*) and Ziphiids (*Z. cavirostris* and *Mesoplodon* spp.) that use Galápagos waters. While more costly, logistically demanding, and requiring welfare considerations, tagging is the most feasible way to reveal the routes of migratory whales (e.g., Silva et al., 2013; Prieto et al., 2014; Hucke-Gaete et al., 2018; Fonseca et al., 2022), which will

TABLE 2 Summary of the proposed priorities for ecological research on cetaceans in Galápagos, along with knowledge gaps, suggested methodological approaches, expected outcomes in the short- (months to years) and long-term (years to decades), and species that are best suited for these approaches.

Priority	Knowledge gap	Methodological approaches	Short-term outcomes (months to years)	Long-term outcomes (years to decades)	Target species
I. Spatiotemporal occurrence	1. Distribution	Sightings, observation and/or photography, passive acoustic monitoring	Distribution maps	Spatiotemporal patterns in occurrence	*T. truncatus, B. edeni brydei*
	2. Local and regional movements	Photo-identification, satellite tagging	Migration routes, home ranges	Local and regional connectivity maps, habitat selection	*T. truncatus, G. macrorhynchus, P. crassidens, O. orca, P. macrocephalus, M. novaeangliae, B. edeni brydei, B. musculus*
II. Population assessment	3. Density	Boat-based or aerial distance sampling	One-off density estimate	Density trends	*S. attenuata, S. longirostris, D. delphis delphis, S. coeruleoalba, G. griseus, G. machrorhynchus, M. novaeangliae, B. musculus*
	4. Abundance	Dedicated photo-identification	One-off population size estimate	Abundance trends, estimates of survival, immigration, emigration, capturability	*T. truncatus, O. orca, B. edeni brydei*
	5. Population structure	Photogrametry, drone-based morphometry, biopsy sampling (genetic sexing)	Individual estimates of sexual maturity, age class, sex	Identification of social units, stocks, or subpopulations, delineation of population structure by sex and age	*O. orca, P. macrocephalus*
III. Health assessment	6. Body condition	Photography, dedicated drone-based morphometry	Baseline nutritional status, one-off health condition	Temporal trends in nutrition status and body conditions relative to life history	*O. orca, P. macrocephalus, B. edeni brydei, M. novaeangliae, B. musculus*
	7. General health status	Dedicated photography, biopsy sampling, breath sampling	Skin lesions and injuries, skin diseases, one-off pollutant load, microbiome	Temporal trends in lesions, diseases, pollutants	*T. truncatus, G. macrorhynchus, O. orca, P. macrocephalus, B. edeni brydei, M. novaeangliae, B. musculus*
IV. Social ecology	8. Social organization	Observation and photography	Group size, group composition	Temporal trends in group composition relative to life history	*T. truncatus, G. macrorhynchus, O. orca, P. macrocephalus*
	9. Social structure	Observation and photography	Identification of previously known social groups	Social units, behaviorally distinct cultural groups	*T. truncatus, G. macrorhynchus, O. orca, P. macrocephalus*
V. Trophic ecology	10. Foraging and diet	Biopsy sampling (stable isotopes), fecal sampling, sloughed skin sampling	Trophic position, diet	Trends in food resources use, interspecific trophic niche overlap	*T. truncatus, G. griseus, G. macrorhynchus, P. macrocephalus, B. musculus*

enable researchers to create connectivity maps across coastal and oceanic habitats in the ETP and beyond (e.g., Davies et al., 2021; Boteler et al., 2022). For the Delphinids and Ziphiids, tagging can provide crucial information on residency, site fidelity, and habitat use (e.g., Baird et al., 2009b; Baird et al., 2013b; Abecassis et al., 2015; Baird, 2016;). Finally, passive acoustic monitoring with towed or moored hydrophones (Mellinger et al., 2007) would be especially useful for detecting deep-diving and cryptic species (*K. sima*, Ziphiids), as well as Odontocetes or Balaenopterids with distinctive acoustic signatures, such as clicking sperm whales and singing humpback and blue whales. Relative to visual methods, acoustic data may not always provide accurate species identification or group size estimates, but recent advances on automated detection of broad-band echolocation clicks and tonal sounds (e.g., Gillispie et al., 2009; Frasier et al., 2017), as well as machine learning tools (e.g., Beslin et al., 2018; Bermant et al., 2019; Woodward et al., 2020) offer promising solutions.

Such multiplatform data collection is increasingly being used to generate predictive habitat suitability maps (e.g., Thorne et al., 2012; Bouchet et al., 2015; Tobeña et al., 2016; Tardin et al., 2017; Fiedler et al., 2018; Tardin et al., 2019; Correia et al., 2021; Fernandez et al., 2021), even with short-term efforts (months to years). In the long term (years to decades), the accumulation of such data will increase the coverage, reliability, and scope of these maps and help refine the characterization of species-specific hotspots of occurrence and their fluctuations in response to environmental variation such as El Niño Southern Oscillation and climate change (e.g., Llapapasca et al., 2018; Becker et al., 2019; Becker et al., 2022). This information could be used to identify cetacean areas of significant importance within Galápagos, as has been done for other locally threatened marine taxa (Edgar et al., 2008; Ventura et al., 2019) as well as for the highly migratory elasmobranchs (Hearn et al., 2010; McKinley et al., 2022). Beyond helping researchers improve their ecological understanding of cetacean occurrence patterns, predictive habitat suitability maps are increasingly used as management tools (e.g., Sahri et al., 2021), and they could help to delineate areas of importance within the GMR that have particularly high conservation significance and yet may be subject to ongoing anthropogenic disturbances.

4.2 Priority II: Population assessment

4.2.1 Knowledge gaps 3 and 4: Density and abundance

Unlike pinnipeds, for which population assessments have been conducted on a regular basis throughout Galápagos (e.g., Páez-Rosas et al., 2021), very few studies have reported population assessments for cetaceans in Galápagos (Palacios and Forney, 2008; O'Hern et al., 2017; Whitehead and Shin, 2022), and there is no formal ongoing program for monitoring cetacean populations. Yet, baseline information on demographic parameters, such as density, abundance, survival, and recruitment, is essential for understanding population status and dynamics, and to unravel the relative importance of competition and predation in structuring the local cetacean community relative to the influences of environmental variability. Ultimately, monitoring temporal trends in population parameters provides information that is immediately useful for guiding conservation decisions (e.g., Taylor et al., 2007; Boyd and Punt, 2021).

4.2.2 Knowledge gap 5: Population structure

Studies are needed to assess the relationship of common bottlenose dolphins in Galápagos to the recently recognized subspecies of offshore bottlenose dolphin (*T. truncatus nuuanu*) or other ecotypes in the ETP (Palacios et al., 2004; Costa et al., 2022) for appropriate management. Other examples include elucidating the relationship of Bryde's whales and sperm whales seen in Galápagos to those that occur in offshore waters and in the jurisdictions of countries bordering the ETP.

4.2.3 Methodological approaches

To estimate demographic parameters of species whose individuals are likely to be re-identified multiple times, such as local populations (*T. truncatus, B. edeni brydei*) or those observed in long-lasting groups (*O. orca*), we suggest designing mark-recapture studies based on photo-identification data (Urian et al., 2015; Wickman et al., 2020; Hammond et al., 2021) (Table 2). In the short term, analyzing photo-identification data with simple mark-recapture models (White and Burnham, 1999) is sufficient to generate one-off estimates of abundance or minimum population size (e.g., Baird et al., 2008; Baird et al., 2009a; Baird et al., 2009b). With an appropriate sampling design for photo-identification effort, long-term data will allow more elaborate mark-recapture modeling to estimate a range of other demographic parameters (e.g., survival, emigration, recruitment; see Pollock et al., 1982; White and Burnham, 1999). Our understanding of population structure and dynamics of cetacean species in Galápagos can be much improved by considering individual covariates, such as sex, age, and/or maturity classes, when estimating parameters with mark-recapture models. This information can be obtained using a variety of field and laboratory approaches: some species are sexually dimorphic (*O. orca, P. macrocephalus*) and others can be sexed genetically with remote biopsy sampling; hormonal analyses can indicate reproductive condition; epigenetic methods can be used for aging individuals (e.g., Polanowski et al., 2014); and boat-based photogrammetry and drone-based morphometry can generate body length estimates, especially of large Odontocetes (e.g., Kotik et al., 2022).

Although some species are common and/or easy to identify, many are unsuited for photo-identification-based mark-recapture modeling, either because the populations and/or their ranging areas are very large (*M. novaeangliae, B. musculus*), or because they are typically seen in large, fast-moving groups (*D. delphis delphis, S. coeruleoalba, S. attenuata, S. longirostris*). For these cases, archipelago-wide efforts would be better suited to distance sampling using line-transect surveys (Buckland et al., 2001; Buckland et al., 2015). This approach can generate one-off density or abundance estimates in the short-term (Palacios and Forney, 2008; O'Hern et al., 2017), as well as trends over time (Table 2). Distance sampling requires dedicated surveys with properly pre-defined transect lines, trained personnel, and careful consideration of assumptions and caveats (Thomas et al., 2007; Faustino et al., 2010), but it remains a cornerstone of cetacean population monitoring. This methodology is typically conducted from large research vessels capable of open-ocean operation (e.g., O'Hern et al., 2017), but has also been adapted to sailboats (e.g., Palacios and Forney, 2008), small boats (Dawson et al., 2008), and aircraft (e.g., Panigada et al., 2011). Line-transect surveys, either boat-based or aerial, can be cost-effective solutions for estimating density and abundance of a wide range of cetacean species in coastal areas (Aragones et al., 1997; Williams and Thomas, 2009; Lambert et al., 2019).

4.3 Priority III: Health assessment

4.3.1 Knowledge gaps 6 and 7: Body condition and general health status

Other than basic documentation of stranding events (Palacios et al., 2004), health assessments for cetaceans in Galápagos are absent. Studies have shown that environmental perturbations such as El Niño as well as exposure to anthropogenic activities near human population centers have impacts on the body condition and general health of teleost fish (Lamb et al., 2018) and pinnipeds (Brock et al., 2013a; Brock et al., 2013b; Paéz-Rosas et al., 2016; Páez-Rosas et al., 2021), suggesting that cetaceans may also be affected by these stressors.

4.3.2 Methodological approaches

Health status in cetaceans can be assessed through monitoring of the nutritional status (Joblon et al., 2014; Christiansen et al., 2020) and the prevalence of cutaneous conditions of individuals and populations (Hart et al., 2012; Soares et al., 2022), which can reveal key insights about population status, the quality of the surrounding environment, and interactions with human activities (e.g., boat traffic, fisheries). A straightforward way to investigate body condition and external lesions and injuries in cetaceans is through visual analyses of photographic and video data. For instance, footage recorded from drones offers a privileged bird's-eye view from which researchers can extract accurate quantitative morphometric data to evaluate body condition and health status (e.g., Christiansen et al., 2020; Horton et al., 2019; Bierlich et al., 2021) (Table 2). Drones can also be adapted to sample the microbial and viral communities in the breath of small and large cetaceans as a complementary approach to assess their health (e.g., Centelleghe et al., 2020). Drone-based photogrammetry and respiratory microbiota sampling may be more suitable for large whales in Galápagos (*B. edeni brydei, B. musculus, M. novaeangliae, P. macrocephalus*) (e.g., Dawson et al., 2017), but coupling drone images with laser altimeters may generate suitable high-resolution aerial photogrammetric data for smaller cetaceans as well (see Bierlich et al., 2021).

While drone sampling requires dedicated research efforts and specific safety and sampling protocols (e.g., Raoult et al., 2020), boat-based photography can provide a quick assessment of general body condition (e.g., "emaciated", "thin", "good") based on fat deposition in specific body parts (e.g., Joblon et al., 2014; Soares et al., 2022; Wachtendonk et al., 2022). Such photographic records can be collected even from opportunistic platforms and can generate insights on the cutaneous lesions and diseases of a range of cetacean species. Visual analyses of the gross characteristics of skin conditions from photographs can indicate cases that are potentially related to viral, fungal, or bacterial aetiology (e.g., Van Bressem et al., 2007; Van Bressem et al., 2009). Photographic records can also be used to assess injuries indicative of traumatic events; wounds and scars, for instance, can suggest predation pressure (Best and Photopoulou, 2016; Baird et al., 2022; Capella et al., 2018; Corsi et al., 2022) as well as negative interactions with anthropogenic activities (e.g., Harnish et al., 2019), entanglement in or interactions with fishing gear (e.g., Baird et al., 2014), or collision with boats (e.g., Toms et al., 2020).

Investigating the underlying causes of body and cutaneous conditions in cetaceans, however, requires further laboratory analyses to determine nutritional status and diagnose disease or injury (Table 2). Therefore, we recommend including biological tissue sampling during dedicated surveys whenever feasible. Proper evaluation of cutaneous conditions includes electron microscopy or molecular analyses of skin tissue to confirm a potential pathology (e.g., Groch et al., 2020). Additional analyses of tissue samples should include pollutant loads (e.g., Alava et al., 2009; Remili et al., 2020). On the other hand, although fresh stranded animals can yield tissue samples opportunistically, any dedicated biopsy sampling requires specialized research efforts (i.e., personnel, equipment, storage, and permitting) and are most feasible for the larger-bodied species (i.e., *T. truncatus, G. griseus, G. macrorhynchus, O. orca, P. macrocephalus, B. edeni brydei, B. musculus, M. novaeangliae*).

4.4 Priority IV: Social ecology

4.4.1 Knowledge gaps 8 and 9: Social organization and social structure

Long-term studies of social ecology in Galápagos marine mammals are among the most world-renowned, including pinnipeds (Wolf et al., 2007), sperm whales (Whitehead, 1985; Whitehead, 2003; Cantor and Whitehead, 2015), and killer whales (Denkinger et al., 2020). While we advocate for the continuation of these efforts, studies on other species or aspects of sociality would advance our understanding of social complexity in cetaceans. Investigating the various social systems present in cetaceans (Mann et al., 2000; Rendell et al., 2019) requires understanding four axes: social organization, social structure, care system, and mating system (Kappeler, 2019). This work requires long-term efforts and can be particularly challenging in the marine realm; however, two of these axes, social structure and social organization, are feasible to measure, even with short-term studies.

The diverse Odontocete fauna of Galápagos represents a variety of unique social systems. Matrilineal species like short-finned pilot whales and killer whales (Denkinger et al., 2020) or species with high levels of fission-fusion social dynamics like common bottlenose dolphins and Risso's dolphins are found in Galápagos. Studying their social organization, in terms of group size and composition, as well as their social structure, in terms of number and strength of social associations, will make for interesting comparisons with other oceanic islands where these species have been studied (Pinela et al., 2009; Hartman et al., 2015; Alves et al., 2019; Servidio et al., 2019; Dinis et al., 2021). Even the social structure of the well-studied sperm whale would benefit from continued investigation. Despite being widespread in deep waters (> 1000 m) around Galápagos (e.g., Palacios and Salazar, 2002; Palacios, 2003; Figures 2F and 3), sperm whale habitat use has shifted over the past four decades between the western, northern, and southern parts of the archipelago (Cantor et al., 2016; Eguiguren et al., 2019). These fluctuations possibly reflect different space use by socially distinct clans over time, but further studies are needed to elucidate their cultural and environmental drivers.

4.4.2 Methodological approaches

Basic information on social organization, such as group size (number of individuals estimated in the field and double-checked with photography) and composition (age and/or sex classes, at least for sexually dimorphic species: *P. macrocephalus*, *O. orca*), can always be recorded during both dedicated surveys and from opportunistic platforms (Table 2). Describing social structure, on the other hand, requires tracking social interactions or associations among individuals identified in groups over time (Whitehead, 2008). The need for recurrent re-sighting makes this effort more suitable for species that are reliably identifiable through standard photo-identification techniques and that are common in Galápagos, such as *T. truncatus*, *P. macrocephalus*, *O. orca*, and *G. macrorhynchus* (Table 2). As such data accumulate, a major goal will be to describe patterns of social structure, for instance subdivisions of the population into stable or more socially connected social communities (Weiss et al., 2021). For species living in medium to high levels of fission-fusion dynamics (e.g., *T. truncatus*), subdivision into communities can reflect important aspects of their ecological environment and the level of competition among individuals (e.g., quality and distribution of resources) and reveal key aspects of their social environment (e.g., social preferences and avoidances, spatial overlap, social clustering around behavioral or biological traits; e.g. Machado et al., 2019). For sperm whales, quantifying temporal stability, geographic range, behavioral variation, and acoustic communication will further reveal how social learning and cultural transmission influences the lives of individual whales and erects social barriers across sympatric clans (Rendell and Whitehead, 2003; Cantor and Whitehead, 2015; Cantor et al., 2015; Eguiguren et al., 2019; Eguiguren et al., 2021; Hersh et al., 2022). The delineation of sperm whale populations into culturally driven vocal clans is a key attribute of their population structure to be considered in regional and international conservation efforts to conserve this broadly roaming species (Brakes et al., 2019).

4.5 Priority V: Trophic ecology

4.5.1 Knowledge gap 10: Foraging and diet

Trophic interactions are central for mapping marine food web structures and understanding ecosystem functioning and dynamics, including nutrient cycling and energy flow. Empirical data on predator-resource interactions are the backbone of food web and ecosystem models, which are typically inferred from foraging observations and analysis of stomach contents and feces. For instance, undigested beaks in fecal samples of sperm whales provide a window into the inaccessible guild of demersal and mesopelagic cephalopods (Smith and Whitehead, 2000; Smith and Whitehead, 2001; Whitehead et al., 2001), and are a reliable proxy of foraging success (Whitehead and Rendell, 2004). In contrast to pinnipeds (Páez-Rosas et al., 2012; Urquía and Páez-Rosas, 2019), elasmobranchs (Páez-Rosas et al., 2018; Salinas-de-León et al., 2019), and seabirds (Jiménez-Uzcátegui et al., 2019), studies of diet in cetaceans in Galápagos have been rarely performed (Smith and Whitehead, 2000; Smith and Whitehead, 2001; Palacios et al., 2004). While fresh specimens (e.g., stomach contents) from stranding events are rarely available in Galápagos (Palacios et al., 2004), the establishment of basic protocols for sample collection from stranded cetaceans by designated and properly trained personnel could help fill this gap, while also informing monitoring and conservation strategies (e.g., Peltier et al., 2014).

Among the oceanic Delphinids occurring in Galápagos, ecologically similar species pairs have somewhat distinct distribution patterns, while mixed-species aggregations are relatively rare. For example, short-beaked common dolphins are predominant in the western and southern parts of the archipelago, while striped dolphins occur more often in the northwestern and northern part (Palacios and Salazar, 2002; Palacios, 2003; Figures 2C and 3). Similarly, Risso's dolphins and short-finned pilot whales are both found in the deep waters surrounding the margins of the archipelago, but Risso's dolphins appear to be more closely associated with the steep slopes of the western part of the archipelago (Palacios and Salazar, 2002; Palacios, 2003; Figures 2E and 3). These intriguing patterns suggest some level of habitat selection or niche partitioning, possibly mediated by foraging specializations (e.g., Whitehead et al., 2001; Quérouil et al., 2008) that deserve further study through methodologies such as those described below.

4.5.2 Methodological approaches

The investigation of the role of prey and predators in ecosystem dynamics can be largely expanded by biochemical tracer analyses (e.g., Boecklen et al., 2011; Pethybridge et al., 2018). Stable isotopes, fatty acid signatures, and other trace elements can complement our understanding of the role of cetaceans as both prey and predators. For instance, combining carbon and nitrogen stable isotopic analysis of bulk tissue and their constituent amino acids can reveal key insights on cetacean diet at the population level, and trophic position and interactions at the community level, over time (Teixeira et al., 2022). Such biomarkers can be accessed from stranded and preserved animals in scientific collections, but also from tissue samples of living animals (e.g., Teixeira et al., 2022). We suggest increased effort for collecting skin and blubber tissues of medium species (*T. truncatus*, *G. griseus*, *G. macrorhynchus*) and large species (*B. musculus*), both with remote biopsy systems and non-invasively, such as collecting sloughed skin of Odontocetes that frequently shed epithelial tissue (*P. macrocephalus*; e.g., Marcoux et al., 2007) (Table 2). Long-term data on biochemical tracers will provide a unique opportunity for assessing trends in resource use over time and space, and for relating these trends to environmental variation (e.g., El Niño Southern Oscillation; Arnés-Urgellés et al., 2021). Beyond contributing to mapping the local Galápagos food webs (e.g., Okey et al., 2004; Alava, 2009), this approach will also allow us to quantify trophic niche overlap between and within species (Enríquez-García et al., 2022), and investigate individual and ontogenetic variation in foraging, and the extent to which such variation is driven by resource partitioning and intra- and interspecific competition (e.g., Teixeira et al., 2022).

5 Discussion

The biologically productive waters surrounding the Galápagos Archipelago form a distinct oceanic insular ecosystem within the greater ETP. Our review confirmed that this ecosystem supports a large and diverse cetacean community, but beyond presence and distribution information, for most species not much more is known about habitat use, population structure, health, and social ecology. In contrast, significantly more efforts have been devoted to the study and monitoring of Galápagos invertebrates (e.g., Edgar et al., 2004; Edgar et al., 2008; Edgar et al., 2011), fishes (e.g., Schiller et al., 2014; Lamb et al., 2018; Salinas-de-León et al., 2019), pinnipeds (e.g., Páez-Rosas et al., 2012; Brock et al., 2013a; Brock et al., 2013b; Paéz-Rosas et al., 2016; Páez-Rosas et al., 2018; Urquía and Páez-Rosas, 2019; Páez-Rosas et al., 2021), and seabirds (e.g., Anchundia et al., 2014; Tompkins et al., 2017; Jiménez-Uzcátegui et al., 2019; Arauco-Shapiro et al., 2020). Admittedly, cetacean research is comparatively more expensive and more logistically demanding. However, at present, the study of cetaceans in Galápagos lags other tropical and subtropical oceanic insular ecosystems around the world, especially the Hawaiian (e.g., Baird et al., 2013b; Baird, 2016; Kratofil et al., 2023) and Macaronesian (e.g., Silva et al., 2014; Hartman et al., 2015; Fais et al., 2016; Tobeña et al., 2016; Alves et al., 2018; Alves et al., 2019; Romagosa et al., 2020; Dinis et al., 2021; Ferreira et al., 2021; Herrera et al., 2021) archipelagoes, where long-term studies have been generating significant new information in recent years. We acknowledge that, being located in the global north, the latter two ecosystems have benefited from established expertise, access to financial resources, and robust legislation mandating marine mammal research and protection that are generally not available in the global south. Further, as cetaceans are not considered extractive resources in Galápagos and additionally receive some level of legal protection throughout Ecuador (whales, at least), they are generally not "on the radar" of government entities in charge of marine resource management.

Given the logistical and funding challenges of conducting cetacean research in Galápagos, we suggest that the development of a collaborative research agenda should include specific actions aimed at establishing and strengthening meaningful partnerships between foreign and local researchers, and include the involvement of governmental and non-governmental entities, as well as stakeholders. Some existing examples of such partnerships include the long-term monitoring of cetacean presence using opportunistic sightings collected by naturalist guides working aboard cruise ships through a program implemented by the Galápagos National Park and the Charles Darwin Foundation (Palacios and Salazar, 2002; Denkinger et al., 2013; Denkinger et al., 2020), or the population assessment surveys for cetaceans conducted through a collaboration between U.S. academics and the Ecuadorian Navy through INOCAR, its institute for oceanographic and Antarctic research (Biggs et al., 2017; O'Hern et al., 2017). Continued partnership with the local tourism industry, in particular, would provide additional opportunities for participation by trained naturalists and citizen scientists in opportunistic but valuable data collection that would enhance and enrich research goals in a relatively inexpensive manner (e.g., Van Cise et al., 2021). An increased presence of researchers and observers in the field would have a side benefit related to the management of human activities in Galápagos by promoting better-guided ecotourism, better regulated vessel traffic, and enhanced surveillance and reporting of illegal fishing activities within the GMR (e.g., Cerutti-Pereyra et al., 2020; Bonaccorso et al., 2021; Global Fishing Watch, 2021).

Other aspects to be considered during development of a collaborative research agenda include capacity building and training of local researchers; optimization the research permit application required by the Galápagos National Park based on the specific needs and requirements cetacean research, including vessel operation and sample collection and export (if appropriate); and fostering the adoption of integrative data sampling and data sharing protocols. On the topic of data sharing, efforts can be optimized if research groups contribute to centralized repositories that provide the technological infrastructure, data access permissions, and terms of use. Such data repositories include those that are taxa-specific but otherwise accept a wide variety of data types (e.g., Halpin et al., 2006), as well as those specializing on photo-identification (e.g., Olson et al., 2020; Berger-Wolf et al., 2017) or tracking data (e.g., Block et al., 2016; Kays et al., 2022). Centralized repositories have the additional advantage of facilitating the curation of citizen science data; for instance, photographs from the public could be perused by specialists to verify species identification (e.g., Jarić et al., 2020), individual photo-identification (e.g., Cheeseman et al., 2021), and assessment of cutaneous and body conditions (e.g., Hart et al., 2012). Ultimately, these collective efforts will foster collaborative research, accelerate discovery, maximize the use of funds, promote the training of local scientists, and create opportunities for the professional development of early-career researchers as well as established scientists and conservation practitioners.

In conclusion, an improved understanding of Galápagos cetaceans will help quantify the ecological role that megafauna plays in connecting oceanic insular ecosystems (Boteler et al., 2022) and further establish the importance of marine reserves for transboundary conservation (e.g., Halpern, 2003; Game et al., 2009; Tetley et al., 2022). Indeed, in the marine realm, cetaceans are firm favorites for raising public awareness about the need for conservation actions (i.e., "flagship species"; Veríssimo et al., 2011) and for expanding these conservation actions to their habitats and ecological communities ("umbrella species"; Caro and O'Doherty, 1999). The information generated from our proposed approaches will also inform the management of the effects of climate change (Dueñas et al., 2021) and of human activities in Galápagos, including the impact of illegal fishing within the GMR, which not only can lead to direct negative interactions (such as megafauna bycatch; Alava et al., 2019; Cerutti-Pereyra et al., 2020) but also contribute to the overexploitation of marine resources (e.g., Usseglio et al., 2016; Bonaccorso et al., 2021). Avoiding such downstream cascading effects on Galápagos' unique biota, environment, and socio-ecological systems (Denkinger and Vinueza, 2014; Walsh and Mena, 2016) will require tailored conservation plans that consider cetaceans as integral components of the ecosystem.

6 Positionality statement

We are biologists and academics in the fields of marine ecology, population ecology, and behavioral ecology, with a focus on marine mammals and other marine megafauna. We share a keen interest in the study of Galápagos cetaceans. As international scientists, we have a variety of experiences conducting cetacean research in Galápagos, but we are neither Ecuadorian citizens nor Galápagos residents. As such, we are not active participants in these communities, nor do we depend, economically or otherwise, from research conducted in Galápagos. We do share cultural aspects with the Ecuadorian people and have professional ties with its research community.

Born and raised in Colombia, DP is a marine ecologist and oceanographer with Ph.D. studies and post-doctoral appointments from institutions in the U.S., where he has resided for 27 years. He has participated in research expeditions in Galápagos in 1993-94, 2000, and 2005, and has additionally visited Galápagos on multiple occasions to participate in scientific workshops. DP is currently an Associate Professor at Oregon State University and remains actively involved in scientific research and conservation throughout Latin America.

MC Is a behavioral ecologist, born and raised in Brazil, who completed undergraduate and graduate degrees at Brazilian institutions before undertaking Ph.D. studies and post-doctoral appointments in universities in the global north. MC has been participating in research expeditions in Galápagos since 2013, starting with his Ph.D. research on the social ecology of sperm whales, as part of a multi-decadal collaboration between a Canadian university and several Ecuadorian and Galápagos institutions. MC is currently an Assistant Professor at Oregon State University in the U.S. and remains an active collaborator in Latin American research projects, including the long-term sperm whale research program in Galápagos.

Despite our collective experience in Galápagos, we acknowledge that we are still external actors. As such, our understanding of the priorities for research in the area is unintentionally influenced by our worldviews, which are themselves biased by our own social and cultural origins, privileges, academic trajectories, and personal experiences. For these reasons, we emphasize that our proposed priorities should be assessed by Ecuadorian and Galápagos governmental institutions in broad and inclusive consultation with stakeholders and the scientific community prior to development and implementation of a research agenda.

Author contributions

DP conceived the study, which was further developed in collaboration with MC. DP prepared Table 1 and Figures 1–5. MC prepared Table 2. DP and MC wrote the manuscript and contributed to revisions. All authors contributed to the article and approved the submitted version.

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Conflict of interest

Publisher's note

References

Abecassis, M., Polovina, J., Baird, R. W., Copeland, A., Drazen, J. C., Domokos, R., et al. (2015). Characterizing a foraging hotspot for short-finned pilot whales and blainville's beaked whales located off the west side of hawai'i island by using tagging and oceanographic data. *PLoS One* 10 (11), e0142628-22. doi: 10.1371/journal.pone.0142628

Acuerdo Ministerial No. 196 (1990). *Ministerio de industrias* (Corte Constitucional del Ecuador). Registro Oficial No. 458.

Acuerdo Ministerial No. MAATE-2022-019 (2022). Ministerio de ambiente, agua y transición ecológica. *Corte Constitucional del Ecuador. Registro Oficial No.* 32, 3–11.

Acuerdo Ministerial No. MAATE-2022-039 (2022). Ministerio de ambiente, agua y transición ecológica. *Corte Constitucional del Ecuador* 59, 2–12. Registro Oficial No.

Acuerdo Ministerial No. MAATE-2022-041 (2022). Ministerio de ambiente, agua y transición ecológica. *Corte Constitucional del Ecuador* 59, 17–31. Registro Oficial No.

Alava, J. J. (2009). Carbon productivity and flux in the marine ecosystems of the Galapagos marine reserve based on cetacean abundances and trophic indices. *Rev. Biol. Mar. Oceanogr.* 44 (1), 109–122. doi: 10.4067/S0718-19572009000100010

Alava, J. J., Ikonomou, M. G., Ross, P. S., Costa, D., Salazar, S., Aurioles-Gamboa, D., et al. (2009). Polychlorinated biphenyls and polybrominated diphenyl ethers in Galapagos sea lions (*Zalophus wollebaeki*). *Environ. Toxicol. Chem.* 28 (11), 2271–2282. doi: 10.1897/08-331.1

Alava, J. J., and Paladines, F. (2017). Illegal fishing on the galápagos high seas. *Science* 357, 1362.1–131362. doi: 10.1126/science.aap7832

Alava, J. J., Tatar, B., Barragán, M. J., Castro, C., Rosero, P., Denkinger, J., et al. (2019). Mitigating cetacean bycatch in coastal Ecuador: governance challenges for small-scale fisheries. *Mar. Pol.* 110, 102769. doi: 10.1016/j.marpol.2017.05.025

Alves, F., Alessandrini, A., Servidio, A., Mendonça, A. S., Hartman, K. L., Prieto, R., et al. (2019). Complex biogeographical patterns support an ecological connectivity network of a large marine predator in the north-east Atlantic. *Divers. Distrib.* 25 (2), 269–284. doi: 10.1111/ddi.12848

Alves, F., Ferreira, R., Fernandes, M., Halicka, Z., Dias, L., and Dinis, A. (2018). Analysis of occurrence patterns and biological factors of cetaceans based on long-term and fine-scale data from platforms of opportunity: Madeira island as a case study. *Mar. Ecol.* 39 (2), e12499-13. doi: 10.1111/maec.12499

Anchundia, D., Huyvaert, K. P., and Anderson, D. J. (2014). Chronic lack of breeding by galápagos blue-footed boobies and associated population decline. *Avian Conserv. Ecol.* 9 (1), art6–ar15. doi: 10.5751/ace-00650-090106

Aragones, L. V., Jefferson, T. A., and Marsh, H. (1997). Marine mammal survey techniques applicable in developing countries. *Asian Mar. Biol.* 14, 15–39.

Arauco-Shapiro, G., Schumacher, K. I., Boersma, D., and Bouzat, J. L. (2020). The role of demographic history and selection in shaping genetic diversity of the galápagos penguin (*Spheniscus mendiculus*). *PloS One* 15, e0226439. doi: 10.1371/journal.pone.0226439

Arnés-Urgellés, C., Salinas-de-León, P., Rastoin-Laplane, E., Vaca-Pita, L., Suárez-Moncada, J., and Páez-Rosas, D. (2021). The effects of climatic variability on the feeding ecology of the scalloped hammerhead shark (*Sphyrna lewini*) in the tropical eastern pacific. *Front. Mar. Sci.* 8. doi: 10.3389/fmars.2021.625748

Awkerman, J. A., Huyvaert, K. P., Mangel, J., Alfaro-Shigueto, J., and Anderson, D. J. (2006). Incidental and intentional catch threatens galápagos waved albatross. *Biol. Cons.* 133 (4), 483–489. doi: 10.1016/j.biocon.2006.07.010

Baird, R. W. (2016). *The lives of hawai'i's dolphins and whales* (Honolulu, Hawai'i: University of Hawai'I Press), 341.

Baird, R. W., Gorgone, A. M., McSweeney, D. J., Ligon, A. D., Deakos, M. H., Webster, D. L., et al. (2009a). Population structure of island-associated dolphins: Evidence from photo-identification of common bottlenose dolphins (*Tursiops truncatus*) in the main Hawaiian islands. *Mar. Mamm. Sci.* 25, 251–274. doi: 10.1111/j.1748-7692.2008.00257.x

Baird, R. W., Mahaffy, S. D., Gorgone, A. M., Cullins, T., McSweeney, D. J., Oleson, E. M., et al. (2014). False killer whales and fisheries interactions in Hawaiian waters: Evidence for sex bias and variation among populations and social groups. *Mar. Mamm. Sci.* 31 (2), 579–590. doi: 10.1111/mms.12177

Baird, R. W., Mahaffy, S. D., and Lerma, J. K. (2022). Site fidelity, spatial use, and behavior of dwarf sperm whales in Hawaiian waters: using small-boat surveys, photo-identification, and unmanned aerial systems to study a difficult-to-study species. *Mar. Mamm. Sci.* 38 (1), 326–348. doi: 10.1111/mms.12861

Baird, R. W., McSweeney, D. J., Schorr, G. S., Mahaffy, S. D., Webster, D. L., Barlow, J., et al. (2009b). "Studies of beaked whales in hawai'i: population size, movements, trophic ecology, social 18rganization and behaviour," in *Proceedings of the ECS workshop "Beaked whale research"*. Eds. S. J. Dolman, C. D. MacLeod and P. G. H. Evans (San Sebastián, Spain: the European Cetacean Society's 21st Annual Conference), 23–25.

Baird, R. W., Oleson, E. M., Barlow, J., Ligon, A. D., Gorgone, A. M., and Mahaffy, S. D. (2013a). Evidence of an island-associated population of false killer whales (*Pseudorca crassidens*) in the northwestern Hawaiian islands. *Pac. Sci.* 67, 513–521. doi: 10.2984/67.4.2

Baird, R. W., Webster, D. L., Aschettino, J. M., Schorr, G. S., and McSweeney, D. J. (2013b). Odontocete cetaceans around the main Hawaiian islands: Habitat use and relative abundance from small-boat sighting surveys. *Aquat. Mamm.* 39 (3), 253–269. doi: 10.1578/am.39.3.2013.253

Baird, R. W., Webster, D. L., Mahaffy, S. D., McSweeney, D. J., Schorr, G. S., and Ligon, A. D. (2008). Site fidelity and association patterns in a deep-water dolphin: Rough-toothed dolphins (*Steno bredanensis*) in the Hawaiian archipelago. *Mar. Mamm. Sci.* 24, 535–553. doi: 10.1111/j.1748-7692.2008.00201.x

Ballance, L. T., Gerrodette, T., Lennert-Cody, C. E., Pitman, R. L., and Squires, D. (2021). A history of the tuna-dolphin problem: successes, failures, and lessons learned. *Front. Mar. Sci.* 8. doi: 10.3389/fmars.2021.754755

Becker, E. A., Forney, K. A., Miller, D. L., Barlow, J., Rojas-Bracho, L., Urbán-R., J., et al. (2022). Dynamic habitat models reflect interannual movement of cetaceans within the California current ecosystem. *Front. Mar. Sci.* 9. doi: 10.3389/fmars.2022.829523

Becker, E. A., Forney, K. A., Redfern, J. V., Barlow, J., Jacox, M. G., Roberts, J. J., et al. (2019). Predicting cetacean abundance and distribution in a changing climate. *Divers. Distrib.* 25, 626–643. doi: 10.1111/ddi.12867

Berger-Wolf, T. Y., Rubenstein, D. I., Stewart, C. V., Holmberg, J. A., Parham, J., Menon, S., et al. (2017). Wildbook: Crowdsourcing, computer vision, and data science for conservation. doi: 10.48550/arXiv.1710.08880 (Accessed January 19, 2023).

Bermant, P. C., Bronstein, M. M., Wood, R. J., Gero, S., and Gruber, D. F. (2019). Deep machine learning techniques for the detection and classification of sperm whale bioacoustics. *Sci. Rep.* 9, 12588. doi: 10.1038/s41598-019-48909-4

Beslin, W. A., Whitehead, H., and Gero, S. (2018). Automatic acoustic estimation of sperm whale size distributions achieved through machine recognition of on-axis clicks. *J. Acoust. Soc Am.* 144, 3485–3495. doi: 10.1121/1.5082291

Best, P. B., and Photopoulou, T. (2016). Identifying the "demon whale-biter": Patterns of scarring on large whales attributed to a cookie-cutter shark isistius sp. *PLoS One* 11 (4), e0152643-20. doi: 10.1371/journal.pone.0152643

Biggs, D. C., Durkacz, S. M., Martin, L. M., Narvaez, M., de la Garza, A., Lombraña, Z., et al. (2017). Bryde's whales (*Balaneoptera brydei*) in an area of upwelling off isla San cristóbal, galápagos. *Neotrop. Biodivers.* 3 (1), 189–195. doi: 10.1080/23766808.2017.1368309

Bierlich, K., Schick, R., Hewitt, J., Dale, J., Goldbogen, J., Friedlaender, A., et al. (2021). Bayesian Approach for predicting photogrammetric uncertainty in morphometric measurements derived from drones. *Mar. Ecol. Prog. Ser.* 673, 193–210. doi: 10.3354/meps13814

Block, B. A., Holbrook, C. M., Simmons, S. E., Holland, K. N., Ault, J. S., Costa, D. P., et al. (2016). Toward a national animal telemetry network for aquatic observations in the united states. *Anim. Biotelemetry* 4, 6. doi: 10.1186/s40317-015-0092-1

Boersma, P. D., Vargas, H., and Merlen, G. (2005). Living laboratory in peril. *Science* 308, 925. doi: 10.1126/science.1114395

Boecklen, W. J., Yarnes, C. T., Cook, B. A., and James, A. C. (2011). On the use of stable isotopes in trophic ecology. *Annu. Rev. Ecol. Evol. Syst.* 42, 411–440. doi: 10.1146/annurev-ecolsys-102209-144726

Bonaccorso, E., Ordóñez-Garza, N., Pazmiño, D. A., Hearn, A., Páez-Rosas, D., Cruz, S., et al. (2021). International fisheries threaten globally endangered sharks in the Eastern tropical pacific ocean: the case of the fu Yuan yu leng 999 reefer vessel seized within the galápagos marine reserve. *Sci. Rep.* 11, 14959. doi: 10.1038/s41598-021-94126-3

Boteler, B., Wagner, D., Durussel, C., Stokes, E., Gaymer, C. F., Friedlander, A. M., et al. (2022). Borderless conservation: Integrating connectivity into high seas conservation efforts for the Salas y gómez and nazca ridges. *Front. Mar. Sci.* 9. doi: 10.3389/fmars.2022.915983

Bouchet, P. J., Meeuwig, J. J., Salgado Kent, C. P., Letessier, T. B., and Jenner, C. K. (2015). Topographic determinants of mobile vertebrate predator hotspots: current knowledge and future directions. *Biol. Rev.* 90, 699–728. doi: 10.1111/brv.12130

Bowen, W. D. (1997). Role of marine mammals in aquatic ecosystems. *Mar. Ecol. Progr. Ser.* 158, 267–274. doi: 10.3354/meps158267

Boyd, C., and Punt, A. E. (2021). Shifting trends: Detecting changes in cetacean population dynamics in shifting habitat. *PloS One* 16 (5), e0251522. doi: 10.1371/journal.pone.0251522

Brakes, P., Dall, S. R. X., Aplin, L. M., Bearhop, S., Carroll, E. L., Ciucci, P., et al. (2019). Animal cultures matter for conservation. *Science* 363, 1032–1034. doi: 10.1126/science.aaw3557

Brock, P., Hall, A., Goodman, S. J., Cruz, M., and Acevedo-Whitehouse, K. (2013a). Applying the tools of ecological immunology to conservation: a test case in the Galapagos sea lion. *Anim. Conserv.* 16, 19–31. doi: 10.1111/j.1469-1795.2012.00567.x

Brock, P. M., Hall, A. J., Goodman, S. J., Cruz, M., and Acevedo-Whitehouse, K. (2013b). Immune activity, body condition and human-associated environmental impacts in a wild marine mammal. *PLoS One* 8 (6), e67132. doi: 10.1371/journal.pone.0067132.s003

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L., and Thomas, L. (2001). *Introduction to distance sampling* (Oxford: Oxford University Press), 432.

Buckland, S. T., Rexstad, E., Marques, T. A., and Oedekoven, C. S. (2015). *Distance sampling: Methods and applications* (Heidelberg: Springer).

Cambra, M., Lara-Lizardi, F., Peñaherrera-Palma, C., Hearn, A., Ketchum, J. T., Zarate, P., et al. (2021). A first assessment of the distribution and abundance of large pelagic species at Cocos ridge seamounts (Eastern tropical pacific) using drifting pelagic baited remote cameras. *PloS One* 16, e0244343. doi: 10.1371/journal.pone.0244343

Cantor, M., Shoemaker, L. G., Cabral, R. B., Flores, C. O., Varga, M., and Whitehead, H. (2015). Multilevel animal societies can emerge from cultural transmission. *Nat. Commun.* 6, 8091. doi: 10.1038/ncomms9091

Cantor, M., and Whitehead, H. (2015). How does social behavior differ among sperm whale clans? *Mar. Mamm. Sci.* 31, 1275–1290. doi: 10.1111/mms.12218

Cantor, M., Eguiguren, A., Merlen, G., and Whitehead, H. (2017). Galápagos sperm whales (*Physeter macrocephalus*): waxing and waning over three decades. *Can. J. Zool.* 95 (9), 645–652. doi: 10.1139/cjz-2016-0266

Cantor, M., Whitehead, H., Gero, S., and Rendell, L. (2016). Cultural turnover among galápagos sperm whales. *R. Soc Open Sci.* 3 (10), 160615. doi: 10.1098/rsos.160615

Capella, J. J., Félix, F., Florez-González, L., Gibbons, J., Haase, B., and Guzman, H. M. (2018). Geographic and temporal patterns of non-lethal attacks on humpback whales by killer whales in the eastern south pacific and the Antarctic peninsula. *Endanger. Species Res.* 37, 207–218. doi: 10.3354/esr00924

Caro, T. M., and O'Doherty, G. (1999). On the use of surrogate species in conservation biology. *Conserv. Biol.* 13, 805–814. doi: 10.1046/j.1523-1739.1999.98338.x

Castro, C. A., Rasmussen, K., Pacheco, A. S., Cardenas, D., Carnero-Huaman, R., Echeverria, G., et al. (2017). Bryde's whale *Balaenoptera edeni* occurrence and movements in coastal 21ater off Ecuador, Peru and Panama. *A preliminary report. paper SC/67^{a}/SH/15 presented to the international whaling commission scientific committee annual meeting* (Bled, Slovenia: International Whaling Commission), 11pp.

Centelleghe, C., Carraro, L., Gonzalvo, J., Rosso, M., Esposti, E., Gili, C., et al. (2020). The use of unmanned aerial vehicles (UAVs) 21aters21os the blow microbiome of small cetaceans. *PLoS One* 15 (7), e0235537. doi: 10.1371/journal.pone.0246177

Cerutti-Pereyra, F., Moity, N., Dureuil, M., Ramírez-González, J., Reyes, H., Budd, K., et al. (2020). Artisanal longline fishing the Galapagos islands–effects on vulnerable megafauna in a UNESCO world heritage site. *Ocean Coast. Manage.* 183, 104995. doi: 10.1016/j.ocecoaman.2019.104995

Cheeseman, T., Southerland, K., Park, J., Olio, M., Flynn, K., Calambokidis, J., et al. (2021). Advanced image recognition: a fully automated, high-accuracy photo-identification matching system for humpback whales. *Mamm. Biol.* 102, 915–929. doi: 10.1007/s42991-021-00180-9

Christiansen, F., Dawson, S. M., Durban, J. W., Fearnbach, H., Miller, C. A., Bejder, L., et al. (2020). Population comparison of right whale body condition reveals poor state of the north Atlantic right whale. *Mar. Ecol. Prog. Ser.* 640, 1–16. doi: 10.3354/meps13299

Correia, A. M., Sousa-Guedes, D., Gil, Á., Valente, R., Rosso, M., Sousa-Pinto, I., et al. (2021). Predicting cetacean distributions in the eastern north Atlantic to support marine management. *Front. Mar. Sci.* 8. doi: 10.3389/fmars.2021.643569

Corsi, E., Calambokidis, J., Flynn, K. R., and Steiger, G. H. (2022). Killer whale predatory scarring on mysticetes: A comparison of rake marks among blue, humpback, and gray whales in the eastern north pacific. *Mar. Mamm. Sci.* 38 (1), 223–234. doi: 10.1111/mms.12863

Costa, A. P. B., Archer, F. I., Rosel, P. E., and Perrin, W. F. (2022). *Tursiops truncatus nuuanu*, a new subspecies of the common bottlenose dolphin from the eastern tropical pacific. *J. Mamm. Evol.*, 1–17. doi: 10.1007/s10914-022-09641-5

Davies, T. E., Carneiro, A. P. B., Campos, B., Hazin, C., Dunn, D. C., Gjerde, K. M., et al. (2021). Tracking data and the conservation of the high seas: Opportunities and challenges. *J. Appl. Ecol.* 58 (12), 2703–2710. doi: 10.1111/1365-2664.14032

Dawson, S. M., Bowman, M. H., Leunissen, E., and Sirguey, P. (2017). Inexpensive aerial photogrammetry for studies of whales and large marine animals. *Front. Mar. Sci.* 4. doi: 10.3389/fmars.2017.00366

Dawson, S., Wade, P., Slooten, E., and Barlow, J. (2008). Design and field methods for sighting surveys of cetaceans in coastal and riverine habitats. *Mamm. Rev.* 38 (1), 19–49. doi: 10.1111/j.1365-2907.2008.00119.x

Day, D. (1994). List of cetaceans seen in galápagos. *Not. Gal. (Gal. Res.)* 53, 5–6.

Decreto Ejecutivo No. 319 (2022) *Gobierno de la república del Ecuador*. Available at: https://www.comunicacion.gob.ec/decreto-ejecutivo-no-319/.

Denkinger, J., Alarcon, D., Espinosa, B., Fowler, L., Manning, C., Oña, J., et al. (2020). Social structure of killer whales (*Orcinus orca*) in a variable low-latitude environment, the galápagos archipelago. *Mar. Mamm. Sci.* 36 (3), 774–785. doi: 10.1111/mms.12672

Denkinger, J., Oña, J., Alarcón, D., Merlen, G., Salazar, S., and Palacios, D. M. (2013). "From whaling to whale watching: Cetacean presence and species diversity in the galápagos marine reserve," in *Science and conservation in the galápagos islands: Frameworks and perspectives, social and ecological interactions in the galápagos islands 1*. Eds. S. J. Walsh and C. F. Mena (New York, NY: Springer Science+Business Media, LCC), 217–235. doi: 10.1007/978-1-4614-5794-7_14

Denkinger, J., and Vinueza, L. (2014). *The Galapagos marine reserve: A dynamic social-ecological system* (London: Springer).

Dinis, A., Molina, C., Tobeña, M., Sambolino, A., Hartman, K., Fernandez, M., et al. (2021). Large-Scale movements of common bottlenose dolphins in the Atlantic: dolphins with an international courtyard. *PeerJ* 9, e11069. doi: 10.7717/peerj.11069

Dueñas, A., Jiménez-Uzcátegui, G., and Bosker, T. (2021). The effects of climate change on wildlife biodiversity of the 22aters22os islands. *Clim. Change. Ecol.* 2, 100026. doi: 10.1016/j.ecochg.2021.100026

Dunn, D. C., Harrison, A.-L., Curtice, C., DeLand, S., Donnelly, B., Fujioka, E., et al. (2019). The importance of migratory connectivity for global ocean policy. *Proc. R. Soc B* 286, 20191472. doi: 10.1098/rspb.2019.1472

Edgar, G. J., Banks, S., Bensted-Smith, R., Calvopiña, M., Chiriboga, A., Garske, L. E., et al. (2008). Conservation of threatened species in the Galapagos marine reserve through identification and protection of marine key biodiversity areas. *Aquat. Conserv.: Mar. Freshw. Ecosyst.* 18, 955–968. doi: 10.1002/aqc.901

Edgar, G. J., Banks, S. A., Bessudo, S., Cortés, J., Guzmán, H. M., Henderson, S., et al. (2011). Variation in reef fish and invertebrate communities with level of protection from fishing across the Eastern tropical pacific seascape. *Global Ecol. Biogeogr.* 20, 730–743. doi: 10.1111/j.1466-8238.2010.00642.x

Edgar, G. J., Banks, S., Fariña, J. M., Calvopiña, M., and Martínez, C. (2004). Regional biogeography of shallow reef fish and macro-invertebrate communities in the Galapagos archipelago. *J. Biogeogr.* 31, 1107–1124. doi: 10.1111/j.1365-2699.2004.01055.x

Eguiguren, A., Pirotta, E., Boerder, K., Cantor, M., Merlen, G., and Whitehead, H. (2021). Historical and contemporary habitat use of sperm whales around the galápagos archipelago: Implications for conservation. *Aquat. Conserv.: Mar. Freshw. Ecosyst.* 31 (6), 1466–1481. doi: 10.1002/aqc.3496

Eguiguren, A., Pirotta, E., Cantor, M., Rendell, L., and Whitehead, H. (2019). Habitat use of culturally distinct galápagos sperm whale *Physeter macrocephalus* clans. *Mar. Ecol. Progr. Ser.* 609, 257–270. doi: 10.3354/meps12822

Enríquez-García, A. B., Villegas-Zurita, F., Tripp-Valdez, A., Moreno-Sánchez, X. G., Galván-Magaña, F., Elorriaga-Verplancken, F. R., et al. (2022). Foraging segregation between spotted (*Stenella attenuata*) and spinner (*Stenella longirostris*) dolphins in the Mexican south pacific. *Mar. Mamm. Sci.* 38 (3), 1070–1087. doi: 10.1111/mms.12912

Estrade, V., and Dulau, V. (2020). Abundance and site fidelity of bottlenose dolphins off a remote oceanic island (Reunion island, southwest Indian ocean). *Mar. Mamm. Sci.* 36 (3), 871–896. doi: 10.1111/mms.12693

Estes, J. A., Tinker, M. T., Williams, T. M., and Doak, D. F. (1998). Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282, 473–476. doi: 10.1126/science.282.5388.473

Evans, D. (1991). Ecuadorian Whale sanctuary is created providing protection for the galápagos islands. *Ambio* 20 (2), 97.

Fais, A., Lewis, T. P., Zitterbart, D. P., Álvarez, O., Tejedor, A., and Soto, N. A. (2016). Abundance and distribution of sperm whales in the canary islands: Can sperm whales in the archipelago sustain the current level of ship-strike mortalities? *PloS One* 11 (3), e0150660-16. doi: 10.1371/journal.pone.0150660

Faustino, C. E. S., Silva, M. A., Marques, T. A., and Thomas, L. (2010). Designing a shipboard line transect survey to estimate cetacean abundance off the Azores archipelago. *Arquipelago (Life Mar. Sciences)* 27, 49–58.

Félix, F., Palacios, D. M., Salazar, S. K., Caballero, S., Haase, B., and Falconí, J. (2011). The 2005 galápagos humpback whale expedition: A first attempt to assess and characterize the population in the archipelago. *J. Cetacean Res. Manage. Special Issue* 3, 291–299.

Fernandez, M., Alves, F., Ferreira, R., Fischer, J., Thake, P., Nunes, N., et al. (2021). Modeling fine-scale cetaceans' distributions in oceanic islands: Madeira archipelago as a case study. *Front. Mar. Sci.* 8. doi: 10.3389/fmars.2021.688248

Ferreira, R., Dinis, A., Badenas, A., Sambolino, A., Marrero-Pérez, J., Crespo, A., et al. (2021). Bryde's whales in the north-East Atlantic: New insights on site fidelity and connectivity between oceanic archipelagos. *Aquat. Conserv.: Mar. Freshw. Ecosyst.* 31 (10), 2938–2950. doi: 10.1002/aqc.3665

Fiedler, P. C., and Lennert-Cody, C. E. (2019). Seasonal and interannual variations in the distributions of tuna-associated dolphins in the eastern tropical pacific ocean. *J. Cetacean Res. Manage.* 20, 67–79. doi: 10.47536/jcrm.v20i1.240

Fiedler, P. C., Redfern, J. V., Forney, K. A., Palacios, D. M., Sheredy, C., Rasmussen, K., et al. (2018). Prediction of large whale distributions: a comparison of presence–absence and presence-only modeling techniques. *Front. Mar. Sci.* 5. doi: 10.3389/fmars.2018.00419

Figueroa, D. (2021). Environmental forcing on zooplankton distribution in the coastal waters of the galápagos islands: spatial and seasonal patterns in the copepod community structure. *Mar. Ecol. Progr. Ser.* 661, 49–69. doi: 10.3354/meps13617

Flanders Marine Institute (2019). Maritime boundaries geodatabase. In: *Maritime boundaries and exclusive economic zones (200NM), version 11.* Available at: https://www.marineregions.org/ (Accessed 6 December 2022).

Fonseca, C. T., Pérez-Jorge, S., Prieto, R., Oliveira, C., Tobeña, M., Scheffer, A., et al. (2022). Dive behavior and activity patterns of fin whales in a migratory habitat. *Front. Mar. Sci.* 9. doi: 10.3389/fmars.2022.875731

Fontoura, L., D'agata, S., Gamoyo, M., Barneche, D. R., Luiz, O. J., Madin, E. M., et al. (2022). Protecting connectivity promotes successful biodiversity and fisheries conservation. *Science* 375, 336–340. doi: 10.1126/science.abg4351

Forryan, A., Garabato, A. C. N., Vic, C., Nurser, A. J. G., and Hearn, A. R. (2021). Galápagos upwelling driven by localized wind–front interactions. *Sci. Rep.* 11, 1277. doi: 10.1038/s41598-020-80609-2

Frasier, K. E., Roch, M. A., Soldevilla, M. S., Wiggins, S. M., Garrison, L. P., and Hildebrand, J. A. (2017). Automated classification of dolphin echolocation click types from the gulf of Mexico. *PloS Comput. Biol.* 13, e1005823. doi: 10.1371/journal.pcbi.1005823

Game, E. T., Grantham, H. S., Hobday, A. J., Pressey, R. L., Lombard, A. T., Beckley, L. E., et al. (2009). Pelagic protected areas: the missing dimension in ocean conservation. *Trends Ecol. Evol.* 24, 360–369. doi: 10.1016/j.tree.2009.01.011

Gillespie, D., Mellinger, D. K., Gordon, J., McLaren, D., Redmond, P., McHugh, R., et al. (2009). PAMGUARD: Semiautomated, open source software for real-time acoustic detection and localisation of cetaceans. *J. Acoust. Soc Am.* 125, 2547. doi: 10.1121/1.4808713

Global Fishing Watch (2021) *Analysis of the southeast pacific distant water squid fleet. GFW-2021-FA-SQUID2020.* Available at: https://globalfishingwatch.org/research/squid-smarts-jumbo-squid-in-the-pacific-ocean/ (Accessed 5 December 2022).

Gove, J. M., McManus, M. A., Neuheimer, A. B., Polovina, J. J., Drazen, J. C., Smith, C. R., et al. (2016). Near-island biological hotspots in barren ocean basins. *Nat. Commun.* 7, 10581. doi: 10.1038/ncomms10581

Groch, K. R., Díaz-Delgado, J., Santos-Neto, E. B., Ikeda, J. M., Carvalho, R. R., Oliveira, R. B., et al. (2020). The pathology of cetacean morbillivirus infection and comorbidities in Guiana dolphins during an unusual mortality event (Brazil 2017–2018). *Vet. Pathol.* 57 (6), 845–857. doi: 10.1177/0300985820954550

Halpern, B. S. (2003). The impact of marine reserves: do reserves work and does reserve size matter? *Ecol. Appl.* 13, 117–137. doi: 10.1890/1051-0761(2003)013[0117:TIOMRD]2.0.CO;2

Halpin, P. N., Read, A., Best, B. D., Hyrenbach, K. D., Fujioka, E., Coyne, M. S., et al. (2006). OBIS-SEAMAP: developing a biogeographic research data commons for the ecological studies of marine mammals, seabirds, and sea turtles. *Mar. Ecol. Progr. Ser.* 316, 239–246. doi: 10.3354/meps316239

Hamilton, T. A., Redfern, J. V., Barlow, J., Ballance, L. T., Gerrodette, T., Holt, R. S., et al. (2009). *Atlas of cetacean sightings from southwest fisheries science center cetacean and ecosystem surveys: U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southwest Fisheries Science Center. 1986 – 2005.* 70.

Hammond, P. S., Francis, T. B., Heinemann, D., Long, K. J., Moore, J. E., Punt, A. E., et al. (2021). Estimating the abundance of marine mammal populations. *Front. Mar. Sci.* 8. doi: 10.3389/fmars.2021.735770

Harnish, A. E., Ault, J., Babbitt, C., Gulland, F. M. D., Johnson, P. C., Shaughnessy, N. L., et al. (2019). Survival of a common bottlenose dolphin (*Tursiops truncatus*) calf with a presumptive gunshot wound to the head. *Aquat. Mamm.* 45 (5), 543–548. doi: 10.1578/AM.45.5.2019.543

Harris, M. P. (1969). Breeding seasons of sea-birds in the Galapagos islands. *J. Zool.* 159, 145–165. doi: 10.1111/j.1469-7998.1969.tb03076.x

Hart, L. B., Rotstein, D. S., Wells, R. S., Allen, J., Barleycorn, A., Balmer, B. C., et al. (2012). Skin lesions on common bottlenose dolphins (Tursiops truncatus) from three sites in the Northwest Atlantic, USA. *PLoS ONE* 7, e33081. doi: 10.1371/journal.pone.0033081

Hartman, K. L., Fernández, M., Wittich, A., and Azevedo, J. M. N. (2015). Sex differences in residency patterns of risso's dolphins (*Grampus griseus*) in the Azores: Causes and management implications. *Mar. Mamm. Sci.* 31 (3), 1153–1167. doi: 10.1111/mms.12209

Hasegawa, D., Lewis, M. R., and Gangopadhyay, A. (2009). How islands cause phytoplankton to bloom in their wakes. *Geophys. Res. Lett.* 36 (20), L20605. doi: 10.1029/2009gl039743

Hearn, A., Ketchum, J., Klimley, A. P., Espinoza, E., and Peñaherrera, C. (2010). Hotspots within hotspots? hammerhead shark movements around wolf island, Galapagos marine reserve. *Mar. Biol.* 157 (9), 1899–1915. doi: 10.1007/s00227-010-1460-2

Herrera, I., Carrillo, M., Esteban, M. C., and Haroun, R. (2021). Distribution of cetaceans in the canary islands (northeast Atlantic ocean): implications for the natura 2000 network and future conservation measures. *Front. Mar. Sci.* 8. doi: 10.3389/fmars.2021.669790

Hersh, T. A., Gero, S., Rendell, L., Cantor, M., Weilgart, L., Amano, M., et al. (2022). Evidence from sperm whale clans of symbolic marking in non-human cultures. *Proc. Natl. Acad. Sci. U.S.A.* 119 (37), e2201692119. doi: 10.1073/pnas.220169211

Heylings, P., Bensted-Smith, R., and Altamirano, M. (2002). "Zonificación e historia de la reserva Marina de galápagos," in *Reserva Marina de galápagos, linea base de la bioversidad.* Eds. E. Danulat and G. J. Edgar (Santa Cruz, Galapagos, Ecuador: Fundación Charles Darwin/Servicio Parque Nacional Galápagos), 10–21.

Hindell, M. A., Reisinger, R. R., Ropert-Coudert, Y., Hückstädt, L. A., Trathan, P. N., Bornemann, H., et al. (2020). Tracking of marine predators to protect southern ocean ecosystems. *Nature* 580, 87–92. doi: 10.1038/s41586-020-2126-y

Hope, P. L., and Whitehead, H. (1991). Sperm whales off the galápagos islands from 1830–50 and comparisons with modern studies. *Rep. Int. Whal. Commn.* 41, 273–283.

Horton, T. W., Hauser, N., Cassel, S., Klaus, K. F., Fettermann, T., and Key, N. (2019). Doctor drone: Non-invasive measurement of humpback whale vital signs using unoccupied aerial system infrared thermography. *Front. Mar. Sci.* 6. doi: 10.3389/fmars.2019.00466

Houvenaghel, G. T. (1978). "Oceanographic conditions in the galápagos archipelago and their relationships with life on the islands," in *Upwelling ecosystems.* Eds. R. Boje and M. Tomczak (Berlin: Springer-Verlag), 181–200.

Hucke-Gaete, R., Bedrinana-Romano, L., Viddi, F. A., Ruiz, J. E., Torres-Florez, J. P., and Zerbini, A. N. (2018). From Chilean Patagonia to Galapagos, Ecuador: novel insights on blue whale migratory pathways along the Eastern south pacific. *PeerJ* 6, e4695. doi: 10.7717/peerj.4695

IUCN-MMPATF (2022). Galápagos archipelago IMMA. In: *Marine mammal protected areas task force (MMPATF).* Available at: https://www.marinemammalhabitat.org/portfolio-item/galapagos-archipelago-imma/ (Accessed 27 November 2022).

Izurieta, A., Delgado, B., Moity, N., Calvopiña, M., Cedeño, I., Banda-Cruz, G., et al. (2018). A collaboratively derived environmental research agenda for galápagos. *Pac. Conserv. Biol.* 24 (2), 207–207. doi: 10.1071/pc17053_co

Jacquet, J., Alava, J. J., Pramod, G., Henderson, S., and Zeller, D. (2008). In hot soup: sharks captured in ecuador's waters. *Env. Sci.* 5 (4), 269–283. doi: 10.1080/15693430802466325

Jarić, I., Correia, R. A., Brook, B. W., Buettel, J. C., Courchamp, F., Di Minin, E., et al. (2020). iEcology: harnessing large online resources to generate ecological insights. *Trends Ecol. Evol.* 35, 630–639. doi: 10.1016/j.tree.2020.03.003

Jiménez-Uzcátegui, G., Vaca, L., Cotín, J., García, C., Costales, A., Sevilla, C., et al. (2019). Using referential values of δ13C and δ15N to infer the foraging ecology of galápagos seabirds. *Mar. Ornithol.* 47, 5–10.

Joblon, M. J., Pokras, M. A., Morse, B., Harry, C. T., Rose, K. S., Sharp, S. M., et al. (2014). Body condition scoring system for delphinids based on short-beaked common dolphins (*Delphinus delphis*). *J. Mar. Anim. Ecol.* 7 (2), 5–13.

Kappeler, P. M. A. (2019). A framework for studying social complexity. *Behav. Ecol. Sociobiol.* 73, 13. doi: 10.1007/s00265-018-2601-8

Kays, R., Davidson, S. C., Berger, M., Bohrer, G., Fiedler, W., Flack, A., et al. (2022). The movebank system for studying global animal movement and demography. *Methods Ecol. Evol.* 13 (2), 419–431. doi: 10.1111/2041-210X.13767

Ketchum, J. T., Hoyos-Padilla, M., Aldana-Moreno, A., Ayres, K., Galván-Magaña, F., Hearn, A., et al. (2020). Shark movement patterns in the Mexican pacific: A conservation and management perspective. *Adv. Mar. Biol.* 85, 1–37. doi: 10.1016/bs.amb.2020.03.002

Kiszka, J. J., Heithaus, M. R., and Wirsing, A. J. (2015). Behavioural drivers of the ecological roles and importance of marine mammals. *Mar. Ecol. Progr. Ser.* 523, 267–281. doi: 10.3354/meps11180

Kiszka, J. J., Méndez-Fernandez, P., Heithaus, M. R., and Ridoux, V. (2014). The foraging ecology of coastal bottlenose dolphins based on stable isotope mixing models and behavioural sampling. *Mar. Biol.* 161, 953–961. doi: 10.1007/s00227-014-2395-9

Kiszka, J. J., Woodstock, M. S., and Heithaus, M. R. (2022). Functional roles and ecological importance of small cetaceans in aquatic ecosystems. *Front. Mar. Sci.* 9. doi: 10.3389/fmars.2022.803173

Klimley, A. P., Arauz, R., Bessudo, S., Chávez, E. J., Chinacalle, N., Espinoza, E., et al. (2022). Studies of the movement ecology of sharks justify the existence and expansion of marine protected areas in the Eastern pacific ocean. *Environ. Biol. Fish.* 105, 2133–2153. doi: 10.1007/s10641-021-01204-6

Kotik, C., Durban, J. W., Fearnbach, H., and Barrett-Lennard, L. G. (2022). Morphometrics of mammal-eating killer whales from drone photogrammetry, with comparison to sympatric fish-eating killer whales in the eastern north pacific. *Mar. Mamm. Sci.* 39 (1), 42–58. doi: 10.1111/mms.12965

Kratofil, M. A., Harnish, A. E., Mahaffy, S. D., Henderson, E. E., Bradford, A. L., Martin, S. W., et al. (2023). Biologically important areas II for cetaceans within U.S. and adjacent waters – Hawai'i Region. *Front. Mar. Sci.* 10, 1053581. doi: 10.3389/fmars.2023.1053581

Lambert, C., Authier, M., Dorémus, G., Gilles, A., Hammond, P., Laran, S., et al. (2019). The effect of a multi-target protocol on cetacean detection and abundance estimation in aerial surveys. *R. Soc Open Sci.* 6, 190296. doi: 10.1098/rsos.190296

Lamb, R. W., Smith, F., Aued, A. W., Salinas-de-León, P., Suarez, J., Gomez-Chiarri, M., et al. (2018). El Niño drives a widespread ulcerative skin disease outbreak in Galapagos marine fishes. *Sci. Rep.* 8, 16602. doi: 10.1038/s41598-018-34929-z

Ley Orgánica de Régimen Especial Para la Provincia de Galápagos. Ley No. 67.

Llapapasca, M. A., Pacheco, A. S., Fiedler, P., Goya, E., Ledesma, J., Peña, C., et al. (2018). Modeling the potential habitats of dusky, commons and bottlenose dolphins in the Humboldt current system off Peru: The influence of non-El niño vs. El niño 1997-98 conditions and potential prey availability. *Prog. Oceanogr.* 168, 169–181. doi: 10.1016/j.pocean.2018.09.003

Lyrholm, T., Kerr, I., Galley, L., and Payne, R. (1992). "Report of the "Expedición siben", Ecuador 1988/89," in *Final report submitted by the Whale Conservation Institute to the Charles Darwin research station and the galápagos national park service* (Puerto Ayora, Islas Galápagos, Ecuador: Whale Conservation Institute), 38.

Machado, A. M. S., Cantor, M., Costa, A. P., Righetti, B. P., Bezamat, C., Valle-Pereira, J., et al. (2019). Homophily around specialized foraging underlies dolphin social preferences. *Biol. Lett.* 15 (4), 20180909. doi: 10.1098/rsbl.2018.0909

MacLeod, C. D., and Mitchell, G. (2006). Key areas for beaked whales worldwide. *J. Cetacean Res. Manage.* 7 (3), 309–322.

Mann, J., Connor, R. C., Tyack, P. L., and Whitehead, H. (Eds.) (2000). *Cetacean societies: Field studies of dolphins and whales* (Chicago: University of Chicago Press).

Marcoux, M., Whitehead, H., and Rendell, L. (2007). Sperm whale feeding variation by location, year, social group and clan: Evidence from stable isotopes. *Mar. Ecol. Progr. Ser.* 333, 309–314. doi: 10.3354/meps333309

Martin, A. H., Pearson, H. C., Saba, G. K., and Olsen, E. M. (2021). Integral functions of marine vertebrates in the ocean carbon cycle and climate change mitigation. *One Earth* 4 (5), 680–693. doi: 10.1016/j.oneear.2021.04.019

McKinley, S. J., Saunders, B. J., Rastoin-Laplane, E., Salinas-de-León, P., and Harvey, E. S. (2022). Functional diversity of reef fish assemblages in the Galapagos archipelago. *J. Exp. Mar. Biol. Ecol.* 549, 151695. doi: 10.1016/j.jembe.2022.151695

Mellinger, D. K., Stafford, K. M., Moore, S. E., Dziak, R. P., and Matsumoto, H. (2007). An overview of fixed passive acoustic observation methods for cetaceans. *Oceanography* 20 (4), 36–45. doi: 10.5670/oceanog.2007.03

Mendelssohn, R., Bograd, S. J., Schwing, F. B., and Palacios, D. M. (2005). Teaching old indices new tricks: A state-space analysis of El niño related climate indices. *Geophys. Res. Lett.* 32, L07709. doi: 10.1029/2005gl022350

Merlen, G. (1992). Ecuadorian Whale refuge. *Noticias Galápagos* 51, 23–24.

Merlen, G. (1995). *A field guide to the marine mammals of Galapagos* (Guayaquil, Ecuador: Instituto Nacional de Pesca), 130.

Neave, E. F., Seim, H., Gifford, S. M., Torano, O., Johnson, Z. I., Páez-Rosas, D., et al. (2021). Protistan plankton communities in the galápagos archipelago respond to changes in deep water masses resulting from the 2015/16 El niño. *Environ. Microbiol.* 24, 1746–1759. doi: 10.1111/1462-2920.15863

O'Hern, J. E., Sculley, M., Jean-Smith, K., Biggs, D., Slowey, N., Ruales, D. A., et al. (2017). Marine mammal distribution in Ecuador: surveys aboard a ship of opportunity as a means of monitoring relative abundance. *Lat. Am. J. Aquat. Mamm.* 12 (1-2), 28–39. doi: 10.5597/lajam00235

Okey, T. A., Banks, S., Born, A. F., Bustamante, R. H., Calvopiña, M., Edgar, G. J., et al. (2004). A trophic model of a galápagos subtidal rocky reef for evaluating fisheries and conservation strategies. *Ecol. Modell.* 172 (2–4), 383–401. doi: 10.1016/j.ecolmodel.2003.09.019

Olson, P. A., Blount, D., Cheeseman, T., Holmberg, J., and Minton, G. (2020). *A cross-reference of flukebook and happywhale platforms* (International Whaling Commission Scientific Committee Annual Meeting), 11pp.

Oremus, M., Poole, M. M., Albertson, G. R., and Baker, C. S. (2012). Pelagic or insular? genetic differentiation of rough-toothed dolphins in the society islands, French Polynesia. *J. Exp. Mar. Biol. Ecol.* 432–433, 37–46. doi: 10.1016/j.jembe.2012.06.027

Pacheco, A. S., Castro, C., Carnero-Huaman, R., Villagra, D., Pinilla, S., Denkinger, J., et al. (2019). Sightings of an adult male killer whale match humpback whale breeding seasons in both hemispheres in the eastern tropical pacific. *Aquat. Mamm.* 45 (3), 320–326. doi: 10.1578/am.45.3.2019.320

Páez-Rosas, D., Aurioles-Gamboa, D., Alava, J. J., and Palacios, D. M. (2012). Stable isotopes indicate differing foraging strategies in two sympatric otariids of the Galapagos islands. *J. Exp. Mar. Biol. Ecol.* 424, 44–52. doi: 10.1016/j.jembe.2012.05.001

Paéz-Rosas, D., Hirschfeld, M., Deresienski, D., and Lewbart, G. A. (2016). Health status of galápagos sea lions (*Zalophus wollebaeki*) on San cristóbal island rookeries determined by hematology, biochemistry, blood gases, and physical examination. *J. Wildl. Dis. 52*, 100–105. doi: 10.7589/2015-04-084

Páez-Rosas, D., Insuasti-Zarate, P., Riofrío-Lazo, M., and Galván-Magaña, F. (2018). Feeding behavior and trophic interaction of three shark species in the Galapagos marine reserve. *PeerJ* 6 (8), e4818–e4821. doi: 10.7717/peerj.4818

Páez-Rosas, D., Torres, J., Espinoza, E., Marchetti, A., Seim, H., and Riofrío-Lazo, M. (2021). Declines and recovery in endangered Galapagos pinnipeds during the El niño event. *Sci. Rep.* 11, 8785. doi: 10.1038/s41598-021-88350-0

Palacios, D. M. (1996). On the specimen of the ginkgo-toothed beaked whale, *Mesoplodon ginkgodens*, from the galápagos islands. *Mar. Mamm. Sci.* 12 (3), 444–446. doi: 10.1111/j.1748-7692.1996.tb00596.x

Palacios, D. M. (1999a). "Marine mammal research in the Galápagos Islands: The 1993-94 Odyssey expedition" *Final report submitted by the Whale Conservation Institute to galápagos national park service and Charles Darwin research station*(Puerto Ayora, Is. Galápagos, Ecuador), 6.

Palacios, D. M. (1999b). Blue whale (*Balaenoptera musculus*) occurrence off the galápagos islands 1978-1995. *J. Cetacean Res. Manage.* 1 (1), 41–51.

Palacios, D. M. (2000). "GalCet2K: A line-transect survey for cetaceans across an environmental gradient off the galápagos islands, 5–19 April 2000," in *Final report submitted to Ocean Alliance to Galápagos National Park Service, Charles Darwin Research Station, Capitanía de Puerto Ayora, and Dirección General de Intereses Marítimos de la Armada Naciona Puerto ayora, and dirección general de intereses maritimos de la armada nacional*(Puerto Ayora, Is. Galápagos, Ecuador: Ocean Alliance), 9.

Palacios, D. M. (2003). Oceanographic conditions around the Galápagos Archipelago and their influence on cetacean community structure. (Corvallis (OR): Oregon State University http://ir.library.oregonstate.edu/concern/graduate_thesis_or_dissertations/xp68kk78c

Palacios, D. M. (2004). Seasonal patterns of sea-surface temperature and ocean color around the galápagos: regional and local influences. *Deep-Sea Res. II: Top. Stud. Oceanogr.* 51 (1-3), 43–57. doi: 10.1016/j.dsr2.2003.08.001

Palacios, D. M., Bograd, S. J., Foley, D. G., and Schwing, F. B. (2006). Oceanographic characteristics of biological hot spots in the north pacific: A remote sensing perspective. *Deep-Sea Res. II: Top. Stud. Oceanogr.* 53 (3-4), 250–269. doi: 10.1016/j.dsr2.2006.03.004

Palacios, D. M., and Forney, K. A. (2008). *Cetacean abundance on the western side of the galápagos islands during April 2000. SC/60/SM7* (Santiago, Chile: International Whaling Commission Scientific Committee), 1–12.

Palacios, D. M., and Salazar, S. (2002). "Cetáceos," in *Reserva Marina de galápagos, línea base de la biodiversidad*. Eds. E. Danulat and G. J. Edgar (Santa Cruz, Galápagos, Ecuador: Fundación Charles Darwin/Servicio Parque Nacional Galápagos), 291–304.

Palacios, D. M., Salazar, S. K., and Day, D. (2004). Cetacean remains and strandings in the galápagos islands 1923-2003. *Lat. Am. J. Aquat. Mamm.* 3, 127–150. doi: 10.5597/lajam00058

Panicker, D., Baumgartner, M., and Stafford, K. (2022). Fine-scale spatial and temporal acoustic occurrence of island-associated odontocetes near a mid-oceanic atoll in the northern Indian ocean. *Mar. Ecol. Prog. Ser.* 683, 195–208. doi: 10.3354/meps13947

Panigada, S., Lauriano, G., Burt, L., Pierantonio, N., and Donovan, G. (2011). Monitoring winter and summer abundance of cetaceans in the pelagos sanctuary (Northwestern Mediterranean Sea) through aerial surveys. *PLoS One* 6, e22878. doi: 10.1371/journal.pone.0022878.t003

Pearson, H. C., Savoca, M. S., Costa, D. P., Lomas, M. W., Molina, R., Pershing, A. J., et al. (2022). Whales in the carbon cycle: can recovery remove carbon dioxide? *Trends Ecol. Evol.* 3074, 1–12. doi: 10.1016/j.tree.2022.10.012

Peltier, H., Jepson, P. D., Dabin, W., Deaville, R., Daniel, P., Canneyt, O. V., et al. (2014). The contribution of stranding data to monitoring and conservation strategies for cetaceans: Developing spatially explicit mortality indicators for common dolphins (*Delphinus delphis*) in the eastern north-Atlantic. *Ecol. Indic.* 39, 203–214. doi: 10.1016/j.ecolind.2013.12.019

Pethybridge, H. R., Choy, C. A., and Polovina, J. J. (2018). Improving marine ecosystem models with biochemical tracers. *Ann. Rev. Mar. Sci.* 10, 199–228. doi: 10.1146/annurev-marine-121916-063256

Pinheiro, H. T., Bernardi, G., Simon, T., Joyeux, J. C., Macieira, R. M., Gasparini, J. L., et al. (2017). Island biogeography of marine organisms. *Nature* 549, 82–85. doi: 10.1038/nature23680

Pinela, A. M., Quérouil, S., Magalhes, S., Silva, M. A., Prieto, R., Matos, J. A., et al. (2009). Population genetics and social organization of the sperm whale (*Physeter macrocephalus*) in the Azores inferred by microsatellite analyses. *Can. J. Zoology* 87 (9), 802–813. doi: 10.1139/z09-066

Polanowski, A. M., Robbins, J., Chandler, D., and Jarman, S. N. (2014). Epigenetic estimation of age in humpback whales. *Mol. Ecol. Resour.* 14 (5), 976–987. doi: 10.1111/1755-0998.12247

Pollock, K. H. (1982). A capture-recapture design robust to unequal probability of capture. *J. Wildl. Manage.* 46, 752–757. doi: 10.2307/3808568

Prieto, R., Silva, M. A., Waring, G. T., and Gonçalves, J. (2014). Sei whale movements and behaviour in the north Atlantic inferred from satellite telemetry. *Endanger. Species Res.* 26 (2), 103–113. doi: 10.3354/esr00630

Quérouil, S., Kiszka, J., Cordeiro, A. R., Cascão, I., Freitas, L., Dinis, A., et al. (2013). Investigating stock structure and trophic relationships among island-associated dolphins in the oceanic waters of the north Atlantic using fatty acid and stable isotope analyses. *Mar. Biol.* 160 (6), 1325–1337. doi: 10.1007/s00227-013-2184-x

Quérouil, S., Silva, M. A., Cascão, I., Magalhães, S., Seabra, M. I., Machete, M. A., et al. (2008). Why do dolphins form mixed-species associations in the Azores? *Ethology* 114, 1183–1194. doi: 10.1111/j.1439-0310.2008.01570.x

Raoult, V., Colefax, A. P., Allan, B. M., Cagnazzi, D., Castelblanco-Martínez, N., Ierodiaconou, D., et al. (2020). Operational protocols for the use of drones in marine animal research. *Drones* 4, 64. doi: 10.3390/drones4040064

Registro Oficial (2000). "Corte constitucional del Ecuador," in *Registro oficial no. 5 del 28 de enero del 2000.*

Registro Oficial (2002). "Corte constitucional del Ecuador," in *Registro oficial no. 679 del 8 de octubre de 2002.*

Remili, A., Gallego, P., Pinzone, M., Castro, C., Jauniaux, T., Garigliany, M.-M., et al. (2020). Humpback whales (*Megaptera novaeangliae*) breeding off Mozambique and Ecuador show geographic variation of persistent organic pollutants and isotopic niches. *Environ. pollut.* 267, 115575. doi: 10.1016/j.envpol.2020.115575

Rendell, L. E., and Whitehead, H. (2003). Vocal clans in sperm whales (*Physeter macrocephalus*). *Proc. R. Soc B: Biol. Sci.* 270 (1512), 225–231. doi: 10.1098/rspb.2002.2239

Rendell, L., Cantor, M., Gero, S., Whitehead, H., and Mann, J. (2019). Causes and consequences of female centrality in cetacean societies. *Philos. Trans. R. Soc B: Biol. Sci.* 374, 20180066. doi: 10.1098/rstb.2018.0066

Rooker, J. R., Dance, M. A., Wells, R. D., Ajemian, M. J., Block, B. A., Castleton, M. R., et al. (2019). Population connectivity of pelagic megafauna in the Cuba-Mexico-United states triangle. *Sci. Rep.* 9, 1663. doi: 10.1038/s41598-018-38144-8

Romagosa, M., Baumgartner, M., Cascão, I., Lammers, M. O., Marques, T. A., Santos, R. S., et al. (2020). Baleen whale acoustic presence and behaviour at a mid-Atlantic migratory habitat, the Azores archipelago. *Sci. Rep.* 10 (1), 4766. doi: 10.1038/s41598-020-61849-8

Ruiz, D. J., Banks, S., and Wolff, M. (2016). Elucidating fishing effects in a large-predator dominated system: The case of Darwin and wolf islands (Galápagos). *J. Sea Res.* 107, 1–11. doi: 10.1016/j.seares.2015.11.001

Ruttenberg, B. I. (2001). Effects of artisanal fishing on marine communities in the galápagos islands. *Conserv. Biol.* 15, 1691–1699. doi: 10.1046/j.1523-1739.2001.99556.x

Sahri, A., Putra, M. I. H., Mustika, P. L. K., Kreb, D., and Murk, A. J. (2021). Cetacean habitat modelling to inform conservation management, marine spatial planning, and as a basis for anthropogenic threat mitigation in Indonesia. *Ocean Coast. Manage.* 205, 105555. doi: 10.1016/j.ocecoaman.2021.105555

Salinas-de-León, P., Fierro-Arcos, D., Suarez-Moncada, J., Proaño, A., Guachisaca-Salinas, J., and Páez-Rosas, D. (2019). A matter of taste: Spatial and ontogenetic variations on the trophic ecology of the tiger shark at the Galapagos marine reserve. *PLoS One* 14 (9), e0222754. doi: 10.1371/journal.pone.0222754

Sambolino, A., Alves, F., Fernandez, M., Krakauer, A. B., Ferreira, R., and Dinis, A. (2022). Spatial and temporal characterization of the exposure of island-associated cetacean populations to whale-watching in Madeira island (NE Atlantic). *Reg. Stud. Mar. Sci.* 49, 102084. doi: 10.1016/j.rsma.2021.102084

Schaeffer, B. A., Morrison, J. M., Kamykowski, D., Feldman, G. C., Xie, L., Liu, Y., et al. (2008). Phytoplankton biomass distribution and identification of productive habitats within the Galapagos marine reserve by MODIS, a surface acquisition system, and *in-situ* measurements. *Remote Sens. Environ.* 112 (6), 3044–3054. doi: 10.1016/j.rse.2008.03.005

Schiller, L., Alava, J. J., Grove, J., Reck, G., and Pauly, D. (2014). The demise of darwin's fishes: evidence of fishing down and illegal shark finning in the galápagos islands. *Aquat. Conserv.: Mar. Freshw. Ecosyst.* 25 (3), 431–446. doi: 10.1002/aqc.2458

Servidio, A., Pérez-Gil, E., Pérez-Gil, M., Cañadas, A., Hammond, P. S., and Martín, V. (2019). Site fidelity and movement patterns of short-finned pilot whales within the canary islands: Evidence for resident and transient populations. *Aquat. Conserv.: Mar. Freshw. Ecosyst.* 29 (S1), 227–241. doi: 10.1002/aqc.3135

Shuster, G. W. (1983). The Galapagos islands: a preliminary study of the effects of sperm whaling on a specific whaling ground. *Rep. Int. Whal Commn Special Issue* 5, 81–82.

Silva, M. A., Prieto, R., Cascão, I., Seabra, M. I., Machete, M., Baumgartner, M., et al. (2014). Spatial and temporal distribution of cetaceans in the mid-Atlantic waters around the Azores. *Mar. Biol. Res.* 10 (2), 123–137. doi: 10.1080/17451000.2013.793814

Silva, M. A., Prieto, R., Jonsen, I., Baumgartner, M. F., and Santos, R. S. (2013). North Atlantic blue and fin whales suspend their spring migration to forage in middle latitudes: building up energy reserves for the journey? *PloS One* 8 (10), e76507. doi: 10.1371/journal.pone.0076507.s004

Silver-Gorges, I., Koval, J., Rodriguez-Zarate, C. J., Paladino, F. V., and Jordan, M. (2020). Large-Scale connectivity, cryptic population structure, and relatedness in Eastern pacific olive ridley sea turtles (Lepidochelys olivacea). *Ecol. Evol.* 10, 8688–8704. doi: 10.1002/ece3.6564

Smith, S. D., and Whitehead, H. (1999). Distribution of dolphins in galápagos waters. *Mar. Mamm. Sci.* 15 (2), 550–555. doi: 10.1111/j.1748-7692.1999.tb00819.x

Smith, S. C., and Whitehead, H. (2000). The diet of Galapagos sperm whales *Physeter macrocephalus* as indicated by fecal sample analysis. *Mar. Mamm. Sci.* 16, 315–325. doi: 10.1111/j.1748-7692.2000.tb00927.x

Smith, S. C., and Whitehead, H. (2001). Reply to r. Clarke and paliza's comment: "The food of sperm whales in the southeast pacific". *Mar. Mamm. Sci.* 17, 430–431. doi: 10.1111/j.1748-7692.2001.tb01288.x

Soares, E. D., Cantor, M., Bracarense, A. P. F. R. L., Groch, K. R., and Domit, C. (2022). Health conditions of Guiana dolphins facing cumulative anthropogenic impacts. *Mamm. Biol.*, 1–16. doi: 10.1007/s42991-022-00299-3

Sonnenholzner, J., Ladah, L., and Lafferty, K. (2009). Cascading effects of fishing on Galapagos rocky reef communities: reanalysis using corrected data. *Mar. Ecol. Prog. Ser.* 375, 209–218. doi: 10.3354/meps07890

Sweet, W. V., Morrison, J. M., Kamykowski, D., Schaeffer, B. A., Banks, S., and McCulloch, A. (2007). Water mass seasonal variability in the galápagos archipelago. *Deep-Sea Res. I: Oceanogr. Res. Pap.* 54 (12), 2023–2035. doi: 10.1016/j.dsr.2007.09.009

Tardin, R. H., Chun, Y., Simão, S. M., and Alves, M. (2017). Modeling habitat use by bryde's whale *Balaenoptera edeni* off southeastern Brazil. *Mar. Ecol. Progr. Ser.* 576, 89–103. doi: 10.3354/meps12228

Tardin, R. H., Chun, Y., Simão, S. M., and Alves, M. A. S. (2019). Habitat use models of spatially auto-correlated data: a case study of the common bottlenose dolphin, *Tursiops truncatus truncatus*, in southeastern Brazil. *Mar. Biol. Res.* 15, 305–316. doi: 10.1080/17451000.2019.1644773

Taylor, B. L., Martinez, M., Gerrodette, T., Barlow, J., and Hrovat, Y. N. (2007). Lessons from monitoring trends in abundance of marine mammals. *Mar. Mamm. Sci.* 23 (1), 157–175. doi: 10.1111/j.1748-7692.2006.00092.x

Tetley, M. J., Braulik, G. T., Lanfredi, C., Minton, G., Panigada, S., Politi, E., et al. (2022). The important marine mammal area network: a tool for systematic spatial planning in response to the marine mammal habitat conservation crisis. *Front. Mar. Sci.* 9. doi: 10.3389/fmars.2022.841789

Thomas, L., Williams, R., and Sandilands, D. (2007). Survey design for complex survey regions. *J. Cetacean Res. Manage.* 9 (1), 1–13.

Thorne, L. H., Johnston, D. W., Urban, D. L., Tyne, J., Bejder, L., Baird, R. W., et al. (2012). Predictive modeling of spinner dolphin (*Stenella longirostris*) resting habitat in the main Hawaiian islands. *PloS One* 7 (8), e43167. doi: 10.1371/journal.pone.0043167.t003

Tobeña, M., Prieto, R., Machete, M., and Silva, M. A. (2016). Modeling the potential distribution and richness of cetaceans in the Azores from fisheries observer program data. *Front. Mar. Sci.* 3. doi: 10.3389/fmars.2016.00202

Todd, V. L. G., and Grove, J. S. (2010). First records of golden trevally (*Gnathodon speciosus*, carangidae), sharp-tail mola (*Masturus lanceolatus*, molidae) and evidence for white shark (*Carcharodon carcharias*, lamnidae) in the galápagos islands, Ecuador. *Mar. Biodivers. Rec.* 3, E104. doi: 10.1017/s1755267210000771

Tompkins, E. M., Townsend, H. M., and Anderson, D. J. (2017). Decadal-scale variation in diet forecasts persistently poor breeding under ocean warming in a tropical seabird. *PloS One* 12 (8), e0182545-24. doi: 10.1371/journal.pone.0182545

Toms, C. N., Stone, T., and Och-Adams, T. (2020). Visual-only assessments of skin lesions on free-ranging common bottlenose dolphins (*Tursiops truncatus*): Reliability and utility of quantitative tools. *Mar. Mamm. Sci.* 36 (3), 744–773. doi: 10.1111/mms.12670

Torres-Florez, J. P., Olson, P. A., Bedriñana-Romano, L., Rosenbaum, H., Ruiz, J., LeDuc, R., et al. (2015). First documented migratory destination for eastern south pacific blue whales. *Mar. Mamm. Sci.* 31 (4), 1580–1586. doi: 10.1111/mms.12239

Tozer, B., Sandwell, D. T., Smith, W. H. F., Olson, C., Beale, J. R., and Wessel, P. (2019). Global bathymetry and topography at 15 arc sec: SRTM15+. *Earth Space Sci.* 6, 1847–1864. doi: 10.1029/2019EA000658

Teixeira, C. R., Troina, G. C., Daura-Jorge, F. G., Simões-Lopes, P. C., and Botta, S. (2022). A practical guide on stable isotope analysis for cetacean research. *Mar. Mamm. Sci.* 38, 1200–1228. doi: 10.1111/mms.12911

Urian, K., Gorgone, A., Read, A., Balmer, B., Wells, R. S., Berggren, P., et al. (2015). Recommendations for photo-identification methods used in capture-recapture models with cetaceans. *Mar. Mamm. Sci.* 31 (1), 298–321. doi: 10.1111/mms.12141

Urquía, D. O., and Páez-Rosas, D. (2019). Δ13C and δ15N values in pup whiskers as a proxy for the trophic behavior of Galapagos sea lion females. *Mamm. Biol.* 96 (1), 28–36. doi: 10.1016/j.mambio.2019.03.012

Usseglio, P., Friedlander, A. M., Koike, H., Zimmerhackel, J., Schuhbauer, A., Eddy, T., et al. (2016). So long and thanks for all the fish: overexploitation of the regionally endemic Galapagos grouper mycteroperca olfax (Jenyns 1840). *PloS One* 11 (10), e0165167. doi: 10.1371/journal.pone.0165167

Van Bressem, M.-F., Van Waerebeek, K., Reyes, J. C., Félix, F., Echegaray, M., Siciliano, S., et al. (2007). A preliminary overview of skin and skeletal diseases and traumata in small cetaceans from south American waters. *Lat. Am. J. Aquat. Mamm.* 6, 7–42. doi: 10.5597/lajam00108

Van Bressem, M.-F., Raga, A., Guardo, G. D., Jepson, P., Duignan, P., Siebert, U., et al. (2009). Emerging infectious diseases in cetaceans worldwide and the possible role of environmental stressors. *Dis. Aquat. Org.* 86, 143–157. doi: 10.3354/dao02101

Van Cise, A., Baird, R., Harnish, A., Currie, J., Stack, S., Cullins, T., et al. (2021). Mark-recapture estimates suggest declines in abundance of common bottlenose dolphin stocks in the main Hawaiian islands. *Endanger. Species Res.* 45, 37–53. doi: 10.3354/esr01117

Ventura, F., Matthiopoulos, J., and Jeglinski, J. W. E. (2019). Minimal overlap between areas of high conservation priority for endangered Galapagos pinnipeds and the conservation zone of the Galapagos marine reserve. *Aquat. Conserv.: Mar. Freshw. Ecosyst.* 29 (1), 115–126. doi: 10.1002/aqc.2943

Veríssimo, D., MacMillan, D. C., and Smith, R. J. (2011). Toward a systematic approach for identifying conservation flagships. *Conserv. Lett.* 4 (1), 1–8. doi: 10.1111/j.1755-263x.2010.00151.x

Wachtendonk, R., Calambokidis, J., and Flynn, K. (2022). Blue whale body condition assessed over a 14-year period in the NE pacific: Annual variation and connection to measures of ocean productivity. *Front. Mar. Sci.* 9. doi: 10.3389/fmars.2022.847032

Wade, P. R., and Gerrodette, T. (1993). Estimates of cetacean abundance and distribution in the eastern tropical pacific. *Rep. Int. Whal. Commn.* 43, 477–493.

Walsh, S. J., and Mena, C. F. (2016). Interactions of social, terrestrial, and marine sub-systems in the Galapagos islands, Ecuador. *Proc. Natl. Acad. Sci. U.S.A.* 113 (51), 14536–14543. doi: 10.1073/pnas.1604990113

Weiss, M. N., Ellis, S., and Croft, D. P. (2021). Diversity and consequences of social network structure in toothed whales. *Front. Mar. Sci.* 8, 688842. doi: 10.3389/fmars.2021.688842

Wellington, G. M., Strong, A. E., and Merlen, G. (2001). Sea Surface temperature variation in the galápagos archipelago: a comparison between AVHRR nighttime satellite data and in-situ instrumentation (1982–1988). *Bull. Mar. Sci.* 69, 27–42.

Whitehead, H. (1985). Studying sperm whales on the galápagos grounds. *Not. Gal. (Gal. Res.)* 42, 18–21.

White, G. C., and Burnham, K. P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 (sup1), S120–S139. doi: 10.1080/00063659909477239

Whitehead, H., Christal, J., and Dufault, S. (1997). Past and distant whaling and the rapid decline of sperm whales off the Galapagos islands. *Conserv. Biol.* 11 (6), 1387–1396. doi: 10.1046/j.1523-1739.1997.96246.x

Whitehead, H., and Hope, P. L. (1991). Sperm whalers off the galápagos islands and in the western north pacific 1830–1850: Ideal free whalers? *Ethol. Sociobiol.* 12 (2), 147–161. doi: 10.1016/0162-3095(91)90018-L

Whitehead, H., MacLeod, C. D., and Rodhouse, P. (2001). Differences in niche breadth among some teuthivorous mesopelagic marine mammals. *Mar. Mamm. Sci.* 19 (2), 400–406. doi: 10.1111/j.1748-7692.2003.tb01118.x

Whitehead, H. (2003). *Sperm whales: social evolution in the ocean* (Chicago: University of Chicago Press).

Whitehead, H. (2008). *Analyzing animal societies: quantitative methods for vertebrate social analysis* (Chicago: University of Chicago Press).

Whitehead, H., and Rendell, L. (2004). Movements, habitat use and feeding success of cultural clans of south pacific sperm whales. *J. Anim. Ecol.* 73, 190–196. doi: 10.1111/j.1365-2656.2004.00798.x

Whitehead, H., and Shin, M. (2022). Current global population size, post-whaling trend and historical trajectory of sperm whales. *Sci. Rep.* 12, 19468. doi: 10.1038/s41598-022-24107-7

White, T. D., Ong, T., Ferretti, F., Block, B. A., McCauley, D. J., Micheli, F., et al. (2020). Tracking the response of industrial fishing fleets to large marine protected areas in the pacific ocean. *Cons. Biol.* 34, 1571–1578. doi: 10.1111/cobi.13584

Wickman, L., Rayment, W., Slooten, E., and Dawson, S. M. (2020). Recommendations for estimating mark rate of cetaceans in photo-ID research: A critique of field sampling protocols and variance estimation. *Mar. Mamm. Sci.* 37 (1), 328–343. doi: 10.1111/mms.12723

Williams, R., and Thomas, L. (2009). Cost-effective abundance estimation of rare animals: Testing performance of small-boat surveys for killer whales in British Columbia. *Biol. Conserv.* 142 (7), 1542–1547. doi: 10.1016/j.biocon.2008.12.028

Wise, J. J. P., Payne, R., Wise, S. S., LaCerte, C., Wise, J. J. P., Gianios, C., et al. (2009). A global assessment of chromium pollution using sperm whales (*Physeter macrocephalus*) as an indicator species. *Chemosphere* 75, 1461–1467. doi: 10.1016/j.chemosphere.2009.02.044

Wolf, J. B., Mawdsley, D., Trillmich, F., and James, R. (2007). Social structure in a colonial mammal: unravelling hidden structural layers and their foundations by network analysis. *Anim. Behav.* 74 (5), 1293–1302. doi: 10.1016/j.anbehav.2007.02.024

Woodward, S. F., Reiss, D., and Magnasco, M. O. (2020). Learning to localize sounds in a highly reverberant environment: Machine-learning tracking of dolphin whistle-like sounds in a pool. *PloS One* 15 (6), e0235155. doi: 10.1371/journal.pone.0235155

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EDITED BY
Filipe Alves,
Center for Marine and Environmental Sciences (MARE), Portugal

REVIEWED BY
Denise Lore Herzing,
Florida Atlantic University, United States
Salvatore Siciliano,
Fundação Oswaldo Cruz (Fiocruz), Brazil

*CORRESPONDENCE
Benjamin de Montgolfier
b.montgolfier@aquasearch.fr

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Site fidelity and population parameters of pantropical spotted dolphins in the Eastern Caribbean through photographic identification

Baptiste Courtin[1,2], Cédric Millon[1], Aurore Feunteun[2], Morjane Safi[2], Nathalie Duporge[2], Jaime Bolaños-Jiménez[3,4], Dalia C. Barragán-Barrera[5,6,7], Laurent Bouveret[1] and Benjamin de Montgolfier[2,8]*

[1]Observatoire des Mammifères Marins de l'Archipel Guadeloupéen (OMMAG), Route Hégésippe Légitimus, Port-Louis, Guadeloupe, [2]Aquasearch, Zone Artisanale et Commerciale (ZAC) Les Côteaux, Sainte-Luce, Martinique, [3]Laboratorio de Mamíferos Marinos (LabMMar-IIB-ICIMAP-UV), Universidad Veracruzana, Xalapa, Mexico, [4]Caribbean-Wide Orca Project (CWOP), Universidad Veracruzana, Xalapa, Mexico, [5]Instituto Javeriano del Agua, Pontificia Universidad Javeriana, Bogotá, Colombia, [6]R&E Ocean Community Conservation Foundation, Oakville, ON, Canada, [7]Fundación Macuáticos Colombia, Medellín, Colombia, [8]Institut des Sciences de la Mer de Rimouski, Rimouski, QC, Canada

The Agoa protected marine area, located in the French West Indies, eastern Caribbean, holds several cetacean species, of which the pantropical spotted dolphin *Stenella attenuata* is the most commonly observed. This species is the focus of whale-watching activities off the leeward coasts of Guadeloupe and Martinique, which has allowed the development of a citizen science program to characterize individuals through the collection of photographic data. Here, we conducted a photo-identification study with a sample of 115,705 photos collected between 2014 and 2019, in which 290 marked individuals (179 in Guadeloupe and 111 in Martinique) were identified. Based on an Agglomerative Hierarchical Classification (AHC) analysis, dolphins from each island were separated into two residency clusters. The Catch–Mark–Release (CMR) POPAN statistical model for open populations estimated the pantropical spotted dolphin populations in Guadeloupe and Martinique at 657 (95% CI: 525–821) and 336 (95% CI: 253–446) individuals for frequent users, respectively, while occasional visitors were estimated at 3,063 (95% CI: 2,133–4,398) and 1,443 (95% CI: 1,024–2,033), respectively. The Martinique population tended to use a reduced coastal area and appeared to be smaller and stable, while the Guadeloupe population showed a slight decline in abundance throughout the study period. These results showed that the leeward coasts of Guadeloupe and Martinique are of particular importance for pantropical spotted dolphin populations, highlighting the need for continued monitoring through both scientific and citizen science programs to fill information gaps on this species in the eastern Caribbean.

KEYWORDS

abundance, distribution, capture-recapture, pantropical spotted dolphin, stenella attenuata, French West Indies

1 Introduction

The monitoring of wild animal species is essential for the effective assessment of the movements, structure, and size of their populations —information that is key to the development of management plans (Gormley et al., 2012; Chan and Karczmarski, 2017). Capture-recapture is one of the most common methods used to estimate these parameters (Cormack, 1964; Jolly, 1965; Seber, 1982; Wells and Scott, 1990; Whitehead, 1990; Hammond, 1990a). Particularly for cetaceans, CMR modeling coupled with non-intrusive and relatively inexpensive techniques such as photo identification have been widely used to determine these parameters, either with systematic surveys (Miller, 1990; Chan and Karczmarski, 2017; Haughey et al., 2020) or *via* opportunistic observations (Robbins et al., 2006; Robbins et al., 2020). This has led to a better understanding of marine mammal ecology, which remained poorly studied because of technical difficulties related to the fact that they have wide distributional ranges and are observable only when they surface (Dufault et al., 1999; Gowans et al., 2007; Shirihai and Jarett, 2007; Jefferson et al., 2015).

Photo identification (Adams et al., 2006; Rosel et al., 2011; Urian et al., 2015; Nowacek et al., 2016) has allowed the identification of inter-island movements of short-finned pilot whales (*Globicephala macrorhynchus*) and sperm whales (*Physeter macrocephalus*) between the Lesser Antillean islands (Gero et al., 2007; De Vries, 2017), annual migrations of humpback whales (*Megaptera novaeangliae*) across the Atlantic (Whitehead and Moore, 1982; Katona and Beard, 1990; Smith et al., 1999), and long-distance movements of common bottlenose dolphins (*Tursiops truncatus*) off the Irish coast (O'Brien et al., 2009). Moreover, combining photo identification with statistical CMR models that take into account population heterogeneity and different residency patterns within a population (Hammond, 1990b; Pradel et al., 1997; Whitehead and Wimmer, 2005; Morteo et al., 2012; Pradel and Sanz-Aguilar, 2012) has allowed the estimation of the structure, size, and residency parameters of dolphin populations such as Indo-Pacific bottlenose dolphins (*Tursiops aduncus*; Zanardo et al., 2016; Hunt et al., 2017; Haughey et al., 2020), common bottlenose dolphins (Silva et al., 2009; Bolaños-Jiménez et al., 2021), and spinner dolphins (*Stenella longirostris*; Tyne et al., 2014). However, no similar studies have been conducted for other *Stenella* dolphins.

The pantropical spotted dolphin (*Stenella attenuata*; hereafter PSD) is distributed worldwide in tropical oceanic zones between latitudes 30–40°N and 20–40°S, and it is one of the most common cetacean species in the Atlantic Ocean (Shirihai and Jarett, 2007; Jefferson et al., 2015; Perrin, 2018; Perrin, 2020). Because of its wide distribution and its top-predator trophic position, it is often considered an umbrella species, meaning that conservation efforts implemented for this species will benefit many other species sharing the same habitat (Jefferson et al., 2015). In the French West Indies, PSD is observed year-round in the western area near the leeward (western) coasts of Guadeloupe and Martinique (Mayol et al., 2016). The species is frequently observed within Agoa Sanctuary, a 140,000 km² marine protected area created in 2010 that covers the entire exclusive economic zone of French waters in the Caribbean, including Guadeloupe and Martinique (Ministère de l'Écologie, du Développement durable, des Transports et du Logement, 2011; Office Français de la Biodiversité, 2012). However, PSD is subject to multiple natural and anthropogenic pressures such as chemical and acoustic pollution, injuries related to commercial fishing, repeated disturbances caused by maritime traffic, climate change, hunting, and bycatch (Cuzange, 2011; Gandilhon, 2012; Mayol et al., 2016; Avila et al., 2018; Feunteun et al., 2018; Safi et al., 2020). Adverse interactions with fisheries and bycatch in particular have been reported as the main threats for PSD worldwide and even in the Caribbean (Avila et al., 2018). For example, populations in the eastern tropical Pacific have experienced dramatic mortalities caused by the purse seine fishery for tuna, with about 3 million individuals being killed from 1959 to 1972; some populations still do not show clear signs of recovery (Gerrodette et al., 2008; Jefferson et al., 2015). Although no information on PSD bycatch is available for the Caribbean, a recent study based on overlapping purse-seine fishing areas and areas of potential PSD distribution suggests that coastal areas of Venezuela as well as surrounding eastern areas have a potentially high risk of bycatch (Pino and Laura, 2021). Thus, this species may be exposed to several pressures that can vary from one island to another in the West Indies (Cuzange, 2011), which highlights the importance of knowing population movements with the aim of proposing adequate conservation plans for each area.

For the islands of Guadeloupe and Martinique, the whale-watching industry has increasingly focused on PSD since it is the most commonly observed cetacean species on the leeward coasts of these islands (more than 50% of observations; Gandilhon, 2012; Mayol et al., 2016; Feunteun et al., 2019). For this reason, PSD conservation is a priority for both ecological and economic reasons. As a result, a citizen science program has been implemented in the area, and the number of observations has allowed the study of PSD for both islands. A preliminary study based on data from 2018 and 2019 (Courtin et al., 2022) suggested separate PSD populations for Guadeloupe and Martinique, with very little exchange between them. In addition, the study showed a heterogeneity in the Martinique population, with two resident clusters: one composed of frequent users and the other of occasional or transient individuals.

Studies on PSD ecology in the Caribbean are scarce (but see, e.g., Mignucci-Giannoni et al., 2003; Barragán-Barrera et al., 2019), and works based on PSD photo-ID data have been conducted only in Hawaii (Psarakos et al., 2003; Machernis et al., 2021). In Martinique and Guadeloupe, a first study using 2018 and 2019 citizen science data revealed preliminary information on the movement, abundance, and residency patterns of PSD individuals between islands (Courtin et al., 2022). Here, we continued that previous work, using a novel dataset on PSD collected from 2014 to 2017 to confirm movements between the islands as well as to determine the size and residency patterns of PSD populations of both islands using the photo-identification technique and CMR statistical modeling. This study shows the effectiveness of a citizen science program to obtain relevant

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Abbreviations: AICc, Akaike Information Criterion corrected; AHC, Agglomerative Hierarchical Classification; CMR, Catch–Mark–Release; EW, Early Wet sampling period; ED, Early Dry sampling period; PSD, Pantropical Spotted Dolphin; LW, Late Wet sampling period; LD, Late Dry sampling period; OMMAG, Observatoire des Mammifères Marins de l'Archipel Guadeloupéen; FU, Frequent Users; OV, Occasional Visitors.

biological, ecological, and population data on a little-studied cetacean species in the Caribbean such as PSD.

2 Materials and methods

2.1 Study area

Martinique and Guadeloupe are two islands in the eastern Caribbean within the French West Indies; PSD is observed off their leeward coasts year-round. These islands are part of Agoa Sanctuary, a maritime area where cetaceans and their habitats are fully protected: killing or approaching within 300 m of an individual is prohibited. However, professional enterprises such as whale-watching companies can approach to within 100 m of cetaceans by following additional regulations and after signing an approach chart (Ministère de l'Écologie, du Développement durable, des Transports et du Logement, 2011; Office Français de la Biodiversité, 2012). The leeward side of these islands offer an area protected from the swell and trade winds of the Atlantic Ocean. In addition, these waters have depths up to 1,000 m near the coast, which appears to be favorable to the presence of PSD (Gowans et al., 2007; Barragán-Barrera et al., 2019). This species occurs relatively close to the coast, within 2.5 and 3.5 nautical miles from Martinique and Guadeloupe, respectively, which facilitates their observation by small and medium-sized whale-watching boats. The islands share a similar climate due to their geographical proximity (Figure 1A). Two seasons are commonly described: the dry season (*carême*) from December to May, and the wet season (*hivernage*) from June to November, which corresponds to the hurricane season (DEAL Guadeloupe, 2012). The seasons are separated by transition periods in terms of rainfall and temperature (Cerema, 2020; Météo France, 2020). Following Courtin et al. (2022), each year was divided into four sampling periods to homogenize the data and refine the statistical models as follows: early dry season: (ED = December to February), late dry season (LD = March to May), early wet season (EW = June to August), and late wet season (LW = September to November), yielding a total of 24 sampling periods (Rosel et al., 2011). Given the overlap of the early dry seasons among years and because December 2013 was not included in our data sample, ED 2014 consists only of January and February 2014 for both islands.

2.2 Data collection

Data were collected between January 2014 and November 2019 from 0730 to 1800 h. Except for LD 2016 in Guadeloupe, when no photos were taken, all sampling periods were covered. Based on the methodology in Courtin et al. (2022), data collection in Guadeloupe was carried out through citizen-based science programs of the "*Observatoire des Mammifères Marins de l'Archipel Guadeloupéen*" (OMMAG), which involves whale-watchers, citizens, and researchers. OMMAG is a network that gathers photos of cetaceans around the Guadeloupe archipelago and classifies them to make them available for science programs. Photos were taken between latitudes 16°23'N and 15°58'N and between longitudes 061°63'W and 061°48'W (Figure 1B). More than 95% of the photos in Guadeloupe were taken by the whale-watching companies *Guadeloupe Evasion Découverte* (GED) and *Cétacés Caraïbes*, which departed from Deshaies and Bouillante, respectively (Figure 1B), while the remaining 5% were taken by other OMMAG members. In Martinique, data were collected by the Aquasearch scientific team during dedicated surveys departing from Trois-îlets or onboard whale-watching boats departing from Grande-Anse d'Arlets and Trois-îlets (Figure 1C). Photos were taken between latitudes 14° 28'N and 14°44'N and between longitudes 61°05'W and 61°17'W (Figure 1C). When a group of PSD was observed, an observation record was created that included date, time, GPS position, estimated group size, predominant activity, heading, and age class of the group (mothers and calves, juveniles, sub-adults, and adults). Age classes were determined by considering the size of individuals and their color pattern, with calves being less than ¾ the size of an adult, showing no spotting, and always staying close to an adult, and juveniles being ¾ the size of an adult, having dark ventral spotting, and usually swimming in close association with an adult (Shirihai and Jarett, 2007; Jefferson et al., 2015; Perrin, 2018). However, for subsequent

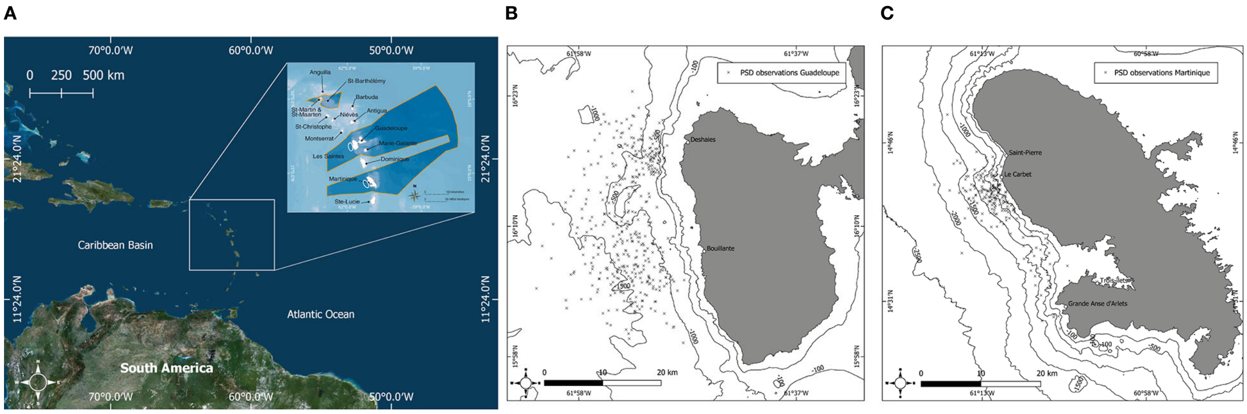

FIGURE 1
(A) Map of the eastern Caribbean showing the location of Agoa Sanctuary (dark blue polygon). The study sites in Guadeloupe and Martinique are shown by white encircled areas. Map of the leeward coasts of Guadeloupe **(B)** and Martinique **(C)** showing the locations of observed pantropical spotted dolphins, *Stenella attenuata*, between 2014 and 2019.

analysis, only data from adults were considered. A group of dolphins was defined as a group of individuals performing the same activity (Shane, 1990) with group members remaining in relative proximity (<50 m; Mann, 1999). Individuals were photographed at each observation, targeting their dorsal fins whenever possible. Whale watchers associated with OMMAG used Nikon D500, D7200, and D3200 cameras mounted with 70- to 200-mm and 18- to 300-mm lenses. Aquasearch observers used Nikon D7100 and D3500 cameras, both with 70- to 300-mm lenses. GPS positions of each observation were compiled to build PSD distributional maps for each island.

2.3 Photo-identification analysis

Dolphin photo-ID analyses were mainly based on the dorsal fin marks of each individual. To avoid false-positive or false-negative identifications because some fin marks were too similar (Würsig and Jefferson, 1990; Urian et al., 2015), analyses were limited to well-marked individuals by a careful sorting of photos according to their quality as well as their distinctiveness (Urian et al., 2015; Passadore et al., 2017). A quality score was assigned to each photo based on its sharpness, contrast, and angle of view of the dorsal fin: Q1 = very good quality, Q2 = good quality, and Q3 = average or poor quality. A score for the distinctiveness of the individual was also assigned, independently of the photo quality score: D1 = very distinctive, D2 = fairly distinctive, and D3 = moderately or not distinctive (Figure 2). Only photos with Q1 and Q2 quality as well as D1 and D2 distinctiveness were used for the analysis (Urian et al., 2015). The best photo (left or right side of the fin) of each individual was chosen to be compared with a catalog that had been developed during the preliminary study (Courtin et al., 2022) with the Windows® software Photos. If there was no match, a new ID was assigned to the individual before adding it to the catalog. An individual was considered "captured" when it was photo-identified for the first time and "recaptured" if it was subsequently photo-identified. These results were compiled into a capture–recapture matrix (or sighting history) for analysis. Discovery curves (Fisher et al., 1943; Colwell et al., 2004) were obtained by compiling the cumulative number of marked individuals identified for the first time according to each consecutive month of sampling.

2.4 Individual encounter rates

The number of photos, observations, identifications, and identified individuals were calculated. The recapture rate $R\%$ was determined for each island using the following equation:

$$R\% = \frac{R}{N}$$

where R is the number of individuals that have been recaptured at least once and N is the total number of individuals identified in the study area.

2.5 Closure test and goodness of fit

The CloseTest program was used to test population closure (Stanley and Burnham, 1999). To avoid any bias in parameter estimations, several assumptions were considered under POPAN models for an open population (Jolly, 1965; Schwarz and Arnason, 1996). To verify the goodness of fit of our data for the POPAN model, the following tests were conducted using a fully parameterized CJS model considering two groups for each island with U-CARE (Choquet et al., 2009): TEST 2, which examined significant difference in capture probabilities between individuals, and TEST 3, which examined whether all identified individuals have the same probability of survival between sampling occasions. These tests were partitioned into four different tests: (1) TEST 2.CT, which tests for a significant trap effect (trap happiness or trap shyness), which, in our case, is a virtual trap effect since individuals are not physically captured; (2) TEST 2.CL, which tests for a significant variation in

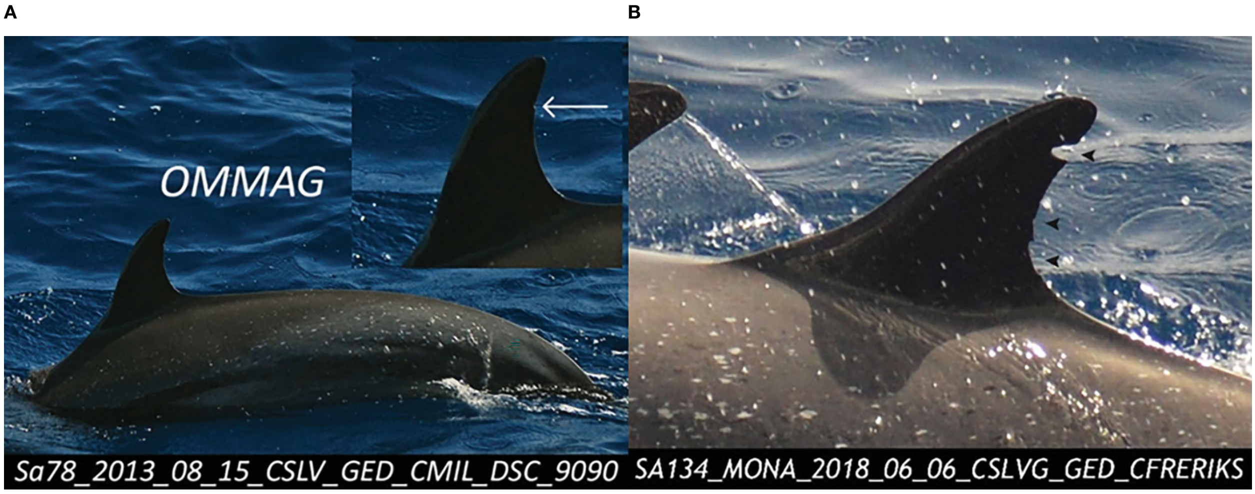

FIGURE 2
Images of a lightly marked individual (D3) pantropical spotted dolphin, *Stenella attenuata*, with a simple superficial notch (**A**, left) *vs*. a well-marked individual (D2) with deep and multiple notches (**B**, right).

the time between re-encounters for captured and non-captured individuals that are assumed to be alive; (3) TEST 3.SR, which tests for a significant excess or lack of transient individuals; and (4) TEST 3.SM, which tests for a significant effect of capture on survival. GLOBAL TEST combines TEST 2 and TEST 3 to assess significant overdispersion of the data (Choquet et al., 2005; Choquet et al., 2009).

2.6 Site fidelity estimates and clustering analysis

The recently developed Standardized Site Fidelity Index (SSFI) IH_4 was used to assess site fidelity and residency patterns at the population level using the following equation (Tschopp et al., 2018):

$$SSFI = \frac{2}{\frac{1}{IT} + \frac{1}{It}}$$

with ITas the permanence, which is the difference between the first and last sighting of an individual, and It as the periodicity, which is the recurrence of an individual, determined by the inverse of the average time (in days) between consecutive recaptures (Balance, 1990; Morteo et al., 2012; Tschopp et al., 2018). If an animal was identified more than once on the same day, only the first observation of the day was retained, and only observations separated by at least 1 day were included in the site fidelity analysis to avoid the probability of data dependency. SSFI indexes were calculated using four sighting histories with different temporal scales: $SSFI_d$ using sighting histories by sampling day, $SSFI_m$ by month, $SSFI_p$ by sampling period, and $SSFI_s$ by season. $SSFI_p$ was used to compare site fidelity between sites and clusters using a Wilcoxon–Mann–Whitney test in R (R Core Team, 2023).

These SSFI indexes were used to separate populations into separate residency clusters with an Agglomerative Hierarchical Classification (AHC) analysis (Zanardo et al., 2016; Hunt et al., 2017; Passadore et al., 2018; Haughey et al., 2020). The Euclidean distance and Ward's method (minimum variance) were used to build the AHC as the dissimilarity measure and the agglomerative clustering algorithm, respectively (Ward, 1963). Clustering analysis was conducted using R 4.0.3 (R Core Team, 2023) with the pvclust package (Suzuki and Shimodaira, 2006) following Passadore et al. (2018; see Acknowledgments).

2.7 Model selection and estimation of population parameters

The capture–recapture history was used to find the most appropriate model for our data using the MARK 9.0 software (White and Burnham, 1999). The POPAN formulation of the Jolly–Seber model for an open population (Jolly, 1965; Schwarz and Arnason, 1996) was used, considering two clusters for each island and 24 sampling periods for Martinique and 23 sampling periods for Guadeloupe (no late wet 2016). Models were compared considering a time (t), group (g), or group and time (g*t) variable structure or constancy (.) for the following parameters (Jolly, 1965; Schwarz and Arnason, 1996): (1) apparent survival φ, which is the probability that an individual or group of individuals captured in sampling period i will survive and not emigrate before sampling period $i+1$; (2) recapture probability p, which is the probability that an individual or group of individuals captured at sampling period i will be recaptured at sampling period $i+1$; and (3) probability β of entry into the population, which is the probability that an individual or group of individuals coming from the superpopulation will survive, not emigrate, and become part of the population in the study area (i.e., the studied population, in our case the marked part of the population). Following the goodness-of-fit tests and based on the separation between two distinct residency groups, only models incorporating both temporal and group variabilities in β were chosen, giving a total of 16 candidate models. The Akaike Information Criterion, corrected for small samples (AICc), was used to determine the best model fitting our data for each island (White and Burnham, 1999; Burnham and Anderson, 2002). That model was then used to estimate p, β, and φ between sampling periods and annually, and seasonal and total abundances of PSD populations in Guadeloupe and Martinique.

2.8 Total population abundance

The POPAN capture–recapture model only estimated the abundance of marked (D1+D2) individuals ($\hat{N}_m$). The superpopulation size and total abundances were determined by incorporating the proportion of unmarked individuals ($1 - \hat{\theta}$) in the calculation (Tyne et al., 2014; Sprogis et al., 2016; Passadore et al., 2017; Haughey et al., 2020). That proportion was calculated for each island by dividing the number of marked individuals (D1+D2) by the number of all individuals (D1+D2+D3) present on high-quality photographs (Q1) (Sprogis et al., 2016). To avoid repeated inclusion of the same D3 individuals, all dolphins, including those marked and previously identified, were counted again. Standard errors from the total population size were calculated following the "delta method" (Seber, 1982; Williams et al., 2002):

$$SE(\hat{N}_t) = \sqrt{\hat{N}_t^2\left(\frac{SE(\hat{N}_m)^2}{\hat{N}_m^2} + \frac{1-\hat{\theta}}{n\hat{\theta}}\right)}$$

Log-normal 95% confidence intervals of the total population size were calculated with upper and lower limits obtained by either multiplying or dividing $\hat{N}_t$ by the factor C following Burnham et al. (1987):

$$C = exp\left(1.96\sqrt{ln\left(1 + \left(\frac{SE(\hat{N}_t)}{\hat{N}_t}\right)^2\right)}\right)$$

3 Results

A total of 783 survey trips (400 in Guadeloupe and 383 in Martinique) conducted between January 2014 and November 2019 resulted in the collection of 115,705 photos, of which 46,825 were usable (Q1 and Q2 = 40%; Table 1). Survey effort is presented in more detail in Figure 3. PSD groups ranged from 1 to 500 individuals in Guadeloupe, with an average group size of 160 (95% CI: 150–170), while group sizes in Martinique ranged from 5 to 500 individuals,

TABLE 1 Data collected on pantropical spotted dolphins, *Stenella attenuata*, in Agoa Sanctuary along the leeward coasts of Guadeloupe and Martinique (Eastern Caribbean).

Island	Year	Survey trips	Photos collected	Usable photos	Identified individuals	New individuals
GUADELOUPE	2014	30	2,766	898	45	41
	2015	69	7,781	2,205	114	64
	2016	71	8,202	2,253	84	27
	2017	60	4,420	956	47	12
	2018	61	5,756	3,249	77	22
	2019	109	26,287	9,907	75	13
	Total	***400***	***55,212***	***19,468***	***442***	***179***
MARTINIQUE	2014	64	5,970	2,350	57	36
	2015	108	14,135	6,447	147	42
	2016	54	9,313	3,876	25	3
	2017	54	8,820	4,185	51	7
	2018	40	6,210	3,466	45	6
	2019	62	16,045	7,033	84	17
	Total	***382***	***60,493***	***27,357***	***409***	***111***
TOTAL	**Total**	**782**	**115,705**	**46,825**	**851**	**290**

Data shown are survey year, number of survey trips, total photos collected, total usable photos, and number of sightings. Bold was used to highlights the total values for each island, and for both combined.

with an average group size of 97 (95% CI: 88–107). A total of 290 marked individuals were identified, 179 in Guadeloupe and 111 in Martinique (Table 2). We identified 29 of the 64 (45%) Guadeloupe individuals and 31 of 54 (57%) Martinique individuals in our 2014–2017 images. None of the 290 identified individuals was found in both Martinique and Guadeloupe. The analyses were therefore carried out considering two distinct populations, one for each island. The proportion of marked individuals $\hat{\theta}$ within the population was estimated at 0.12 (SE = 0.02) in Guadeloupe and 0.09 (SE = 0.02) in Martinique.

3.1 Pantropical spotted dolphin distributions off the coasts of Guadeloupe and Martinique

The PSD population in Guadeloupe seemed to be distributed homogeneously in waters with bathymetries ranging from 500 m to 1,500 m (Figure 1B). Conversely, PSD population in Martinique preferred shallower waters, mainly concentrating in waters with bathymetries ranging from 100 m to 1,500 m depth off the town of Le Carbet, located south of the bay of Saint-Pierre (Figure 1C).

3.2 Goodness-of-fit tests and clustering analysis

Closure for each population was tested and revealed that both populations were open (Stanley & Burnham Closure Test in Guadeloupe *p*-value< 0.01; in Martinique *p*-value< 0.01). Goodness-of-fit tests were first performed considering total populations for each island, and significant excesses of transient individuals were detected for both (TEST3.SR in Guadeloupe, *p*-value = 3.4e-06; TEST3.SR in Martinique, *p*-value = 8.7e-07). A significant trap-happiness effect was also detected for the Guadeloupe population (TEST2.CT, *p*-value

TABLE 2 Summary of the number of individuals identified, maximum number of captures, recapture rates, Standardized Site Fidelity Index by sampling period (SSFIp), and abundance estimates for the marked ($\hat{N}_M$) and total ($\hat{N}_T$) population of pantropical spotted dolphins *Stenella attenuata* off Guadeloupe and Martinique (eastern Caribbean) between 2014 and 2019 according to the total population and the residency cluster [frequent users (FU) or occasional visitors (OV)].

Population		Ident. ind.	N_{max} of captures	Recapture rate	SSFI$_p$ (95% CI)	$\hat{N}_M$ (95% CI)	$\hat{N}_T$ (95% CI)
GUAD.	**Total**	179	21	42%	0.10 (0.08–0.13)	453 (NA)	3720 (NA)
	FU	69	21	100%	0.27 (0.24–0.30)	80 (74–93)	657 (525–821)
	OV	110	1	6%	0.001 (0–0.002)	373 (280–516)	3,063 (2,133–4,398)
MART.	**Total**	111	21	62%	0.16 (0.13–0.20)	156 (NA)	1779 (NA)
	FU	30	21	100%	0.43 (0.38–0.48)	30 (30–30)	336 (253–446)
	OV	81	2	48%	0.06 (0.04–0.08)	126 (107–159)	1,443 (1,024–2,033)

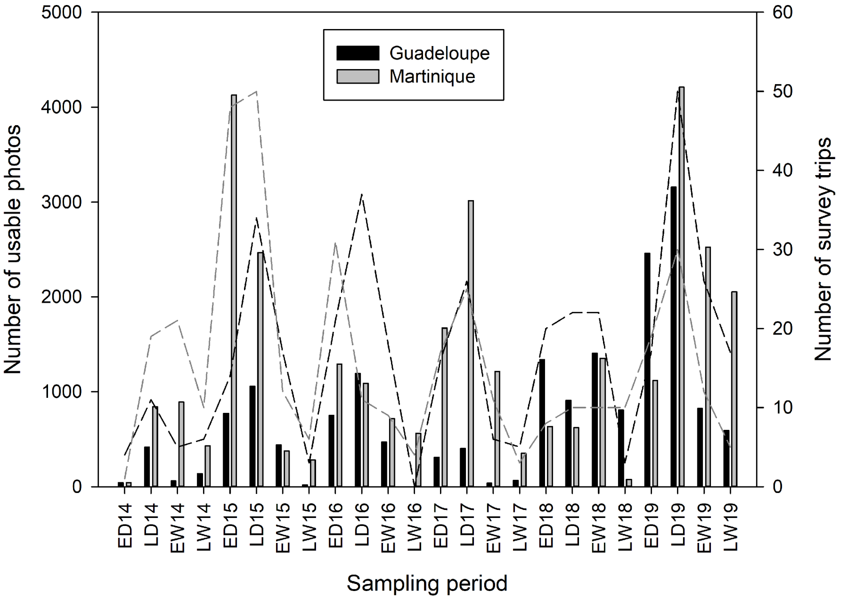

FIGURE 3
Sampling effort of pantropical spotted dolphins, *Stenella attenuata*, in Agoa Sanctuary along the leeward coasts of Guadeloupe and Martinique islands between 2014 and 2019, covering the early dry season (ED = December to February), late dry season (LD = March to May), early wet season (EW = June to August), and late wet season (LW = September to November).

= 0.01). To refine the population analysis, populations were separated into separate residency clusters. The AHC analysis separated each marked population into two residency clusters, which were classified as frequent users (FU) or occasional visitors (OV). These clusters in Guadeloupe consisted of 69 FU (38%) and 110 OV individuals (62%), while in Martinique, they consisted of 30 FU (27%) and 81 OV individuals (73%; Table 2). Goodness-of-fit tests were again performed considering FU and OV clusters, and while no significant excess of transient individuals was detected, a significant trap-happiness effect was still present for the Guadeloupe population (TEST2.CT, *p*-value = 0.02). GLOBAL TEST did not detect any overdispersion of the data considering two clusters for each population (GLOBAL TEST for Guadeloupe: χ^2 = 56.30, DF = 56, *p*-value = 0.46; GLOBAL TEST for Martinique: χ^2 = 48.84, DF = 71, *p*-value = 0.98), indicating a good fit of our model to the data.

3.3 Encounter rates of pantropical spotted dolphin

The cumulative number of newly identified individuals did not reach a plateau in the total marked population discovery curve for

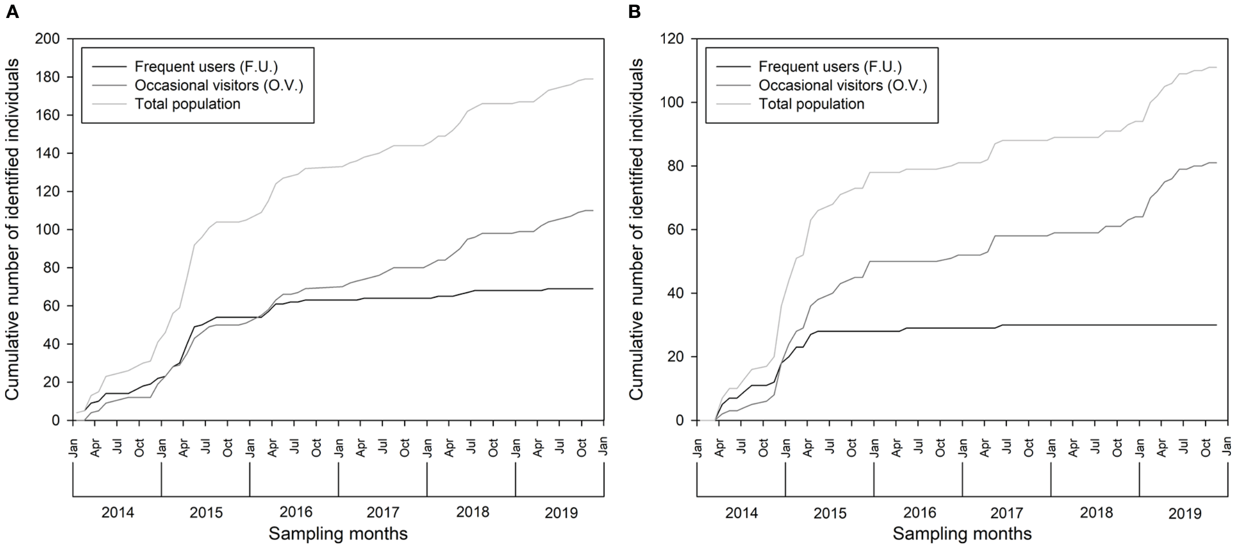

FIGURE 4
Discovery curve of identified pantropical spotted dolphin, *Stenella attenuata*, in **(A)** Guadeloupe and **(B)** Martinique between 2014 and 2019.

TABLE 3 POPAN model results considering 24 sampling periods and two residency groups [frequent users (FU) or occasional visitors (OV)] of pantropical spotted dolphins *Stenella attenuata* in Guadeloupe and Martinique (eastern Caribbean).

Model	AICc	Delta AICc	AICc Weights	Model likelihood	Num. Par	Deviance
Guadeloupe						
{φ(g) p(t) β(g*t)}	1,215.042	0	1	1	67	−128.037
{φ(g) p(g*t) β(g*t)}	1,265.642	50.600	0	0	94	−165.940
{φ(g*t) p(t) β(g*t)}	1,271.665	56.623	0	0	102	−189.552
{φ(.) p(g*t) β(g*t)}	1,302.624	87.582	0	0	93	−125.374
{φ(t) p(g*t) β(g*t)}	1,311.119	96.077	0	0	103	−153.926
{φ(g) p(.) β(g*t)}	1,343.465	128.423	0	0	49	51.142
{φ(g) p(g) β(g*t)}	1,345.279	130.237	0	0	50	50.286
{φ(g*t) p(g*t) β(g*t)}	1,350.078	135.036	0	0	124	−202.534
Martinique						
{φ(g) p(t) β(g*t)}	1,208.403	0	0.999	1	70	278.628
{φ(.) p(g*t) β(g*t)}	1,222.774	14.371	0.001	0.001	97	190.910
{φ(g) p(g*t) β(g*t)}	1,226.302	17.899	0.000	0.0001	98	190.155
{φ(g) p(g) β(g*t)}	1,259.850	51.446	0	0	52	386.217
{φ(t) p(g*t) β(g*t)}	1,262.489	54.086	0	0	110	171.590
{φ(.) p(t) β(g*t)}	1,290.804	82.401	0	0	73	350.839
{φ(.) p(g) β(g*t)}	1,294.051	85.648	0	0	51	423.307
{φ(g) p(.) β(g*t)}	1,297.269	88.866	0	0	51	426.525

The table provides an overview of the corrected Akaike Information Criterion (AICc), difference in AICc, AICc weight, model likelihood, number of parameters used in the model fit, and deviance explained. The models used were either constant (.), group (g), or time (t) variable for each of their parameters, i.e., φ (survivability), p (capture probability), and β (probability of entrance into the superpopulation).

The models are ranked by the lowest AIC.

Guadeloupe (Figure 4A), but it seems to approach an asymptote. A plateau was reached for FU individuals while new OV individuals were continuously identified in the area (Figure 4A). Similar results were obtained in Martinique for both FU and OV (Figure 4B), indicating that most FU of both islands were identified while more OV individuals, which have not been identified, were present in the area. The maximum number of recaptures of the same individual in Guadeloupe was 21 for individual SA081 "ARNOLD," while 100% of the FU, 6% of the OV, and 42% of the total population were recaptured at least once (Table 2). In Martinique, the maximum number of recaptures was 21 for SA159 "PIKACHU," while 100% of the FU, 48% of the OV, and 62% of the total population were recaptured at least once (Table 2).

3.4 Estimation of pantropical spotted dolphin site fidelity

The site fidelity index ($SSFI_p$; Table 2) in Guadeloupe was estimated at 0.10 (95% CI: 0.08–0.13) for the whole marked population, 0.27 (95% CI: 0.24–0.30) for FU, and 0.001 (95% CI: 0–0.002) for OV. In Martinique, it was estimated at 0.16 (95% CI: 0.13–0.20) for the whole marked population, 0.43 (95% CI: 0.38–0.48) for FU, and 0.06 (95% CI: 0.04–0.08) for OV.

3.5 Survival rates and abundance of pantropical spotted dolphin

The model that best fit out data was the same for both islands (Table 3). In Guadeloupe, the apparent survival φ of the marked population was constant over time but differed among residency clusters. It was estimated at 0.94 (95% CI: 0.92–0.96) for FU and 0.33 (95% CI: 0.23–0.45) for OV between sampling periods, and at 0.80 (95% CI: 0.72–0.85) for FU and 0.01 (95% CI: 0.003–0.04) for OV annually. The recapture probability p was constant among clusters but varied temporally and was higher during dry seasons (p_{ds} = 0.14–0.65) than during wet seasons (p_{ws} = 0–0.56; Figure 5A), likely because of variations in sampling effort. The probabilities β of entry into the population varied with both time and cluster. Approximately 6% of the FU individuals were present in the study area just before the start of the study. β values were higher at the start of the study, with a maximum of 0.63 (95% CI = 0.36–0.83) between late wet 2014 and early dry 2015 and almost null during subsequent intervals (Figure 5B), indicating that more than 80% of FU recruitment from the super-population occurred before early dry 2015. For OV, probabilities β of entry varied according to intervals, with a maximum at 0.28 (95% CI = 0.17–0.43) reached between late wet 2014 and early dry 2015 (Figure 5B), indicating that more than 40% of recruitment from the super-population occurred before early dry 2015. No OV individuals were present just before the start of the study. The

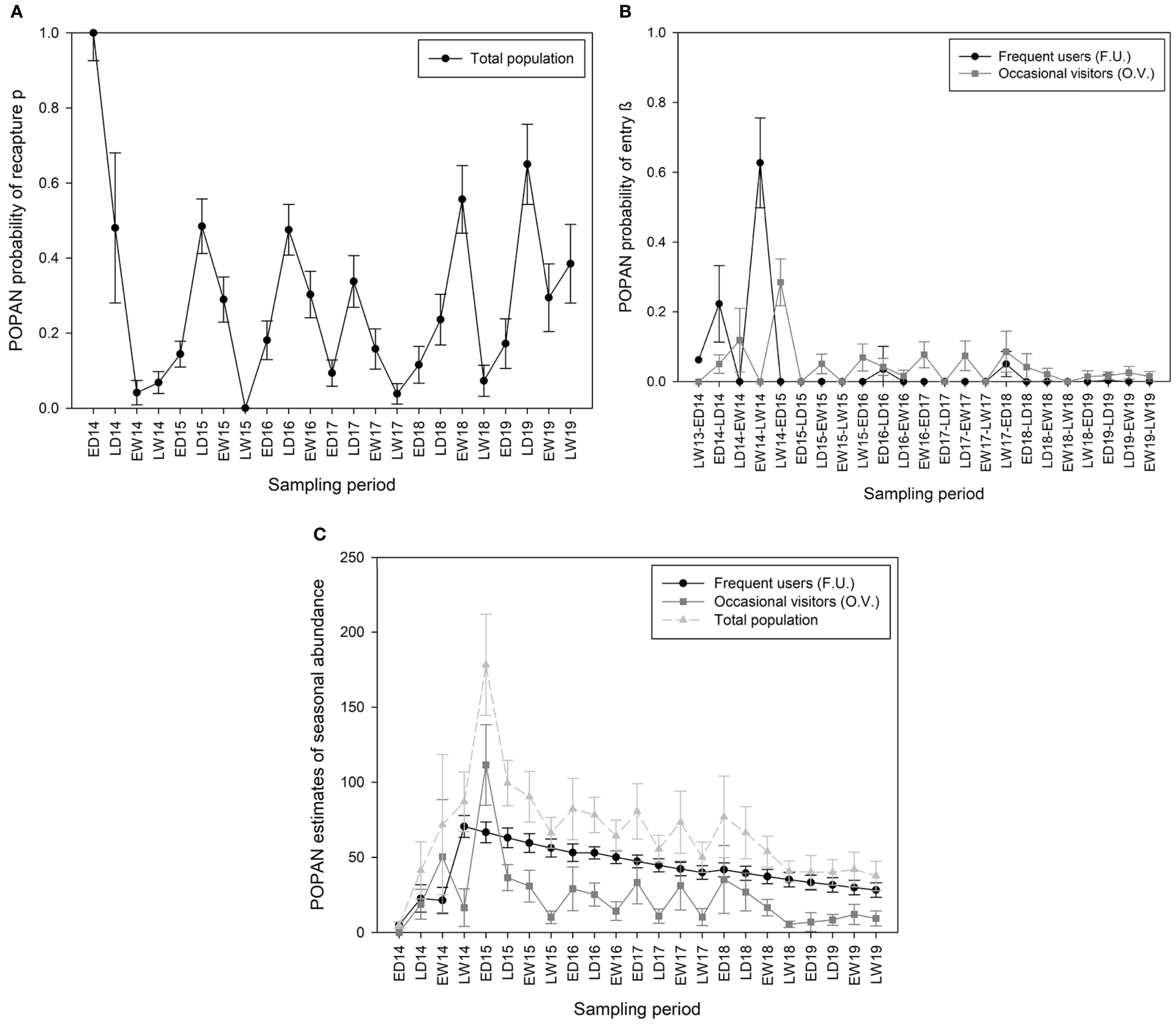

FIGURE 5
POPAN estimates of **(A)** capture probability, **(B)** probability β of entry, and **(C)** abundance among sampling periods of pantropical spotted dolphin, *Stenella attenuata*, in Guadeloupe between 2014 and 2019. Bars show estimated standard error.

maximum number of FU individuals in the area ($\hat{N}_{M\text{FU}}$ = 71, 95% CI: 58–86) was reached during late wet 2014, after which their abundance showed a progressive and stable decline until the end of the study period ($\hat{N}_{M\text{LW19}}$ = 28, 95% CI = 10–39; Figure 5C). Abundances of OV individuals in the area varied among sampling periods, showing higher values during dry seasons ($\hat{N}_{M\text{ds}}$ = 7–111) than during wet seasons ($\hat{N}_{M\text{ws}}$ = 5–50), and they decreased until the end of the study period ($\hat{N}_{M\text{OV/2019}}$ = 5–12). The total population followed the same tendency, with a maximum of 179 marked individuals in early dry 2015, followed by slight variations caused by the proportion of OV individuals and a slow decline in abundance until the study's end in late wet 2019 ($\hat{N}_{M\text{Tot/2019}}$ = 38–42). The total number of marked individuals $\hat{N}_M$ throughout the study period was estimated at 80 FU individuals (95% CI: 74–93) and 373 OV individuals (95% CI: 280–516; Table 2). The total population size $\hat{N}_T$ in Guadeloupe, including the non-marked proportion of the population, was estimated at 657 FU individuals (95% CI: 525–821) and 3,063 OV (95% CI: 2,133–4,398; Table 2).

In Martinique, the apparent survival φ of the marked population was constant over time and varied by cluster. It was higher than in Guadeloupe for both clusters and was estimated at 1 for FU (95% CI: 1–1) and 0.84 for OV (95% CI: 0.79–0.88) among sampling periods, and at 1 for F.U. (95% CI: 1–1) and 0.50 for OV (95% CI: 0.39–0.60) annually (Table 2). Like Guadeloupe, the recapture probability p in Martinique was constant between clusters but varied temporally and was higher during dry seasons (p_{ds} = 0.11–0.60) than during wet seasons (p_{ws} = 0.03–0.50; Figure 6A), following the patterns of sampling effort (Figure 3). Probabilities β of entry in Martinique also followed the same tendency as in Guadeloupe. For FU, β values were higher at the start of the study, with an average maximum of 0.50 (95% CI = 0.23–0.77) between late wet 2014 and early dry 2015, and 0.48 (95% CI = 0.21–0.76) between late dry 2014 and early wet 2014. Probabilities β of entry were almost null during subsequent intervals (Figure 6B), and more than 95% of the FU superpopulation was captured before early dry 2015. No FU or OV individuals were present in the study area just before the start of the study. For OV, β varied according to the intervals, with a maximum of 0.25 (95% CI = 0.04–0.74) between early wet 2014 and late wet 2014 (Figure 6B), and only 35% of the OV superpopulation was captured before early dry 2015. The number of FU individuals was stable for most

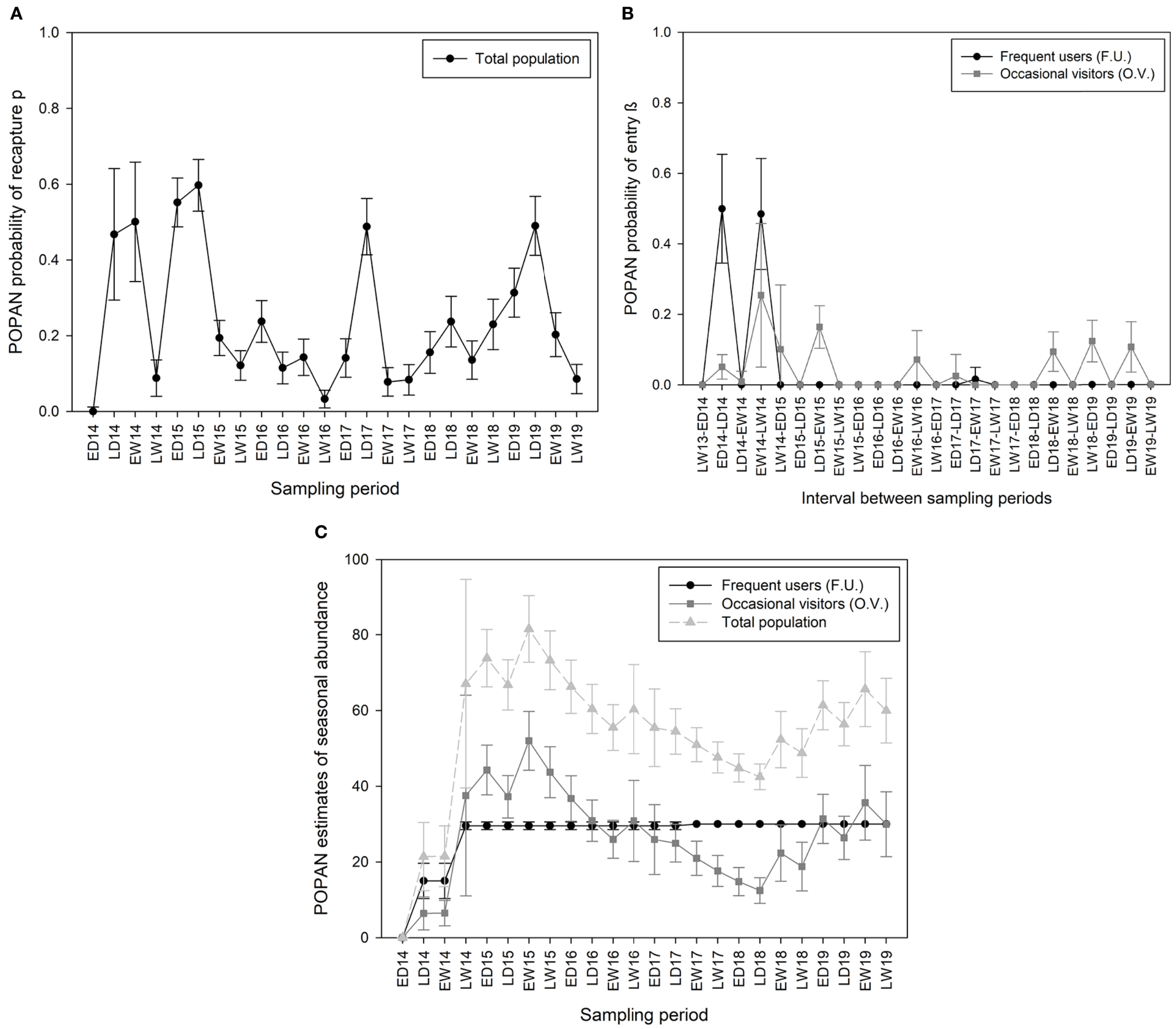

FIGURE 6
POPAN estimates of **(A)** capture probability, **(B)** probability β of entry, and **(C)** abundance among sampling periods of pantropical spotted dolphin, *Stenella attenuata*, in Martinique between 2014 and 2019. Bars show estimated standard error.

of the study period ($\hat{N}_{MFU} = 30$) while the abundance of OV individuals varied according to the sampling period, with a maximum during early wet 2015 ($\hat{N}_{MEW15} = 52$, 95% CI = 39–70) and a minimum during late dry 2018 ($\hat{N}_{MLD18} = 12$, 95% CI = 7–21). OV abundance seemed to be stable between the start and the end of the study ($\hat{N}_{MLW14} = 38$, 95% CI = 11–131 and $\hat{N}_{MLW19} = 30$, 95% CI = 17–52, Figure 6C). Like the OV cluster, total population abundance varied according to the sampling periods. The total number of marked individuals in the Martinique area over the entire study period was lower than in Guadeloupe, with estimations of 30 for FU (95% CI: 30–30) and 126 for OV (95% CI: 107–159, Table 2). The total population size in Martinique ($\hat{N}_T$) was estimated at 336 for FU (95% CI: 253–446) and 1,443 for OV (95% CI: 1,024–2,033; Table 2).

4 Discussion

This study extended the preliminary work reported by Courtin et al. (2022) and allowed the identification of 179 marked PSD individuals in Guadeloupe (115 newly identified individuals) and 111 marked PSD individuals in Martinique (57 newly identified) over a period of six consecutive years. Although there are some difficulties in accurately counting the number of cetaceans because all individuals may not surface while being observed, we provide some insights into PSD individuals present for both Guadeloupe and Martinique islands.

4.1 Sampling effort and group size

The number of usable photos for both islands were lower during wet seasons (Figure 3), which is the consequence of fewer survey trips during these periods. Indeed, the wet (hurricane) season (Cerema, 2020; Météo France, 2020), with poor sea conditions, did not allow the same sampling effort as during the dry season. However, this should not affect estimates produced by the POPAN model since it does not assume equal sampling effort (Cooch and White, 2019). Even though the number of usable photos in Martinique (27,357 photos) was higher than in Guadeloupe (19,468 photos), more marked individuals were identified in Guadeloupe (179) than in Martinique (111). Conversely, the previous study (Courtin et al., 2022) showed a higher number of usable photos in Guadeloupe (13,156 photos) than in Martinique (10,499 photos), reporting 70 and 54 individuals for each island, respectively. Consequently, these findings suggest that differences in abundances are not related to sampling effort; thus, it is possible that the population of marked PSD is larger in Guadeloupe than in Martinique. These results are consistent with the group sizes observed for both islands, with larger groups observed in Guadeloupe (mean group size = 160, 95% CI: 150–170) than in Martinique (mean group size = 97, 95% CI: 88–107). PSD group sizes are generally higher in most populations worldwide, but these estimates can vary among populations and localities. For example, the coastal group size of PSD in Murcielago Archipelago, Costa Rican Pacific, was estimated to be between 1 and 50 (mean = 9.95, SE = 10.28; May-Collado and Forcada, 2012), while offshore groups of PSD in Hawaii were found to range from 10 to 150 individuals (mean = 60, SE = 26; Baird et al., 2001). Larger groups have been reported in the Northern Gulf of Mexico, ranging from 5 to 210 (mean = 49, SE = 4.5) and 3 to 650 individuals (mean = 71.3, SE = 3.45; Mullin et al., 2004; Maze-Foley and Mullin, 2007); in Brazil, with groups from 3 to 250 individuals off the coast (Moreno et al., 2005); and in Golfo Dulce, Costa Rica, with groups from 50 to 300 individuals (Cubero-Pardo, 2007). The small groups of PSD reported in Guadeloupe and Martinique could suggest that dolphins are mainly coastal individuals.

4.2 Goodness of fit and residency clusters

The heterogeneity in the data detected by the goodness-of-fit tests separated each population into two residency clusters. These clusters do not necessarily correspond to social groups of individuals, but rather to individuals sharing a common residency pattern (Whitehead and Wimmer, 2005; Haughey et al., 2020). However, the heterogeneity previously detected in Martinique (Courtin et al., 2022) was confirmed, and the heterogeneity tests also detected a significant excess of transient (OV) individuals in Guadeloupe, which was not detected previously, probably because of the short study period (2 years).

PSD groups preferring different geographic areas have been reported worldwide, with coastal populations occurring close to islands and the mainland while others are distributed in offshore waters, thus showing slight differences in ecological niches and habits (Jefferson et al., 2015; Perrin, 2018). The existence of different residency clusters in populations from both Guadeloupe and Martinique may suggest that both coastal and offshore individuals are transiting the Eastern Caribbean island waters, with FU individuals belonging to the coastal form and OV individuals belonging to the offshore one. This remains to be confirmed.

The trap-happiness effect detected in the goodness-of-fit tests showed that the survey method in Guadeloupe resulted in an increased probability for some marked individuals to be captured, which can result in an underestimation of the parameters produced by the models, such as the size of the marked population $\hat{N}_M$ (Pollock et al., 1990; Pradel, 1993; Parra et al., 2006; Pradel and Sanz-Aguilar, 2012). Determining the factors leading to a trap-happiness effect can be laborious (Choquet et al., 2005). However, the regularly observed bow-riding behavior of PSD (Jefferson et al., 2015; Perrin, 2018), which attracts some individuals to boats, might be one of the reasons. Moreover, observers in Guadeloupe acknowledged that distinctively marked individuals were more frequently photographed than less distinct or unmarked individuals (Millon, personal observation) compared to the situation in Martinique, where the scientific team was on the boat, randomly photographing individuals. In addition, some individuals showed strong site fidelity, which could induce heterogeneity in recapture probability (Pradel, 1993). This effect would probably be less prevalent in Guadeloupe than in Martinique, where site fidelity is higher. In addition, because marked individuals in Guadeloupe might be overrepresented in photographs, the total size $\hat{N}_T$ of that population might be underestimated by an exaggerated mark ratio $\hat{\theta}$ (Eguchi, 2014; Wickman et al., 2021).

4.3 Distribution and site fidelity of pantropical spotted dolphins in Guadeloupe and Martinique

Most PSD observations in Guadeloupe were made in areas where the bathymetries ranged between 500 and 1,500 m while bathymetries ranged between 100 m and 1,500 m in Martinique. PSD occurrence at these depths is consistent with previous observations (600 m to 2,500 m; Mignucci-Giannoni et al., 2003) and with predictions from ecological niche modeling (500 m to 1,600 m; Barragán-Barrera et al., 2019) in the Caribbean, but they are shallower than depths predicted from observations (850 m to 4,000 m; Moreno et al., 2005) and ecological niche modeling (1,500 m to 5,000 m; do Amaral et al., 2015) off Brazil in the southern Atlantic Ocean. The apparent preference by PSD for “shallower” waters in the Eastern Caribbean may be related to prey availability: coastal Caribbean waters are oligotrophic environments (Corredor, 1979); hence, PSD tend to travel long distances looking for food ((Davis et al., 2002; Barragán-Barrera et al., 2019).

Most FU individuals from both islands were identified in contrast to OV individuals; this is consistent with their respective residency patterns. FU individuals, which are regularly present and are probably mainly of the coastal form that prefers shallower areas, are more likely to be identified than OV individuals, who are likely offshore individuals ranging over a broader area and who periodically enter and leave the area. The high site fidelity of FU from both islands indicates that the same individuals return regularly to the study area while OV rarely return to the study area because of low site fidelity. Both islands have resident individuals, which could be indicative of the high ecological suitability of their leeward coasts. Indeed, these areas are sheltered from climate hazards, especially during the hurricane season, and may offer several advantages for delphinid species, such as complex and shallow habitats for protection from predators (Wells et al., 1999; Connor, 2000), as well as predictable food resources (Gowans et al., 2007). These factors might be more diffuse along the Guadeloupe coast, where PSD observations are more spread out. PSD near Martinique are frequently sighted offshore of Le Carbet and are likely the coastal form, making them attractive for whale-watching activities (Mayol et al., 2016).

Habitat use by delphinids may differ according to age and sex (Heithaus and Dill, 2002; Gowans et al., 2007) since individuals form structured age and sex groups throughout their lifetimes (Gowans et al., 2007; Jefferson et al., 2015). In Martinique, marked individuals may not be evenly distributed according to age or sex (Safi et al., 2020), which could lead to an overrepresentation of age and sex classes in the observed distribution. However, the areas of observation seem to be the same whether or not marked individuals are present in the group (de Montgolfier, personal observation; Mayol et al., 2016; Safi et al., 2020). More information on individuals' sex and their social structure is needed to determine whether spatial segregation according to social groups exists in these two islands.

4.4 Movement of pantropical spotted dolphins between Guadeloupe and Martinique

Photo-identification studies between islands in Agoa Sanctuary have shown movements of short-finned pilot whales (De Vries, 2017) and sperm whales (Gero et al., 2007; De Vries, 2017), confirming the effectiveness of the technique to assess cetacean migration and movement patterns. However, no PSD individual was observed in both Guadeloupe and Martinique between 2014 and 2019, showing that exchanges between these two populations are very low, as suggested by the preliminary study (Courtin et al., 2022). Only one individual, known as SA054 "Victoire," was observed at both islands. This individual was first identified in Martinique on 12 January 2013 and again in Guadeloupe on 23 June 2013 (Bouveret, Millon, and de Montgolfier, unpublished data). Victoire was subsequently identified twice in Guadeloupe, on 26 April 2015 and 13 May 2019, but never again in Martinique. This movement is likely exceptional behavior; thus, movements of marked PSD between Guadeloupe and Martinique appear to be extremely rare.

Nevertheless, undetected movements of PSD individuals may occur if conducted by unmarked or slightly marked dolphins, which were not distinctive enough to be identified in this study. It would be possible to examine this with an increased and more systematic research effort. The presence of transient individuals in both populations suggest that a high proportion of individuals move outside of the study area. Even if some anecdotal observations of PSD have been reported in other areas (Windward-coast and Grand-Cul-de-Sac-Marin in Guadeloupe, Robert and François bays in Martinique), most populations tend to be concentrated on the leeward coast (Cuzange, 2011; Mayol et al., 2016). It is likely that these transient individuals move further offshore from the island, toward either the Caribbean or the Atlantic basin. PSD have also been reported off the coasts of various other islands of the West Indies, such as Dominica (Watkins, 1985), Sainte-Lucie (Burks and Swartz, 2000), and Saint-Vincent (Caldwell et al., 1971). As Dominica is located between Guadeloupe and Martinique, transient individuals from both populations might move to Dominica, maintaining genetic connectivity between these populations, even if no direct movements between Guadeloupe and Martinique exist. It is also possible that transient individuals from Martinique may move further south to nearby islands such as St Lucia or St Vincent. However, no studies have been published on the populations of these islands. Research focusing on the connectivity of these populations by similar photo-identification techniques linked to genetic assessments would help to better understand the population genetic structure and movements of this species in the West Indies.

4.5 Modeling estimation of population parameters

It is difficult to estimate the true survivability of long-lived species (Hunt et al., 2017; Passadore et al., 2017; Haughey et al., 2020) because it is challenging to separate permanent emigration from the survival probability of one individual (Jolly, 1965). PSD are long-living mammals (Shirihai and Jarett, 2007; Edwards et al., 2013; Jefferson et al., 2015; Perrin, 2018); hence, it is not expected that natural mortality would affect the survivability estimate during our 6-year study period. Furthermore, only a few PSD stranding events were reported in both islands between 2014 and 2019 (two and three strandings in Guadeloupe and Martinique, respectively; Réseau National Échouage, 2021), which is not indicative of unusual mortality events. However, currents and trade winds from the Atlantic Ocean may carry dead animals offshore instead of bringing them to the coast.

FU individuals from both islands display higher residency patterns than OV individuals, while OV individuals, which include transients, are more mobile and less regularly present, leading to higher permanent emigration since they likely rely on a habitat larger than our study area (Haughey et al., 2020; Bolaños-Jiménez et al., 2021). This is particularly evident for the Guadeloupe population, where the annual apparent survival of FU individuals ($\varphi = 0.80$, 95% CI: 0.72–0.85) is 80 times higher than that of OV individuals ($\varphi = 0.01$, 95% CI: 0.003–0.04), but is also seen in the Martinique population of ($\varphi = 1$, 95% CI: 1–1 for FU and $\varphi = 0.50$, 95% CI: 0.39–0.60 for OV). The PSD population in Martinique displayed higher apparent survival than that in Guadeloupe, perhaps because of the increased dispersion of individuals in Guadeloupe. The annual apparent survivability of the FU individuals in Guadeloupe was slightly lower ($\varphi = 0.80$) while that of FU individuals in Martinique was similar ($\varphi = 1$). Likewise, other resident populations of *Stenella* worldwide showed similar survival estimations, such as spinner dolphins in Hawaii ($\varphi = 0.97 \pm 0.05$; Tyne et al., 2014), which were suggested to be representative of closed populations with little movement in or out of the study area, or other resident delphinids such as common bottlenose dolphins of the southwestern Gulf of Mexico ($\varphi = 1$; 95% CI: 1–1; Bolaños-Jiménez et al., 2021). Thus, the lower FU survival rate in Guadeloupe might be the result of some individuals moving in or out from the study area, whereas FU survival rates in Martinique indicate both high survival and very low emigration rates.

Variations in recapture probability in both islands appeared to be the result of variations in sampling effort, which is common with POPAN models (Chan and Karczmarski, 2017; Hunt et al., 2017; Passadore et al., 2017). Recapture probabilities are lower when few survey trips are made—and few photos taken—as it is the case during the wet hurricane season (Cerema, 2020). In CJS models that consider temporal variations in recapture probability, it is common that the recapture probability of the first period is not estimated correctly

(Cooch and White, 2019). This explains why the recapture probability of early dry 2014 in both islands appear to represent extreme and imprecise values ($p = 1$, 95% CI: 0–1 in Guadeloupe and $p = 0$, 95% CI: 0.00–0.02 in Martinique). Almost all FU individuals of both islands were recruited at the start of the study: they are regularly present in the area and thus are more likely to be observed and identified. This can also explain the low abundances estimated for the first year, when only a small portion of individuals had been identified. Conversely, OV individuals were recruited continuously throughout the study period when new individuals entered the population. After most FU individuals had been identified, their abundance remained constant while the number of OV individuals varied according to the arrival of new individuals and the emigration of identified individuals.

The number of PSD individuals in Guadeloupe declined slightly and continuously during the study. In Guadeloupe and Martinique, marine species are subject to multiple anthropogenic pressures, such as maritime traffic, fishing activities, and water pollution (Cuzange, 2011; Mayol et al., 2016; Feunteun et al., 2019), which can lead to injury and death (Read and Murray, 2000; Reynolds et al., 2009; Luksenburg, 2014). However, stressors like maritime traffic and competition for food linked to fishing are more important on the Caribbean coast of Martinique than in Guadeloupe (Cuzange, 2011). A decrease in PSD abundance seemed to occur in Martinique from 2018 to 2019 (Courtin et al., 2022), but extending the study period from 2014 to 2019 showed that PSD abundance was relatively constant over the years. It is likely that the decrease in PSD abundance was the result of permanent emigration out of the study area rather than an increase in mortality. Productive ecosystems in the Caribbean basin such as coral reefs have been greatly perturbed (Pandolfi et al., 2003); this has reduced food availability and could force PSD to travel further offshore to find prey (Barragán-Barrera et al., 2019). The decline in PSD abundance needs to be monitored more closely to understand better its causes and consequences.

The number of individuals in the superpopulation estimated by POPAN were two to three times larger in Guadeloupe ($\hat{N}_{MFU} = 80$, $\hat{N}_{MOV} = 373$) than in Martinique ($\hat{N}_{MFU} = 30$, $\hat{N}_{MOV} = 126$), and the total population size estimates were two times larger in Guadeloupe ($\hat{N}_{TFU} = 657$, $\hat{N}_{TOV} = 3063$) than in Martinique ($\hat{N}_{TFU} = 336$, $\hat{N}_{TOV} = 1443$), which confirms preliminary findings regarding the number of identifications and abundances for each island (Courtin et al., 2022). However, the presence of a trap-happiness effect in Guadeloupe may have produced an underestimation of the marked population estimates (Pradel, 1993; Parra et al., 2006; Pradel and Sanz-Aguilar, 2012), which may be even more important because increased photographing of distinctively marked individuals might lead to a higher mark ratio, and thus a lower estimate of the total population size (Wickman et al., 2021). To overcome such biases on the trap effect and the mark ratio estimations, the sampling method should specify that photographs be taken randomly of all individuals, whether or not they have distinctive markings and by taking a number of photographs proportional to the size of the group observed (Eguchi, 2014; Wickman et al., 2021). Our abundance estimates, which were determined from a relatively small study area, seem to indicate rather large populations. For comparison, our estimates were similar to the number of PSD estimated from much larger study areas, e.g., the southeastern Atlantic off the US (N = 6,593, CV = 0.51; Garrison, 2020), the northwestern Gulf of Mexico (N = 5,876, CV = 0.43 and N = 5,097, CV = 0.24; Jefferson, 1996 and Mullin et al., 2004, respectively), and in Pacific waters off Colombia (N = 3,934, 95% CI: 1,755–8,820; Palacios et al., 2012).

4.6 Implications for the conservation of pantropical spotted dolphins in Agoa Sanctuary

The management and conservation of marine species can be complex due to the lack of baseline studies on the species and the environment in which they live (O'Brien and Whitehead, 2013; Haughey et al., 2020). It is essential to improve the current knowledge of these species to carry out specific and effective action plans to protect them (Holt, 2009). Our results indicate that PSD populations in Guadeloupe and Martinique consist of individuals with different levels of residency—individuals showing high site fidelity and transients displaying low site fidelity, with individuals regularly entering and leaving the study area. Despite the presence of mobile transient individuals, there is little to no exchange between the populations of Guadeloupe and Martinique apart from the exceptional case documented in 2013. PSD individuals in Martinique seemed to be concentrated in one specific area, off the coast of Carbet, and their abundance in the study area, although lower than in Guadeloupe, appeared to be stable. Conversely, the larger Guadeloupe population seemed to be more dispersed off the leeward coast and showed a continuous decline in numbers. It is highly recommended that management measures be implemented within Agoa Sanctuary considering these new findings to most effectively protect the species.

To protect mobile species whose habitats include the waters of several countries, international cooperation is essential, especially in the West Indies, where islands are frequently located less than a hundred kilometers from each other and with national jurisdictions of marine territories varying from one island to the next. This concern led to the creation of the Cartagena Convention Protocol Concerning the Protection of Areas and Wildlife (CAR-SPAW), which has been signed by various Caribbean countries with the aim of coordinating protection measures (Vanzella-Khouri, 1998) and would be an excellent support to carry out such projects. Coordinated cetacean monitoring, both visual and acoustics, as well as genetic studies with neighboring islands would permit the assessment of genetic connectivity between populations and allow a better understanding of the range and distribution of PSD in the West Indies.

Resident marine mammal populations are more sensitive to anthropogenic pressures because their site fidelity is high (e.g., Currey et al., 2009; Atkins et al., 2016; Barragán-Barrera et al., 2017), and fortunately, they are also the most responsive to targeted conservation actions (Gormley et al., 2012). Considering resident individuals in Martinique, a reduction or limitation in the anthropogenic pressures off the Carbet coast is essential as well as determining the reasons for PSD concentrations in this area in the first place. Regarding PSD in Guadeloupe, factors influencing their apparent population decline should be investigated so that they can be controlled by future action plans.

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 Office français de la biodiversité - Sanctuaire Agoa.

Author contributions

BC collected field data with CM,MS, AF and ND. BC made data analysis with JB-J, DB-B, LB and BM. LB and BM supervised this study. BC wrote the first draft of the manuscript and JB-J, DB-B and BM critically reviewed 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.

Publisher's note

References

Adams, J. D., Speakman, T., Zolman, E., and Schwacke, L. H. (2006). Automating image matching, cataloging, and analysis for photo-identification research. *Aquat. Mammals* 32, 374–384. doi: 10.1578/AM.32.3.2006.374

Atkins, S., Cantor, M., Pillay, N., Cliff, G., Keith, M., and Parra, G. J. (2016). Net loss of endangered humpback dolphins: integrating residency, site fidelity, and bycatch in shark nets. *Mar. Ecol. Prog. Ser.* 555, 249–260. doi: 10.3354/meps11835

Avila, I. C., Kaschner, K., and Dormann, C. F. (2018). Current global risks to marine mammals: Taking stock of the threats. *Biol. Conserv.* 221, 44–58. doi: 10.1016/j.biocon.2018.02.021

Baird, R. W., Ligon, A. D., Hooker, S. K., and Gorgone, A. M. (2001). Subsurface and nighttime behaviour of pantropical spotted dolphins in hawai'i. *Can. J. Zool.* 79, 9. doi: 10.1139/cjz-79-6-988

Balance, L. T. (1990). "Residence patterns, group organization, and surfacing associations of bottlenose dolphins in kino bay, gulf of California, Mexico," in *The bottlenose dolphin*. Eds. S. Leatherwood and R. R. Reeves (San Diego: Academic Press), 267–283.

Barragán-Barrera, D. C., May-Collado, L. J., Tezanos-Pinto, G., Islas-Villanueva, V., Correa-Cárdenas, C. A., Caballero, S., et al (2017). High genetic structure and low mitochondrial diversity in bottlenose dolphins of the Archipelago of Bocas del Toro, Panama: A population at risk? *PLoS One* 12, e0189370. doi: 10.1371/journal.pone.0189370

Barragán-Barrera, D. C., do Amaral, K. B., Chávez-Carreño, P. A., Farías-Curtidor, N., Lancheros-Neva, R., Botero-Acosta, N., et al. (2019). Ecological niche modelling of three species of stenella dolphins in the Caribbean basin, with application to the seaflower biosphere reserve. *Front. Mar. Sci.* 6. doi: 10.3389/fmars.2019.00010

Bolaños-Jiménez, J., Morteo, E., Delfín-Alfonso, C. A., Fruet, P. F., Secchi, E. R., and Bello-Pineda, J. (2021). Population dynamics reveal a core community of the common bottlenose dolphin (*Tursiops truncatus*) in open waters of the south-Western gulf of Mexico. *Front. Mar. Sci.* 8. doi: 10.3389/fmars.2021.753484

Burks, C., and Swartz, S. L. (2000). *Cruise results, windwards humpback (Megaptera novaeangliae) survey: NOAA ship Gordon Gunter cruise GU-00-01, 9 February to 3 April 2000*. 31. (Miami, FL USA: U.S. Department of Commerce, NOAA Technical Memorandum NMFS-SEFSC-438).

Burnham, K. P., and Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach. 2nd edn* (New York: Springer-Verlag).

Burnham, K. P., Anderson, D. R., White, G. C., Brownie, C., and Pollock, K. H. (1987). *Design and analysis methods for fish survival experiments based on release-recapture* (Bethesda, MD USA: American Fisheries Society Monographs) No 5, 414–420.

Caldwell, D. K., Caldwell, M. C., Rathjen, W. F., and Sullivan, J. R. (1971). Cetaceans from lesser antillean island of St-Vincent. *Fish. Bull. Natl. Oceanic Atmospheric Administration* 69, 303.

Cerema (2020) *Dynamiques et évolution du littoral fascicule 13 : Synthèse des connaissances de l'archipel de Guadeloupe*. Available at: https://www.cerema.fr/fr/centre-ressources/boutique/general/.

Chan, S. C. Y., and Karczmarski, L. (2017). Indo-pacific humpback dolphins (*Sousa chinensis*) in Hong Kong: Modelling demographic parameters with mark-recapture techniques. *PloS One* 12, e0174029. doi: 10.1371/journal.pone.0174029

Choquet, R., Lebreton, J.-D., Gimenez, O., Reboulet, A.-M., and Pradel, R. (2009). U-CARE: Utilities for performing goodness of fit tests and manipulating CApture–REcapture data. *Ecography* 32, 1071–1074. doi: 10.1111/j.1600-0587.2009.05968.x

Choquet, R., Reboulet, A.-M., Lebreton, J.-D., Gimenez, O., and Pradel, R. (2005). *U-CARE 2.2 (Utilities–CApture-REcapture) user's manual* (Montpellier, France: CEFE). Available at: https://www.cefe.cnrs.fr/fr/recherche/bc/bbp/264-logiciels.

Colwell, R. K., Mao, C. X., and Chang, J. (2004). Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology* 85, 2717–2727. doi: 10.1890/03-0557

Connor, R. C. (2000). "Group living in whales and dolphins," in *Cetacean societies: Field studies of dolphins and whales*. Eds. J. Mann, R. C. Connor, P. L. Tyack and H. Whitehead (Chicago, IL.: University of Chicago Press), 199–218.

Cooch, E. G., and White, G. C. (2019). *Program MARK - a gentle introduction. 19th edition* (Fort Collins: Colorado State University).

Cormack, R. M. (1964). Estimates of survival from the sighting of marked animals. *Biometrika* 51, 429–438. doi: 10.1093/biomet/51.3-4.429

Corredor, J. E. (1979). Phytoplankton response to low level nutrient enrichment through upwelling in the Columbian Caribbean basin. *Deep Sea Res. Part A Oceanogr. Res. Papers* 26, 731–741. doi: 10.1016/0198-0149(79)90010-4

Courtin, B., Millon, C., Feunteun, A., Safi, M., Duporge, N., Bolaños-Jiménez, J., et al. (2022). Insights on the residency status and inter-island movement patterns of pantropical spotted dolphins *Stenella attenuata* in the agoa sanctuary, Eastern Caribbean. *Latin Am. J. Aquat. Mammals* 17, 22–34. doi: 10.5597/lajam00277

Cubero-Pardo, P. (2007). Environmental factors governing the distribution of the bottlenose (*Tursiops truncatus*) and the spotted dolphin (*Stenella attenuata*) in golfo dulce, south pacific, off Costa Rica. *Investigaciones marinas* 35, 15–23. doi: 10.4067/S0717-71782007000200002

Currey, R. J., Dawson, S. M., Slooten, E., Schneider, K., Lusseau, D., Boisseau, O. J., et al. (2009). Survival rates for a declining population of bottlenose dolphins in doubtful sound, new Zealand: an information theoretic approach to assessing the role of human impacts. *Aquat. Conserv.: Mar. Freshw. Ecosyst.* 19, 658–670. doi: 10.1002/aqc.1015

Cuzange, P.-A. (2011). Les Pressions anthropiques s'exerçant dans le sanctuaire pour les mammifères marins aux antilles françaises (Agoa). 200. Office Français de la Biodiversité. Available at: http://oai.afbiodiversite.fr/cindocoai/download/AAMP/91/1/536AAMP_2011_Rapport_Agoa_CUZANG20011E.pdf/.

Davis, R. W., Ortega-Ortiz, J. G., Ribic, C. A., Evans, W. E., Biggs, D. C., Ressler, P. H., et al. (2002). Cetacean habitat in the northern oceanic gulf of Mexico. *Deep Sea Res. Part I: Oceanogr. Res. Papers* 49, 121–142. doi: 10.1016/S0967-0637(01)00035-8

DEAL Guadeloupe (2012). *Profil environnemental régional de la Guadeloupe* (France: Ministère de l'Écologie, du Développement durable et de l'Énergie). Available at: http://www.guadeloupe.developpement-durable.gouv.fr/IMG/pdf/.

De Vries, L. (2017). *First characterization of cetacean's movement in the eastern Caribbean: application to sperm whale, short-finned pilot whale and bottlenose dolphin* (France: Université Jean Monnet (Saint-Étienne).

do Amaral, K. B., Alvares, D. J., Heinzelmann, L., Borges-Martins, M., Siciliano, S., and Moreno, I. B. (2015). Ecological niche modeling of stenella dolphins (Cetartiodactyla: Delphinidae) in the southwestern Atlantic ocean. *J. Exp. Mar. Biol. Ecol.* 472, 166–179. doi: 10.1016/j.jembe.2015.07.013

Dufault, S., Whitehead, H., and Dillon, M. (1999). An examination of the current knowledge on the stock structure of sperm whales (*Physeter macrocephalus*) worldwide. *J. cetacean Res. Manage.* 1, 1–10. doi: 10.47536/jcrm.v1i1.447

Edwards, E. F., Kellar, N. M., and Perrin, W. F. (2013). *Form, function and pathology in the pantropical spotted dolphin (Stenella attenuata)*. 81. (La Jolla, USA: NOAA technical memorandum NMFS NOAA-TMNMFS-SWFSC-516).

Eguchi, T. (2014). Estimating the proportion of identifiable individuals and group sizes in photographic identification studies. *Mar. Mammal Sci.* 30, 1122–1139. doi: 10.1111/mms.12119

Feunteun, A., de Schrevel, C., Verhaegen, M., Chevallier, D., Duchemin, M., Ziani, N., et al. (2018). First evaluation of the cookie-cutter sharks (*Isistius* sp.) predation pattern on different cetacean species in Martinique. *Environ. Biol. Fish.* 101, 749–759. doi: 10.1007/s10641-018-0735-1

Feunteun, A., Safi, M., and de Mongolfier, B. (2019) *État des connaissances sur la fréquentation des cétacés en baie de fort-De-France et les risques de perturbations liés au trafic maritime*. Available at: https://www.grandebaiemartinique.com/document/etat-de-frequentation-baie-cetaces-feunteun-et-al-2019-gpmm-v1/.

Fisher, R. A., Corbet, A. S., and Williams, C. B. (1943). The relation between the number of species and the number of individuals in a random sample of an animal population. *J. Anim. Ecol.* 12, 42. doi: 10.2307/1411

Gandilhon, N. (2012). *Contribution au recensement des cétacés dans l'archipel de Guadeloupe* (Pointe-à-Pitre, France: Université des Antilles et de la Guyane, Campus Fouillole).

Garrison, L. (2020) *Abundance of marine mammals in waters of the U.S. southeastern Atlantic during summer 2016*. Available at: https://repository.library.noaa.gov/view/noaa/27294.

Gero, S., Gordon, J., Carlson, C., Evans, P., and Whitehead, H. (2007). Population estimate and inter-island movement of sperm whales, *Physeter macrocephalus*, in the Eastern Caribbean Sea. *J. Cetacean Res. Manage.* 9, 143–150.

Gerrodette, T., Waters, G., Perryman, W., and Balance, L. T. (2008). *Estimates of 2006 dolphin abundance in the eastern tropical pacific, with revised estimates from 1986-2003 43. NOAA technical memorandum NOAA-TM-NMFS-SWFSC-422* (La Jolla, CA: NOAA National Marine Fisheries Service.).

Gormley, A. M., Slooten, E., Dawson, S., Barker, R. J., Rayment, W., du Fresne, S., et al. (2012). First evidence that marine protected areas can work for marine mammals: Protected areas for marine mammals. *J. Appl. Ecol.* 49, 474–480. doi: 10.1111/j.1365-2664.2012.02121.x

Gowans, S., Würsig, B., and Karczmarski, L. (2007). The social structure and strategies of delphinids: predictions based on an ecological framework. *Adv. Mar. Biol.* 53, 195–294. doi: 10.1016/s0065-2881(07)53003-8

Hammond, P. S. (1990a). Capturing whales on film–estimating cetacean population parameters from individual recognition data. *Mammal Rev.* 20, 17–22. doi: 10.1111/j.1365-2907.1990.tb00099.x

Hammond, P. S. (1990b). Heterogeneity in the gulf of Maine? estimating humpback whale population size when capture probabilities are not equal. *Rep. Int. Whaling Commission Special Issue* 12, 135–139.

Haughey, R., Hunt, T., Hanf, D., Rankin, R. W., and Parra, G. J. (2020). Photographic capture-recapture analysis reveals a Large population of indo-pacific bottlenose dolphins (*Tursiops aduncus)* with low site fidelity off the north West cape, Western Australia. *Front. Mar. Sci.* 6. doi: 10.3389/fmars.2019.00781

Heithaus, M. R., and Dill, L. M. (2002). Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology* 83, 480–491. doi: 10.1890/0012-9658(2002)083[0480:FAATSP]2.0.CO;2

Holt, E. (2009). "Marine protected areas," in *Encyclopedia of marine mammals*. Eds. B. Würsig, W. F. Perrin and J. G. M."Hans" Thewissen (Amsterdam: Elsevier), 696–705.

Hunt, T., Bejder, L., Allen, S., Rankin, R., Hanf, D., and Parra, G. (2017). Demographic characteristics of Australian humpback dolphins reveal important habitat toward the southwestern limit of their range. *Endangered Species Res.* 32, 71–88. doi: 10.3354/esr00784

Jefferson, T. A. (1996). Estimates of abundance of cetaceans in offshore waters of the northwestern gulf of Mexico 1992-1993. *Southwestern Nat.* 41, 279–287.

Jefferson, T. A., Webber, M. A., Pitman, R. L., and Gorter, U. (2015). *Marine mammals of the world: a comprehensive guide to their identification. 2nd edn* (London, UK: Academic Press/Elsevier).

Jolly, G. M. (1965). Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* 52, 225. doi: 10.2307/2333826

Katona, S. K., and Beard, J. A. (1990). Population size, migrations and feeding aggregations of the humpback whale (*Megaptera novaeangliae*) in the western north Atlantic ocean. *Rep. Int. Whaling Commission Special Issue* 12, 295–306.

Luksenburg, J. A. (2014). Prevalence of external injuries in small cetaceans in aruban waters, southern Caribbean. *PloS One* 9, e88988. doi: 10.1371/journal.pone.0088988

Machernis, A. F., Stack, S. H., Olson, G. L., Sullivan, F. A., and Currie, J. J. (2021). External scarring as an indicator of fisheries interactions with bottlenose (*Tursiops truncatus*) and pantropical spotted (*Stenella attenuata*) dolphins in Maui nui, hawai'i. *Aquat. Mammals* 47, 482–498. doi: 10.1578/AM.47.5.2021.482

Mann, J. (1999). Behavioral sampling methods for cetaceans: A review and critique. *Mar. Mammal Sci.* 15, 102–122. doi: 10.1111/j.1748-7692.1999.tb00784.x

May-Collado, L. J., and Forcada, J. (2012). Small-scale estimation of relative abundance for the coastal spotted dolphins (*Stenella attenuata*) in Costa Rica: the effect of habitat and seasonality. *Rev. Biología Trop.* 60, 133. doi: 10.15517/rbt.v60i2.19997

Mayol, P., de Montgolfier, B., Ratel, M., Bordes, R., Costales, L., Iatropoulos, D., et al. (2016) *). caractérisation des activités d'observation commerciale des cétacés à l'échelle du sanctuaire agoa*. Available at: http://www.souffleursdecume.com/docs/.

Maze-Foley, K., and Mullin, K. (2007). Cetaceans of the oceanic northern gulf of Mexico: Distributions, group sizes and interspecific associations. *J. Cetacean Res. Manage.* 8, 203.

Météo France (2020) *Bulletin climatique annuel 2015 - 2020 - Martinique*. Available at: https://donneespubliques.meteofrance.fr/.

Mignucci-Giannoni, A. A., Schartz, S. L., Martinez, A., Burks, C. M., and Watkins, W. A. (2003). First records of the pantropical spotted dolphin (*Stenella attenuata*) for the Puerto Rican bank, with a review of the species in the Caribbean. *Caribbean J. Sci.* 39, 381–392.

Miller, E. J. (1990). Photo-identification techniques applied to dall's porpoise (*Phocoenoides dalli*) in puget sound, Washington. *Rep. Int. Whaling Commission Special Issue* 12, 429–437.

Ministère de l'Écologie, du Développement durable, des Transports et du Logement (2011). Arrêté du 1er juillet 2011 fixant la liste des mammifères marins protégés sur le territoire national et les modalités de leur protection. *J. Officiel de la République Française*. France.

Moreno, I., Zerbini, A., Danilewicz, D., de Oliveira Sa, S., Simões-Lopes, P., Lailson-Brito, J., et al. (2005). Distribution and habitat characteristics of dolphins of the genus stenella (Cetacea: Delphinidae) in the southwest Atlantic ocean. *Mar. Ecol. Prog. Ser.* 300, 229–240. doi: 10.3354/meps300229

Morteo, E., Rocha-Olivares, A., and Morteo, R. (2012). Sensitivity analysis of residency and site fidelity estimations to variations in sampling effort and individual catchability. *Rev. Mexicana Biodiversidad* 83, 487–495. doi: 10.22201/ib.20078706e.2012.2.972

Mullin, K. D., Hoggard, W., and Hansen, L. J. (2004). Abundance and seasonal occurrence of cetaceans in outer continental shelf and slope waters of the north-central and northwestern gulf of Mexico. *Gulf Mexico Sci.* 22, 62–73. doi: 10.18785/goms.2201.06

Nowacek, D. P., Christiansen, F., Bejder, L., Goldbogen, J. A., and Friedlaender, A. S. (2016). Studying cetacean behaviour: new technological approaches and conservation applications. *Anim. Behav.* 120, 235–244. doi: 10.1016/j.anbehav.2016.07.019

O'Brien, J. M., Berrow, S. D., Ryan, C., Mcgrath, D., O'Connor, I., Pesante, G., et al. (2009). A note on long-distance matches of bottlenose dolphins (*Tursiops truncatus*) around the Irish coast using photo-identification. *J. Cetacean Res. Manage.* 11, 71–76.

O'Brien, K., and Whitehead, H. (2013). Population analysis of endangered northern bottlenose whales on the scotian shelf seven years after the establishment of a marine protected area. *Endangered Species Res.* 21, 273–284. doi: 10.3354/esr00533

Office Français de la Biodiversité (2012) *Plan de gestion du sanctuaire AGOA*. Available at: http://www.aires-marines.fr/Documentation/.

Palacios, D. M., Herrera, J. C., Gerrodette, T., Garcia, C., Soler, G. A., Avila, I. C., et al. (2012). Cetacean distribution and relative abundance in colombia's pacific EEZ from survey cruises and platforms of opportunity. *J. Cetacean Res. Manage.* 12, 45–60.

Pandolfi, J. M., Bradbury, R. H., Sala, E., Hughes, T. P., Bjorndal, K. A., Cooke, R. G., et al. (2003). Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301, 955–958. doi: 10.1126/science.1085706

Parra, G. J., Corkeron, P. J., and Marsh, H. (2006). Population sizes, site fidelity and residence patterns of Australian snubfin and indo-pacific humpback dolphins: Implications for conservation. *Biol. Conserv.* 129, 167–180. doi: 10.1016/j.biocon.2005.10.031

Passadore, C., Möller, L., Diaz-Aguirre, F., and Parra, G. J. (2017). Demography of southern Australian bottlenose dolphins living in a protected inverse estuary. *Aquat. Conserv.: Mar. Freshw. Ecosyst.* 27, 1186–1197. doi: 10.1002/aqc.2772

Passadore, C., Möller, L., Diaz-Aguirre, F., and Parra, G. J. (2018). High site fidelity and restricted ranging patterns in southern Australian bottlenose dolphins. *Ecol. Evol.* 8, 242–256. doi: 10.1002/ece3.3674

Perrin, W. F. (2018). "Pantropical spotted dolphin," in *Encyclopedia of marine mammals*, *2nd edn*. Eds. B. Würsig, W. F. Perrin and J. G. M."Hans" Thewissen (London, UK.: Academic Press Inc.), 676–678.

Perrin, W. F. (2020) *World cetacea database*. Available at: http://www.marinespecies.org/cetacea/ (Accessed 16 Feb 2020).

Pino, O., and Laura, V. (2021). *Riesgo potencial de captura incidental del delfín manchado pantropical (Stenella attenuata) por pesquerías de atún en el Pacífico Oriental Tropical y el Gran Caribe*. (Santiago de Cali, Colombia: Universidad del Valle).

Pollock, K. H., Nichols, J. D., Brownie, C., and Hines, J. E. (1990). Statistical inference for capture-recapture experiments. *Wildlife Monographs*, 3–97.

Pradel, R. (1993). "Flexibility in survival analysis from recapture data: Handling Trap-Dependence," in *Marked individuals in the study of bird populations*. Eds. P. M. North and J.-D. Lebreton (Bale, Switzerland: Birkhäuser Verlag), 29–37.

Pradel, R., Hines, J. E., Lebreton, J.-D., and Nichols, J. D. (1997). Capture-recapture survival models taking account of transients. *Biometrics* 53, 60–72. doi: 10.2307/2533097

Pradel, R., and Sanz-Aguilar, A. (2012). Modeling trap-awareness and related phenomena in capture-recapture studies. *PloS One* 7, e32666. doi: 10.1371/journal.pone.0032666

Psarakos, S., Herzing, D. L., and Marten, K. (2003). Mixed-species associations between pantropical spotted dolphins (*Stenella attenuata*) and Hawaiian spinner dolphins (*Stenella longirostris*) off Oahu, Hawaii. *Aquat. Mammals* 29, 390–395. doi: 10.1578/01675420360736578

R Core Team (2023). *R: A language and environment for statistical computing*. (Vienna: R Foundation for Statistical Computing).

Read, A. J., and Murray, K. T. (2000). *Gross evidence of human-induced mortality in small cetaceans*. 21. (Silver Spring, MD USA: U. S. Department of Commerce, NOAA Technical Memorandum NMFS-OPR-15).

Réseau National Échouage (2021) *BDD ECHOUAGE : Histogrammes & cartes echouage*. Available at: http://pelagis.in2p3.fr/public/histo-carto/ (Accessed 4 Sep 2021).

Reynolds, J. E.III, Marsh, H., and Ragen, T. J. (2009). Marine mammal conservation. *Endangered Species Res.* 7, 23–28. doi: 10.3354/esr00179

Robbins, J., Allen, J. M., Clapham, P. J., and Mattila, D. K. (2006). Stock identity of a humpback whale taken in a southeastern Caribbean hunt. *J. Cetacean Res. Manage.* 8, 29–31.

Robbins, J. R., Babey, L., and Embling, C. B. (2020). Citizen science in the marine environment: estimating common dolphin densities in the north-east Atlantic. *PeerJ* 8, e8335. doi: 10.7717/peerj.8335

Rosel, P. E., Mullin, K. D., Garrison, L., Schwacke, L., Adams, J., Balmer, B., et al. (2011). *Photo-identification capture-mark-recapture techniques for estimating abundance of bay, sound and estuary populations of bottlenose dolphins along the U.S. East coast and gulf of Mexico: a workshop report*. 38. (Cajundome Boulevard Lafayette, LA, USA: U.S. Department of Commerce, NOAA Technical Memorandum NMFS-SEFSC-621).

Safi, M., Eymard, M., Janssen, A., Feunteun, A., and de Mongolfier, B. (2020) *Etat de santé des populations résidentes et semi-résidentes des cétacés présentes dans les eaux de la Martinique*. Available at: https://projets.beecee.fr/baie-fdf/document/.

Schwarz, C. J., and Arnason, A. N. (1996). A general methodology for the analysis of capture-recapture experiments in open populations. *Biometrics* 52, 860–873. doi: 10.2307/2533048

Seber, G. A. F. (1982). *The estimation of animal abundance and related parameters* (New York, NY: MacMillan).

Shane, S. H. (1990). "Behavior and ecology of the bottlenose dolphin at sanibel island, Florida," in *The Bottlenose Dolphin* eds. S. Leatherwood and R. R. Reeves (San Diego: The Bottlenose Dolphin, Academic Press), 245–265.

Shirihai, H., and Jarett, B. (2007). *Guide des mammifères marins du monde* (Paris: Delachaux et Niestlé).

Silva, M., Magalhães, S., Prieto, R., Santos, R., and Hammond, P. (2009). Estimating survival and abundance in a bottlenose dolphin population taking into account transience and temporary emigration. *Mar. Ecol. Prog. Ser.* 392, 263–276. doi: 10.3354/meps08233

Smith, T. D., Allen, J., Clapham, P. J., Hammond, P. S., Katona, S., Larsen, F., et al. (1999). An ocean-Basin-Wide mark-recapture study of the north Atlantic humpback whale (*Megaptera novaeangliae*). *Mar. Mammal Sci.* 15, 1–32. doi: 10.1111/j.1748-7692.1999.tb00779.x

Sprogis, K. R., Pollock, K. H., Raudino, H. C., Allen, S. J., Kopps, A. M., Manlik, O., et al. (2016). Sex-specific patterns in abundance, temporary emigration and survival of indo-pacific bottlenose dolphins (*Tursiops aduncus*) in coastal and estuarine waters. *Front. Mar. Sci.* 3. doi: 10.3389/fmars.2016.00012

Stanley, T. R., and Burnham, K. P. (1999). A closure test for time-specific capture-recapture data. *Environ. Ecol. Stat* 6, 197–209. doi: 10.1023/A:1009674322348

Suzuki, R., and Shimodaira, H. (2006). Pvclust: an r package for assessing the uncertainty in hierarchical clustering. *Bioinformatics* 22, 1540–1542. doi: 10.1093/bioinformatics/btl117

Tschopp, A., Ferrari, M. A., Crespo, E. A., and Coscarella, M. A. (2018). Development of a site fidelity index based on population capture-recapture data. *PeerJ* 6, e4782. doi: 10.7717/peerj.4782

Tyne, J. A., Pollock, K. H., Johnston, D. W., and Bejder, L. (2014). Abundance and survival rates of the hawai'i island associated spinner dolphin (*Stenella longirostris*) stock. *PloS One* 9, e86132. doi: 10.1371/journal.pone.0086132

Urian, K., Gorgone, A., Read, A., Balmer, B., Wells, R. S., Berggren, P., et al. (2015). Recommendations for photo-identification methods used in capture-recapture models with cetaceans. *Mar. Mammal Sci.* 31, 298–321. doi: 10.1111/mms.12141

Vanzella-Khouri, A. (1998). Implementation of the protocol concerning specially protected areas and wildlife (SPAW) in the wider Caribbean region. *Univ. Miami Inter-American Law Rev.* 30, 53–83.

Ward, J. J. H. (1963). Hierarchical grouping to optimize an objective function. *J. Am. Stat. Assoc.* 58, 236–244. doi: 10.1080/01621459.1963.10500845

Watkins, W. A. (1985). Investigations of sperm whale acoustic behaviors in the southeast Caribbean. *Cetology* 49, 1–15.

Wells, R., Boness, D., and Rathbun, G. (1999). "Behavior," in *Biology of Marine Mammals*, eds. J. E. Reynolds III and S. Rommell (Washington, DC: Biology of Marine Mammals. Smithsonian Institution Press), 324–422.

Wells, R. S., and Scott, M. D. (1990). Estimating bottlenose dolphin population parameters from individual identification and capture-release techniques. *Rep. Int. Whaling Commission Special Issue* 12, 407–415.

White, G. C., and Burnham, K. P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study* 46, S120–S139. doi: 10.1080/00063659909477239

Whitehead, H. (1990). Mark-recapture estimates with emigration and re-immigration. *Biometrics* 46, 473–479. doi: 10.2307/2531451

Whitehead, H., and Moore, M. J. (1982). Distribution and movements of West Indian humpback whales in winter. *Can. J. Zool.* 60, 2203–2211. doi: 10.1139/z82-282

Whitehead, H., and Wimmer, T. (2005). Heterogeneity and the mark–recapture assessment of the scotian shelf population of northern bottlenose whales (*Hyperoodon ampullatus*). *Can. J. Fish. Aquat. Sci.* 62, 2573–2585. doi: 10.1139/f05-178

Wickman, L., Rayment, W., Slooten, E., and Dawson, S. M. (2021). Recommendations for estimating mark rate of cetaceans in photo-ID research: A critique of field sampling protocols and variance estimation. *Mar. Mammal Sci.* 37, 328–343. doi: 10.1111/mms.12723

Williams, B. K., Nichols, J. D., and Conroy, M. J. (2002). *Analysis and management of animal populations*. (San Diego, CA, USA: Academic Press).

Würsig, B., and Jefferson, T. A. (1990). Methods of photo-identification for small cetaceans. *Rep. Int. Whaling Commission Special Issue* 12, 43–52.

Zanardo, N. J., Parra, G. M., and Möller, L. (2016). Site fidelity, residency, and abundance of bottlenose dolphins (*Tursiops* sp.) in adelaide's coastal waters, south Australia. *Mar. Mammal Sci.* 32, 1381–1401. doi: 10.1111/mms.12335

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EDITED BY
Nuno Queiroz,
Centro de Investigacao em Biodiversidade e Recursos Geneticos (CIBIO-InBIO), Portugal

REVIEWED BY
Matthieu Authier,
Université de la Rochelle, France
Lara Loureiro Sousa,
University of Oxford, United Kingdom
Lola Gilbert,
Université de la Rochelle, La Rochelle, France in collaboration with reviewer MA

*CORRESPONDENCE
Andrea Fariñas-Bermejo
afarinas@iim.csic.es

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Response of cetaceans to fluctuations of pelagic fish stocks and environmental conditions within the Celtic Sea ecosystem

Andrea Fariñas-Bermejo[1,2,3]*, Simon Berrow[3,4], Michaël Gras[5,6], Ciaran O'Donnell[5], Vasilis Valavanis[7], Dave Wall[4] and Graham J. Pierce[4]

[1]Instituto de Investigaciones Marinas (IIM), Consejo Superior de Investigaciones Científicas (CSIC), Vigo, Spain, [2]Faculty of Sciences, Ghent University, Ghent, Belgium, [3]Marine and Freshwater Research Centre, Atlantic Technological University, Galway, Ireland, [4]Irish Whale and Dolphin Group, Merchants Quay, Kilrush, County Clare, Ireland, [5]Marine Institute, Oranmore, County Galway, Ireland, [6]European Commission Joint Research Center, Ispra, Italy, [7]Institute of Marine Biological Resources and Inland Waters, Hellenic Centre for Marine Research, Athens, Greece

Inshore waters off the south coast of Ireland are an important foraging area for a range of cetacean species. Some of the main prey species of these cetaceans are herring and sprat, two economically valuable fish species in the region. The Celtic Sea herring stock suffered a marked decline in 2013. The present study aimed to investigate potential changes in the ecosystem associated to the herring decline and to determine the potential impacts on predators. Here we analyzed sightings information of common dolphins, fin, minke, humpback and unidentified whale species, acoustic data of herring and sprat, and a range of environmental variables mainly derived from satellites. Firstly, we characterized spatio-temporal patterns in the relative abundance of predator and prey species, and environmental variables, and compared periods before and since the herring decline. Since the 2013 herring decline, (i) the herring stock has mainly concentrated in south-eastern coastal waters and southern offshore Irish waters, (ii) sprat density has increased, (iii) chlorophyll concentration has decreased, (iv) sea surface temperature has risen, and (v) the euphotic layer has extended deeper. Secondly, we modelled the effects of prey density and environmental conditions on the relative abundance and distribution of cetaceans, as well as the effects of environmental conditions on prey density, between 2005-2018 by applying Hurdle Generalized Additive Models. The models for herring and sprat support the idea that these species have different environmental relationships, for example herring tended to be found in shallower waters than was the case for sprat. The presence and relative abundance of common dolphins were significantly affected by both environmental conditions and herring density, whereas whale species presence and relative abundance were found to be correlated with sea surface temperature and prey density. The model results suggest differences in prey choice among whale species. Understanding the dynamic relationships between predators, prey and the environment is important to inform an ecosystem-based approach to fisheries management.

KEYWORDS

cetaceans, ecosystem-based management (EBM), prey-predator relationships, environmental change, herring stock decline, Celtic Sea, hurdle generalized additive model

1 Introduction

The distribution and local abundance of cetaceans around the North Atlantic has been shown to be influenced by a range of environmental variables such as sea surface temperature, chlorophyll concentration, depth, wind components and large scale environmental indices such as the North Atlantic Oscillation index (e.g. Ramp et al., 2015; Tobeña et al., 2016; Prieto et al., 2017; Saavedra et al., 2017; Correia et al., 2019; Castro et al., 2020). Prey availability is also an important predictor (e.g. Pendleton et al., 2012; Zerbini et al., 2016). Cetaceans are often considered as opportunistic predators, modifying their diet in response to changes in prey availability (e.g. Piatt et al., 1989; Santos et al., 2013; Surma et al., 2018). To a large extent, the apparent influence of environmental predictors on cetacean distribution could be considered as a proxy for prey availability, although other factors such as thermal limits and diving capabilities are also relevant (e.g. Macleod et al., 2004; Lambert et al., 2014).

The Celtic Sea hosts a wide range and high abundance of cetacean species (O'Brien et al., 2009; Wall et al., 2013; Whooley and Berrow, 2019). Off the south and south-west coasts of Ireland, they are especially abundant during autumn and winter, when small pelagic fish concentrate in schools before migrating to spawning grounds (Molloy, 2006; Wall et al., 2013). Common dolphins (*Delphinus delphis*), fin (*Balaenoptera physalus*), minke (*Balaenoptera acutorostrata*) and humpback (*Megaptera novaeangliae*) whales are frequently recorded in this important foraging area (Whooley et al., 2011; Ryan et al., 2015; Volkenandt et al., 2015).

Common dolphins are piscivorous predators feeding mainly, on small pelagic shoaling fish, with preference for energy-rich species with high calorific content such as herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) (Pusineri et al., 2007; Meynier et al., 2008; Spitz et al., 2010; Santos et al., 2014). Meynier et al. (2008) observed seasonal variation in the diet of common dolphins (i.e. species composition and prey size) which appears to be related to the availability of the prey species (e.g. sprat almost absent in the diet during winter and autumn). Similarly, Santos et al. (2013) demostrated that the observed lack of evidence for selective predation of common dolphins on sardine (*Sardina pilchardus*) may be related to the low stock abundance in the area. Dietary differences between inshore and offshore common dolphins in the Celtic Sea have also been observed. Specifically, in inshore individuals, herring and sprat account for the 1.2% and 2.3% of the total number of prey items respectively, while they were no present in the analyzed offshore common dolphins (Brophy et al., 2009).

In the study area, fin and humpback whales have been seen in association with seasonal inshore presence of spawning herring and sprat (Whooley et al., 2011; Ryan et al., 2013a; Volkenandt et al., 2015). Individual fin and humpback whales have shown some fidelity to the area. Fin whales have been recorded in five out of seven years surveyed by Whooley et al., 2011, while fidelity of humpback whales has been hypothesized from the high recapture frequency observed from a photo-identification study of 15 years developed by Ryan et al., 2015. Herring and sprat, especially age 0 (young of the year) fish have been identified as the main prey for baleen whales in the Celtic sea, together with northern krill (*Meganyctiphanes norvegica*) (Trenkel et al., 2005; Ryan et al., 2013a; Volkenandt et al., 2015; Baines et al., 2017). The proportion of these pelagic fish species in the diet of baleen whales in this area is high in comparison to other sites in the Northeast Atlantic and in the Mediterranean, where krill (mainly *M. norvegica*) is the major component of their diet (Gannier, 2002; Pierce et al., 2004; Visser et al., 2011; Ryan et al., 2013b; Víkingsson et al., 2014; Spitz et al., 2018).

Herring and sprat are key components of the ecosystem, transferring high-calorific energy to higher trophic levels (Pikitch et al., 2004; Engelhard et al., 2014). They are also valuable species for European and, specifically, Irish pelagic fisheries (Gerritsen and Lordan, 2014). The Celtic Sea ecoregion is one of the most productive pelagic fishing grounds in European waters (CSHMAC, 2018; STECF, 2019). Atlantic herring and sprat are the most important species (by weight) landed in European Union (EU) Member States in the Northeast Atlantic, accounting for 21.3% and 14.8% of the total catch respectively (Eurostat, 2020). Herring is also one of the most economically valuable commercial fish species in Ireland (Molloy, 2006; Marine Institute, 2013; O'Donnell et al., 2018). Irish boats take the majority of allocated total allowable catch (TAC) for herring inside the Exclusive Economic Zone (87% in 2012; Gerritsen and Lordan, 2014). Catches of both herring and sprat are mainly concentrated in the southern Irish waters (Gerritsen and Lordan, 2014).

Currently the Celtic Seas sprat stock is in assessment category 5, i.e. the only reliable source of information available to be used in an assessment is the landing declarations (ICES, 2017). According to published information, no clear trend has been detected in the abundance of the sprat stock over the study period. The status of the Celtic Seas herring stock is clearer. The raw acoustic abundance index obtained during the annual Celtic Sea Herring Acoustic Surveys (CSHAS) suggested a sharp decline since 2013 (O'Donnell et al., 2020), which was later confirmed by the stock assessment modelling initiated in 2012 (ICES, 2021b). Recruitment fell from 2011 to 2018 and since 2013 it has been below the long-term average. Even though an increase in the abundance of immature fish was observed in 2019 (O'Donnell et al., al., 2020), the perception of the status of the stock did not improve and the spawning stock biomass (SSB) remained under the Maximum Sustainable Yield approach (MSY $B_{trigger}$) since 2015 (ICES, 2021b). Fishing mortality (F) has been above the F_{MSY} level since 2015, although below the F_{MSY} level in 2020 (ICES, 2021a). It was concluded that the stock was being harvested unsustainably as a result of continued poor recruitment within the stock and ICES advised zero catches in 2020 and 2021 (ICES, 2019; ICES, 2020a; ICES, 2021a). In 2018, the Celtic Sea Herring Fishery lost its Marine Stewardship Council (MSC) certification (CSHMAC, 2018). In 2019, the main fishery closed early in the of the majority of sampled herring were below the Minimum Conservation Reference Size (ICES, 2020b).

At a smaller scale, the proportion of spawning herring in the autumn-western spawning ground of the Celtic Seas herring stock has declined since the 1990s (Harma et al., 2012; Volkenandt et al., 2014), dropping sharply in 2013, when no spawning was detected but, it was recorded in the winter-eastern spawning ground off the southern Irish coast (ICES, 2018a). While high fishing mortality seems to have been part of the problem, the changes seen in herring stock status may also be, at least in part, environmentally driven. Environmental conditions affect all life-stages of pelagic fishes, including the spawning success (Winters and Wheeler, 1996; Rijnsdorp et al., 2009; Brunel and Dickey-collas, 2010). Winter spawning has been shown to be favored over autumn spawning in years with warmer sea surface temperatures (Haegele and Schweigert, 1985). In other clupeid species such as sardine, variation in recruitment success and in abundance has been linked to environmental variation (e.g. Santos et al., 2012).

The decline of the Celtic Sea herring stock has led to concern about possible effects on predators such as cetaceans. Whooley (2019) found an unexplained decline in fin whale sightings during 2008 to 2018 in Irish offshore waters which could be related to changes in prey abundance. All odontocete and mysticete species are protected under national (Wildlife Act (1976) and Amendments) and international (EU Habitats Directive; Council Directive 92/43/EEC, 1992) law and within the Marine Strategy Framework Directive (MSFD; Directive 2008/56/EC, 2008). Moreover, cetaceans are considered indicator species under Descriptor 1 of Biodiversity of the MSFD for the assessment of the ocean health, and their monitoring is required for every EU member state (Santos and Pierce, 2015; Palialexis et al., 2019).

Here we investigated how cetacean distribution and abundance has changed with changes in prey availability, specifically the decline in herring over the past decade, in particular to the apparent decline of the herring stock during the study period (2005-2018). Since changes in fish distribution and abundance maybe at least partially driven by environmental factors, and both environmental conditions and prey availability are expected to influence cetacean distribution and abundance, we also examine the relationships between environmental factors, prey availability and cetacean abundance in the Celtic Sea. To address this aim, we compared ecosystem characteristics before and since the apparent herring stock decline, and we modelled the effects of environmental characteristics on the fish and the cetaceans, as well as the effect of fish density on local abundance of cetaceans using Hurdle Generalized Additive Models.

2 Materials and methods

2.1 Study area

The study area, to the south of Ireland, falls within the Celtic Sea Ecoregion as defined by ICES and includes portions of ICES Divisions 7.a, 7.b, 7.f, 7.g and 7.j.2 covering 87.065 km^2 between 11°- 5.5°W and 50.25°- 52.8°N (Figure 1).

The Celtic Sea is a shelf sea area strongly influenced by the North Atlantic Current, as well as by the Shelf Edge Current, the

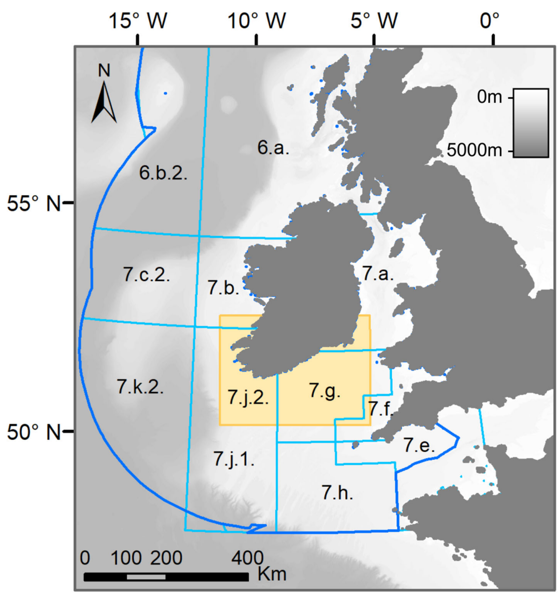

FIGURE 1
Map of the study area (yellow rectangle) and International Council for the Exploration of the Sea (ICES) Divisions (light blue lines) of the Celtic Sea ecoregion (darker blue line). The labels within the map indicate the names of the ICES Divisions, which shapefile was obtained from ICES website. The grey shading represents the bathymetry, which was obtained from General Bathymetric Chart of the Oceans (GEBCO) website.

Irish Coastal Current and the Irish Shelf Front (Pingree, 1980). The water column in the shallower areas remains mixed over the whole year due to the action of the tides, while in deeper zones stratification occurs in summer, leading to lower productivity, which is interrupted by pelagic mesoscale structures such as productivity fronts (Pingree et al., 1982). Consistent with global warming, an increase in the average sea surface temperature of 0.3° C has been observed in Irish waters between 1850 and 2008, with the strongest warming trend detected in south-western waters (Cannaby and Hüsrevolu, 2009).

2.2 Data collection

Since 2004, the Marine Institute in Ireland has conducted an annual acoustic survey (Celtic Sea Herring Acoustic Survey - CSHAS) to derive an index of abundance of the Celtic herring stock, which is later used in the assessment models. The present study analyzed data collected during the surveys from 2005 to 2018. All CSHAS were conducted on-board *RV Celtic Explorer* and lasted for three weeks, typically between 6 and 26 October. Acoustic data were collected continuously (i.e. over 24 hours per day). Echo-integration was carried out for herring over the 24-hour period based on its behavioral characteristics in this region (no night time dispersion to surface waters) whereas echo-integration for sprat uses only data collected during daylight hours due its diurnal behavior and the effects of day-night bias (Cardinale et al., 2003).

Marine mammal and seabird (relative) abundance and distribution were determined through sighting surveys carried out during daylight hours. Data collection was interrupted only during trawl sampling and CTD deployments, since the vessel reduced speed (to 4 knots) or stopped, respectively. The vessel followed systematic parallel line transects and additional survey legs were carried out in areas of high herring abundance within the core survey area. The survey design and effort has changed only slightly between years, although the precise area covered has shifted over time to match shifts in fish distribution (O'Donnell et al., 2018; Figure 2A). The present study analyzed acoustic data on herring and sprat abundance, plus cetacean sightings, from 2005 to 2018.

2.2.1 Environmental variables

We analyzed the relationships between the environmental conditions and the cetaceans response by using eight dynamic and two static environmental variables (Table 1), based on their known influence on cetacean distribution and abundance (Forney, 2000; Anderwald et al., 2012; Ramp et al., 2015; Tobeña et al., 2016), which is generally related to their expected influence on distribution of prey. The dynamic variables were the mean and standard deviation of: sea surface temperature (SST; °C), chlorophyll-a concentration (CHL; mg m^{-3}), photosynthetically available radiation (PAR; Einstein m^{-2} day^{-1}), euphotic depth (ZEU; m), which were obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS) on board the Aqua satellite (data available at the OceanColorWeb: https://oceancolor.gsfc.nasa.gov/l3/). Products of L3-SMI (Level 3 – Standard Mapped Images) with monthly and 4km resolution were downloaded and processed using Arc Macro Language in ArcGIS (ESRI, 2011) in order to transform distribution format to GIS-usable format. Data for the month when CSHASs are usually conducted and data from the previous and subsequent months (i.e. September, October, November) were used to calculate the average and standard deviation for each variable per grid cell per studied year (for further details about the number of records available for the analysis, see Table 1). Two static environmental variables, bathymetry and distance to coast, were also included. Bathymetry (with a 30-arc second resolution) was extracted from the General Bathymetric Chart of the Ocean (GEBCO: https://www.gebco.net/). Distances from the coast to the center of each grid cell were calculated in ArcGIS (ArcMap 10.4.1, ESRI, 2016) using the Near Table Proximity tool from the Analysis tool package (one value per grid cell).

2.2.2 Fisheries acoustic data

Acoustic information on the density of pelagic fish was collected using a Simrad EK60 scientific echosounder, operating with transducers at frequencies of 18, 38, 120 and 200 kHz. The nautical area scattering coefficient (NASC) was extracted and echo-integrated over the local sea depth for 1.85km horizontal segments into effort blocks known as elementary distance sampling units (EDSUs) (Simmonds and Maclennan, 2007). Echotraces were identified to species level and multi-species schools were catalogued as a mix of species, with the dominant species being specified when possible. Directed trawling was carried out to groundtruth the species composition of insonified echotraces. The process of when to trawl was largely subjective and carried out by a scientist with experience in school identification in this area.

Abundance and biomass estimates for the fish were available only at the scale of the whole study area, as annual snapshot estimates of abundance. Therefore, the raw acoustic (NASC) data were used for modelling the fine-scale prey-predator relationships. For a better understanding of the limitations of using NASC as a proxy of fish abundance, we explored the trends of the annual averages of (1) raw NASC values, (2) abundance and biomass estimated from the NASC (i.e. total stock abundance (TSN), spawning stock biomass (SSB; for herring) and total stock biomass (TSB; for sprat); O'Donnell et al. (2020)) and (3) recruitment calculated using the herring stock assessment models (ICES, 2021b). Following the Marine Institute's protocols for the estimation of the abundance and biomass (O'Donnell et al., 2018), this study used only those echotraces identified as "definitely" or "probably" herring, sprat or a mixture of both in which one of these species was dominant. Thus, echotraces classified as "possible" herring or "possible" sprat (less than 2% of the total) were not included in the analysis.

2.2.3 Marine mammal data

Marine mammal observers (MMO) collected data on marine mammal sightings during daylight hours. Observations on effort were conducted in favorable weather conditions (sea state<6 and visibility >1km). Trained and experienced MMOs were used during each survey and in some cases two marine mammal observers were onboard. In such instances, observers alternated with each other to maximize observer effort during daylight hours. Observers scanned the horizon by eye, focusing 90° either side of the survey track line,

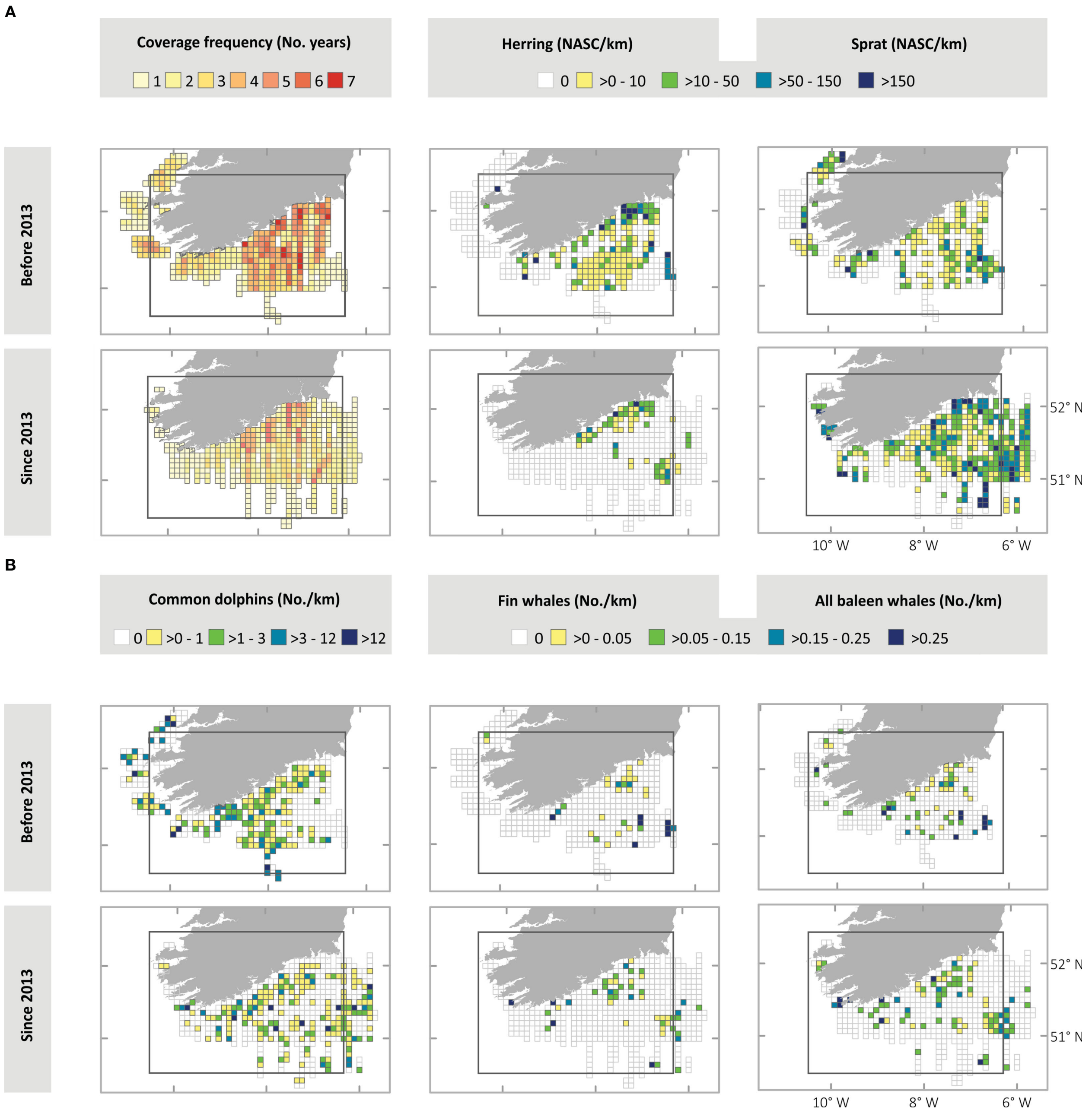

FIGURE 2
These maps represent spatialized data obtained from the annual Celtic Sea Herring Acoustic Surveys (CSHAS) in both study periods, i.e. before (from 2005 to 2012, 8 years) and since (from 2013 to 2018, 6 years) the herring decline. **(A)** First column of maps represents the area coverage by the surveys expressed as the number of years in which each cell grid was surveyed. Second and third columns of maps represent the relative abundance of the prey species before and since 2013. **(B)** Maps representing the relative abundance of the predator species before and since 2013. The grid cells (8 km x 8 km) represent the area sampled at least by one annual survey during each study period. The rectangle indicates the approximate area surveyed for all species and years of the study period, so apparent increases or decreases outside this area cannot be confirmed. NASC (Nautical Area Scattering Coefficient).

and using binoculars when required (e.g. to confirm species identification and group size). The main observation platform was the crow's nest, situated 18m above sea level, but if weather conditions were unsuitable, observations were conducted from the ships bridge, which was located at 11m above sea level. Logger 2000 software (IFAW, 2000) was used to store the sightings information and environmental conditions. The latter were recorded every 30 minutes or whenever conditions or the survey track line changed. Sightings data recorded included location, time, species, number of individuals, sea state (Beaufort scale) and visibility (on a six-point scale: 1 =< 1km, 2 = 1 – 5km, 3 = 6 – 10km, 4 = 11 – 15km, 5 = 16 – 20km, 6 =>20km). Whenever identification to species level was not possible, cetaceans were identified to the nearest possible taxonomic level (e.g. dolphin species or large whale species).

Data from three types of cetaceans were analyzed, including the two most frequently sighted species, namely common dolphins

TABLE 1 Response and explanatory variables included in the models, units, spatial and temporal resolution, data source and total number of records followed by their range of values per grid cell per year between brackets.

Variables	Units	Spatial resolution	Temporal resolution	Source	Number of records
Explanatory variables					
Presence and abundance of predators					
Common dolphins	*Presence and number of individuals*	-	-	*CSHAS*	*796 (0-10)*
Fin whales	*Presence and number of individuals*	-	-	*CSHAS*	*130 (0-7)*
All baleen whales	*Presence and number of individuals*	-	-	*CSHAS*	*291 (0-7)*
Explanatory variables					
Detection probability					
Effort applied	*m*	-	-	*CSHAS*	*2160 (1)*
Sea state	*Beaufort scale*	-	*30 min*	*CSHAS*	*2553 (0-52)*
Visibility	*6 ranges from<1km up to >20km**	-	*30 min*	*CSHAS*	*2553 (0-52)*
Spatio-temporal variability					
Year	*Year*	-	-	*CSHAS*	*2160 (1)*
Latitude and longitude	*Decimal degrees*	-	-	*CSHAS*	*2160 (1)*
Prey availability					
Herring density	*NASC*	*1 nautical mile*	*15 min*	*CSHAS*	*4025 (0-181)*
Sprat density	*NASC*	*1 nautical mile*	*15 min*	*CSHAS*	*6805 (0-218)*
Environmental variables					
Distance to the coast	*m*	-	-	*ArcMap*	*2160 (1)*
Bathymetry	*m*	*30-arc second*	-	*GEBCO*	*407070 (188-189)*
SST and SSTSTD	*°C*	*4km*	*monthly*	*MODIS*	*103680 (48)*
PAR and PARSTD	*Einstein m-2 day $^{-1}$*	*4km*	*monthly*	*MODIS*	*103680 (48)*
CHL and CHLSTD	*mg m-3*	*4km*	*monthly*	*MODIS*	*103680 (48)*
ZEU and ZEUSTD	*m*	*4km*	*monthly*	*MODIS*	*103680 (48)*

SST (Sea Surface Temperature), PAR (Photosynthetically Available Radiation), CHL (Chlorophyll-a Concentration), ZEU (Euphotic Depth); STD (standard deviation of the corresponding variable), NASC (Nautical Area Scattering Coefficient); CSHAS (Celtic Sea Herring Acoustic Survey); GEBCO (General Bathymetric Chart of the Ocean); MODIS (Moderate Resolution Imaging Spectroradiometer). * Visibility ranges: 1 (< 1 km), 2 (1 – 5 km), 3 (6 – 10 km), 4 (11 – 15 km), 5 (16 – 20 km), 6 (> 20 km).

(n=410) and fin whales (n=83). In order to account for the other baleen whale species (which had a low number of observations when considered separately), fin, minke, humpback whales together with unidentified baleen whales were treated as a third category, i.e. “all baleen whales” (n=160). All sightings recorded on-effort were included in the present analysis, whether or not conditions were suitable for detection of cetaceans (Barlow, 2015). To account for the lower probability of seeing animals in poorer conditions (i.e. extrinsic variability of the response variable), sea state and visibility were included in the models as explanatory variables.

2.3 Data processing

Data were imported and processed in ArcGIS using tools available in ArcToolbox (ArcMap 10.4.1, ESRI, 2016). In order to avoid possible distortion of some spatial features from differing data sources a customized Projected Coordinate System, centered on the study area (i.e.: central meridian = -8.5°; latitude of origin = 51.5°; scale factor = 1), was created for the project (MacLeod, 2013).

A fixed square grid was created using the “Fishnet” tool and used in order to extract the final data in a standardized format. The cell size was set at 8 x 8 km based on knowledge of the effective prey detection range for baleen whales in the Celtic Sea - estimated at 8km by Volkenandt et al. (2015), the association distance between common dolphins with their prey - estimated as between 0 and 14.82 km in the Bay of Biscay by Lambert et al. (2018), and considering the spatial resolution of the oceanographic variables (4km).

Only segments of the tracklines for which the echosounder and MMO were simultaneously on effort were included. Using a combination of Intersect and Spatial Join tools, the cetacean sightings (numbers of individuals of each species, and presence/absence), together with the prey detections (average NASC values, and presence/absence) and oceanographic data (dynamic and static variables) were extracted per cell grid for each year. For creating the relative abundance maps of the prey and cetacean species, cetacean sightings and prey NASC data were standardized by dividing the total number of detections by the total length (km) of the segments on common effort in each grid cell (i.e. total number of individuals or sum of NASC values per km on effort by species). For modelling the data were not standardized by effort because effort was included as an explanatory variable in the models.

2.4 Data analysis

A detailed data exploration was carried out in R statistical software (R Core Team, 2018) following recommendations by Zuur et al. (2010) to assess possible outliers, normality, distribution, collinearity and relationships among the variables. After examining the distributions of the sightings and acoustic data and fitting some preliminary models, several outliers were detected all associated with grid cells with low survey effort. In order to exclude these outliers we excluded all grid cells with less than 500m of effort. Fifteen cells out of 2176 were thus removed, 5 of which had cetacean sightings and 10 of which had detections of sprat. In addition, herring and sprat NASC variables were log-transformed due to having right-skewed distributions, i.e. the majority of values were concentrated at the lower end of the range with very few high values. Potential outliers were identified based on hat-values (a hat-value of 1 or over indicates a data point with unacceptably high influence on the model results; see Zuur et al., 2007). Three cetacean detections were excluded from the analysis because of the unusually high number of individuals recorded in the cell (even if genuine) could unduly influence the model output. Collinearity among explanatory variables was assessed by Pearson correlation matrices and visualization in pair plots. Mean CHL was excluded from subsequent analysis since it was highly correlated with the its standard deviation (CHLSTD) and several other explanatory variables (Supplementary Figure 1). Due to its right-skewed distribution, CHLSTD was log-transformed to reduce the influence of very high values.

2.4.1 Spatio-temporal characterization

In order to provide an overview of the changes which have occurred in the distributions of the predator and prey species studied and the ecosystem conditions, we examined the trends over time and compared spatial distributions from 2005-2012 and from 2013-2018, i.e. before and since the herring decline (accordingly with the NASC values used in this study).

Prior to comparing the abundance indices for prey and predators and the oceanographic conditions, between the two periods, it is necessary to consider the annual survey coverage. Consequently, we represented the distribution and frequency of the effort applied in graduated color maps. These maps show the variation on effort over the study timeframe, adapting to the changes in herring distribution. Temporal trends in predator and prey species were observed and compared by time series graphs of the annual averaged abundance index values. Additionally, as mentioned in previous section 2.2.2. for herring and sprat we compared the annual averages of (1) raw NASC values, (2) abundance and biomass estimated from the NASC (i.e. TSN, SSB and TSB; O'Donnell et al., 2020) and (3) recruitment calculated using the herring stock assessment models (ICES, 2021b), to provide a better understanding of the relationships among these stock parameters. For the dynamic oceanographic variables, the temporal trends of their values and the changes over the studied period, were visually compared using a heatmap, an Integrative Trend Analysis technique (ICES, 2018b) which represents the individual variation of different types of variables, all normalized to range between 0 and 1, by graduated colors.

We produced maps for both periods using ArcGIS (ArcMap 10.4.1, ESRI, 2016). The averaged density (NASC) for the pelagic fishes and the average number of individuals for cetacean species, both variables standardized per unit of effort for each of the grid cells, were calculated to represent the relative abundance of both prey and predator species by graduated colors. For a better understanding, we produced a map representing the distribution of prey and predator species including all grid cells surveyed at least once during each study period (i.e. before and since the herring decline; Figures 2A, B) and another map representing all the squares covered (at least once) in the whole study period (Supplementary Figure 2).

2.4.2 Modelling

Regarding the oceanographic conditions, in order to support their characterization using visual tools as described below, models were also applied. General Additive Models (GAMs) were fitted with a gamma distribution family and log link function, to the time series of annual average values for every oceanographic variable and we also compared values before and since 2013 (Equations 1 and 2, using the variable CHL as an example):

$$\text{gam}\,(CHL^{\sim}\ s(Year),\ \text{family} = \text{Gamma}\ (\text{link} = \text{“log”})) \qquad \text{(Equation 1)}$$

$$\text{gam}\,(CHL^{\sim}\ Periods,\ \text{family} = \text{Gamma}\ (\text{link} = \text{“log”})) \qquad \text{(Equation 2)}$$

where *Periods* is a Bernoulli variable in which the years 2005-2012 take the value 0, and for years 2013-2018 take the value 1.

Concerning predator and prey occurrence and distribution, models were used to explore the relationships among ecosystem components. Exploration of the data suggested the existence of non-linear relationships between predator and prey response and explanatory variables; therefore, Generalized Additive Models (GAMs) were used. These models are one of the recommended techniques for developing an integrative trend analysis to explore the relationships among ecosystem components including different trophic levels and environmental variables (ICES, 2018b). Moreover, they are extensively used for cetacean habitat modelling and prey-predator interactions studies (e.g. Nøttestad et al., 2015; Zerbini et al., 2016; Derville et al., 2018; González García et al., 2018; Virgili et al., 2019).

Specifically, Hurdle GAM models (models in two stages) (Cragg, 1971) were used to deal with the large number of zero values in our cetacean and prey count data. For the first stage, a binomial distribution and logit link function were used to fit a model to presence-absence data on the cetaceans and fish. For the second stage, the presence only data were modelled, using a negative binomial model with logit link function and the optimizer 'perf' was used (the data did not fit well to a Poisson distribution, e.g. Supplementary Figure 3) for cetacean models, and a gamma model with log link function for fish abundance models. The theta value showed little variation between different models for a given taxonomic group and the theta value was therefore not fixed. Models were fitted using the 'mgvc' library (Wood, 2013) in the R software (R Core Team, 2018).

The cetacean models included six response variables: annual presence/absence (i.e. sighted animals or not) and relative abundance (i.e. number) of common dolphins, fin whales and all baleen whales in each grid cell per year. The explanatory variables fall into several categories: variables affecting the detection probability of cetaceans (observation effort, sea state and visibility conditions), spatio-temporal variables (year, latitude and longitude), prey availability (densities of herring and sprat), static environmental variables (depth and distance from the coast), and oceanographic variables (SST, CHL, PAR, ZEU and their standard deviations) (Table 1). Firstly, we explored the extrinsic variability of cetacean presence and abundance due to their detection probability using this category of variables. Then, three different sets of models were run with the spatio-temporal, prey and environmental variables. Lastly, models were fitted using explanatory variables from all the above subsets.

The prey models included four response variables: the presence/absence and acoustic density (i.e. NASC values) of herring and sprat. The explanatory variables used were the recorded variables that could affect to the echosounder (time on effort and sea state), as well as the static environmental and dynamic oceanographic variables used in the cetacean models. A general model for each prey response variable was constructed using all the mentioned explanatory variables.

To avoid over-fitting and ensure that biologically realistic relationships were obtained, the degrees of freedom for the smoothers for the explanatory variables were limited to a maximum value of 3 by setting the number of knots (k) at 4, following recommendations by Wood (2006) and agreeing with other studies (e.g. González García et al., 2018; Virgili et al., 2019). The spatiotemporal variables are expected to have more complicated effects on the response variables so higher numbers of knots were permitted for the variables *Year* and *Latitude x Longitude* (latitude and longitude were included in the same smoother term thus accounting for their main effects and their interaction). The function 'gam.check' was used to verify that the number of knots used was adequate.

Optimal models for both predator and prey species, were determined following a forward stepwise selection process based on the Akaike information criterion (AIC; Anderson and Burnham, 2002) as well as considering the significance of the explanatory variables (p-values), deviance explained and R^2. In general, the most suitable models were selected based on the lowest AIC. Where two models had similar AIC values ($\delta AIC<2$) an ANOVA Chi-square test was used to verify their similarity, and where similar models differed in complexity applied the principle of parsimony (i.e. giving preference to the simpler model). The final models assumptions were validated by checking for outliers or influential values and the homogeneity of variance (by fitted values vs residuals plots). When a hat value higher than 1 was identified (indicating a data point with high influence), the corresponding model was compared with and without that value. The performance of the model was validated by testing the correlation between fitted values (after inverse transformation) and observed values (Spearman test) and checking these results visually by plotting fitted values vs observed values. The results from the Spearman test are included in the Supplementary Table 4.

For the interpretation of the effects of the significant continuous exploratory variables included in the models, we looked at the partial effects plots from the GAMs output. When a horizontal line (i.e. zero trend) could be fitted within the 95% confidence intervals illustrated in these plots, the trend (within the relevant range of values of the explanatory variable) could be considered non-significant. This was frequently relevant for the extreme values of the explanatory variables, where the wide 95% confident intervals reflect the lower number of observations.

3 Results

3.1 Exploratory analysis of the spatio-temporal variation

3.1.1 Survey effort

A total of 16,718.8 km (a daily average of 59.7 km) was covered (simultaneously) by both MMOs and echosounder on effort during 280 days from 14 surveys. The frequency of coverage per cell grid showed differences between periods before and since 2013 (Figure 2A). The south-western coast of Ireland was surveyed only during the first period, while more effort was applied in the south-eastern part of the study area since 2013, because of the survey adapting to evidence of changes in the distribution of herring and commercial fishing effort (Ciaran O'Donnell, Personal observation, 5th October 2021). The central zone accumulated most of the effort over the whole time series.

3.1.2 Oceanographic variables

Several trends in the oceanographic variables were observed from the models, maps and heatmap. CHL was lower since 2013 (Figure 3) decreasing significantly between 2009 and 2014 and increased in the last years ($p<0.0001$, Supplementary Figure 4; Supplementary Table 1), which is especially noticeable in coastal zones (Figure 4). CHLSTD has also decreased significantly in the latter period ($p=0.001$, Supplementary Figure 4, Supplementary Table 1 and Figure 3) showing a spatial pattern which reflects weaker variability in oceanic waters and stronger variability in coastal areas, although this trend was less clear since 2013 (Figure 3). In addition, euphotic depth (ZEU) has increased since the herring decline (Figures 3, 4) significantly from 2009 to 2014 (Supplementary Figure 4; Supplementary Table 1), specifically in central and southern areas, while its variability (ZEUSTD) was higher in coastal waters in both periods (Figure 4).

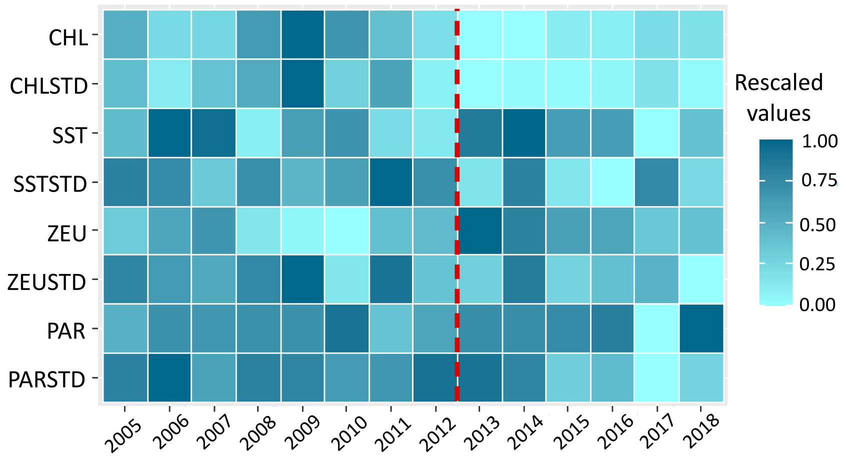

FIGURE 3
Heatmap representing the temporal trends of the oceanographic variables included in the study rescaled between the values 0 and 1. The lightest blue represents the minimum value of the annual average over the study area of each variable, while the darkest represents the maximum. The red dashed line highlights the year since the herring began to decline. Variables represented on Y-axis are: chlorophyll concentration (CHL); sea surface temperature (SST); Euphotic Depth (ZEU); Photosynthetically Available Radiation (PAR); and the standard deviation of the oceanographic variables (CHLSTD; SSTSTD; ZEUSTD; PARSTD). Data source: OceanColorWeb.

From the maps of another proxy of primary productivity (Photosynthetically Available Radiation, PAR) it appears to have increased considerably in recent years, more so in coastal and adjacent waters as well as in the strip between coordinates 10° W – 8° W (Figure 4). However, no significant trend was found from the GAMs results (Supplementary Table 1). From the heatmap, lower variability of PAR (i.e. lower PARSTD) in also apparent from the heatmap over the last few years of the study period (Figure 4)

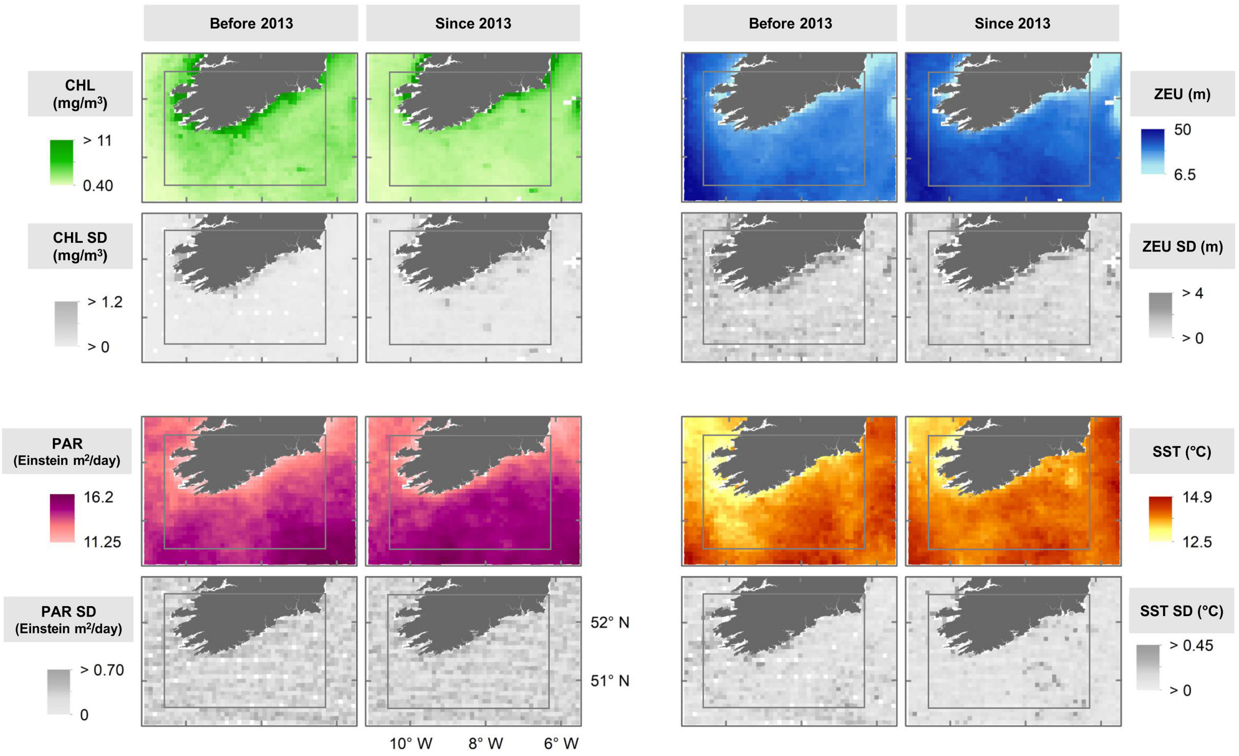

FIGURE 4
Maps showing the spatial patterns of the average annual mean and standard deviations (SD) between the periods 2005-2012 and 2013-2018 of the four oceanographic variables included in the study: Chlorophyll concentration (CHL), Euphotic Depth (ZEU), Photosynthetically Available Radiation (PAR) and Sea Surface Temperature (SST). The rectangle indicates the approximate area surveyed for all species and years of the study period. Data source: OceanColorWeb.

and from the significant results from the corresponding model (p=0.005, Supplementary Figure 4; Supplementary Table 1). The maps (Figure 4) show an increase of SST since the herring decline in both the south west and south east of the study area, although it is more noticeable in the former zone. In the same areas, the variability of sea surface temperature (SSTSTD) was stronger before 2013 and more evident in the south east since then. Despite some apparent contradictions in the signals, it appears that productivity was lower after the herring decline.

3.1.3 Prey and cetacean species occurrence and distribution

Over the study period, herring SSB and TSN followed very similar trends, differing from both NASC and recruitment. It appears that between 2008 and 2010, SSB and TSN increased while NASC remained stable near its lowest values. The average NASC showed three peaks, the largest occurring in 2012 and corresponding to peaks in SSB and TSN. Since then, these three parameters decreased sharply. Slightly earlier, the herring recruitment estimated by the stock assessment models, showed a peak in 2011 from which it decreased until the end of the study period (Figure 5).

The sprat stock indicators TSN and TSB showed similar trends, with an increase from 2007 to 2015 and a second peak in 2017 (higher than in 2015 for TSN but lower than 2015 in the case of TSB). The NASC trend was again different, reaching a maximum value in 2013 (Figure 6).

Common dolphins were the most abundant cetacean species recorded during the CSHASs, with an annual average of 911.6 ± 598.3 individuals recorded. Fin whales were the most frequently recorded baleen whale species, with an annual mean of 16 ± 13.5 individuals, which corresponds to approximately half of the average of all baleen whale species recorded, the latter group including fin, minke, humpback and unidentified baleen whales (30.6 ± 17.4 individuals).

The relative abundance of the three cetacean groups generally showed different year-to-year trends over the study period. The relative abundance in the area of common dolphins peaked in 2007 and 2016, while fin whales were most abundant in 2011 and the group of all baleen whales peaked in 2014 (Figure 7). However, all three groups showed similar trends during 2011-2015, with a low value in 2013 (the year in which herring abundance fell drastically).

The distribution of the species changed between the periods before and since the decrease in the herring stock (Figures 2A, B and Supplementary Figure 2). The maps suggest that both prey and predator species have been more concentrated towards the south-eastern part of the study area since the herring decline. As previously commented the surveyed area was adjusted over time to account for the observed shift in herring spawning area. Herring density, as observed from survey data, showed a consistent decline year-on-year beginning in 2013, especially off the south and southwest coasts. Conversely, the maps suggest an increase in sprat density post-2013 off the southeast coast (Figure 2A). Predator abundance and distribution followed a similar pattern with an increase in abundance in the southeast and a decrease off the west coast. Maximum numbers of common dolphins were recorded off the southeast coast post-2013. In contrast, the highest concentrations of fin whales occurred pre-2013.

3.2 Modelling the environmental influence on prey

The presence of herring increased when increasing effort was applied and sea state worsens. Herring presence increased towards shallower waters and from the coastline up to 60km offshore (the trend for the latter variable was significant only relatively close to the coast; in deeper waters confidence limits were too wide to see a clear trend). Three dynamic oceanographic variables had a significant effect on the presence of herring. The presence of herring increased from the lowest PAR values up to 14 and also increased from values of -4 to -2 of the log-transformed standard deviation of chlorophyll concentration (logCHLSTD). The herring occurrence was inversely related to SST at temperatures higher than 14°C (Supplementary Figure 5A; Table 2B).

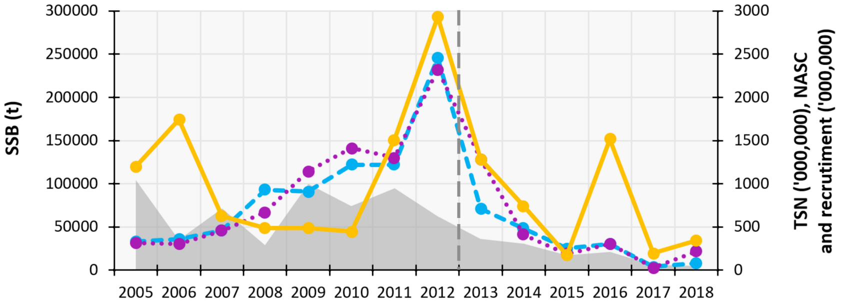

FIGURE 5
Time series graph representing the herring (*Clupea harengus*) annual average values of the Total Stock Abundance (TSN, millions of fish, right axis; purple dotted line), Spawning Stock Biomass (SSB, t, left axis; blue dashed line), Nautical Area Scattering Coefficient (NASC, unitless, right axis; orange solid line), recruitment (millions of fish, right axis; light grey shaded area) and year since the herring began to decline (dark grey dashed line). Data source: Annual Celtic Sea Herring Acoustic Surveys, except for the recruitment which was calculated from the herring stock assessment models by ICES (2021b).

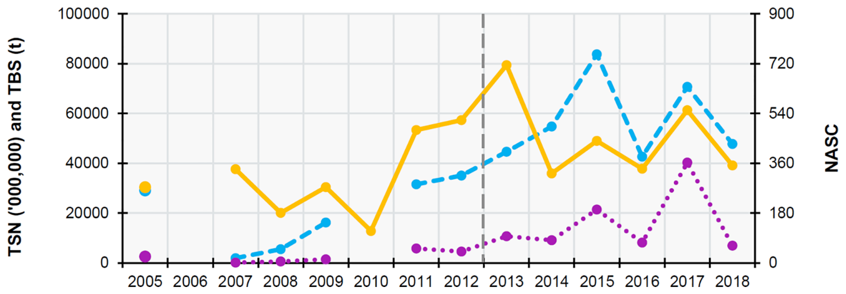

FIGURE 6
Time series graph representing the sprat (*Sprattus sprattus*) annual average values of the Total Stock Abundance (TSN, millions of fish, left axis; purple dotted line), Total Stock Biomass (TSB, t, left axis; blue dashed line),Nautical Area Scattering Coefficient (NASC, unitless, right axis; orange solid line) and year since the herring began to decline (dark grey dashed line). Data source: Annual Celtic Sea Herring Acoustic Surveys. Note the for 2006 there are no data and in 2010 TSN and TSB could not be calculated.

Where herring occurred, its acoustic density tended to be greater in shallower waters but also higher further from the shore. It should be borne in mind these are partial effects, i.e. at shorter distances from the shore density is higher if the water is shallower. The density also decreased from sea states 2 to 4 (Supplementary Figure 5B; Table 2B).

The presence of sprat increased when higher survey effort was applied and decreased from sea states 1 to 4. The presence of sprat was higher at medium distances from the shoreline and at medium depths. Sprat presence decreased as PAR increased up to a PAR value of 14 and increased for higher values of PAR. The presence of sprat increased significantly between 12.5°C and 14°C and decreased at higher temperatures. The effect of the log-transformed standard deviation of chlorophyll concentration was non-significant (p= 0.056) but including this variable improved the model (from an AIC value of 1947.41 to 1943.86). The presence of sprat showed a weak negative relationship with the variability of chlorophyll concentration (Supplementary Figure 6A; Table 2B).

The acoustic density of sprat (where present) was related to the same variables as in the presence model. Sprat density was negatively related to both SST (between 13°C and 15°C) and PAR (from PAR values of 13 to 16.5) (Supplementary Figure 6B; Table 2B). Validation tests for every prey model indicated no problems. For further details about the model selection process for herring and sprat, see Supplementary Tables 2, 3.

3.3 Modelling of cetacean distribution and abundance

3.3.1 Presence of common dolphins

The presence of common dolphins increased when higher survey effort occurred and sea state decreased. Based on visual examination of the smoother plots (Figure 8A), the effects of these variables became non-significant when survey effort was higher than 25km per cell and sea state was ≤1 or ≥4. From the contour plot, even though the probability of presence was quite high in southern waters, a coastal hot-spot occurred in the center of the study area. The presence of common dolphins fluctuated over the years, reaching a peak in 2016. Common dolphins were less likely to be present in the shallowest waters and occurrence increased towards deeper waters, up to approximately 80m. Over greater water depths, the trend became non-significant. The depth of the euphotic zone (ZEU) was the only dynamic oceanographic variable that showed a significant effect on common dolphin presence, with the highest probability of presence when ZEU was around 30m and decreasing as ZEU approached 40 m. Outside this range of ZEU values, the very wide confidence intervals mean that there was no clear significant trend. None of the prey species abundance indices showed a significant effect on the presence of this species (see Table 2A). For further details about the model selection process for the three groups of cetaceans species, see Supplementary Tables 4, 5.

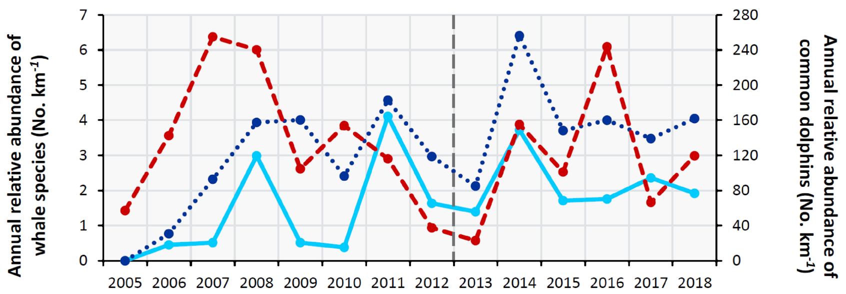

FIGURE 7
Time series graph of the annual number of individuals sighted standardized per km surveyed of each predator species. Common dolphin: red dashed line (right y-axis); sum of all baleen whale species: dark blue dotted line; fin whales: light blue solid line; year since the herring began to decline: dark grey dashed line. Data source: Annual Celtic Sea Herring Acoustic Surveys.

TABLE 2 Summary of the final binomial (presence) and negative binomial (abundance or acoustic density, where the species is present) models for (a) common dolphins, fin whales, all baleen whale species, (b) herring and sprat.

(a) Group of models	Explanatory variables											Estimated parameters		
	Sea state	Visibility	Effort	Depth	SST	PAR	ZEU	Lat,Lon	Year	Herring	Sprat	DE	R-sq	AIC
Common dolphins														
Presence/Absence	***		***	***			*	***	**			18.20	0.163	1655.32
Abundance	**	**			***	*				***		19.60	0.107	3395.96
Fin whales														
Presence/Absence	***		***					*			***	31.70	0.176	534.73
Abundance									**			18.90	0.083	329.09
All baleen whales														
Presence/Absence	***		***					*	*	*	***	26.60	0.201	865.99
Abundance (A)	.	*	**		*							29.20	0.171	612.37
Abundance (B)	*	**	*							·		29.30	0.139	613.41

(b) Group of models	Exploratory variables							Estimated parameters		
	Sea state	Effort	Depth	Distance	SST	PAR	logCHLS-TD	DE	R-sq	AIC
Herring										
Presence/Absence	***	***	***	***	***	***	**	0.18	0.157	1274.69
Abundance	*	***		***				0.25	0.079	3928.99
Sprat										
Presence/Absence	**	***	***	***	**	***	·	0.12	0.136	1943.86
Abundance					***	**		0.11	0.063	7503.76

Significance levels: · 0.1 > p > 0.05; * p< 0.05; ** p< 0.01; *** p< 0.001. SST (Sea Surface Temperature), PAR (Photosynthetically Available Radiation), ZEU (Euphotic Depth), Lat,Lon (Latitude, Longitude), logCHLSTD (log-transformed standard deviation of the chlorophyll concentration). See methods section for a full list of the explanatory variables considered.

For each final model, the table shows the p-value associated with each explanatory variable included, and the values obtained for percentage of deviance explained (DE), R-squared (R-sq) and AIC. When a variable was not included in the model, the corresponding cell was center blank. Explanatory variables that were not significant in any of the models were excluded from the table.

3.3.2 Abundance-given-presence of common dolphins

Where common dolphins were present, their abundance decreased when sea state increased and was lowest when visibility was highest. The abundance of this species (given presence) did not vary significantly over space and time once effects of other explanatory variables were considered. Abundance was lowest at around 13-14°C but increased in both colder and warmer waters. PAR had a weakly positive effect on common dolphin abundance. The trends associated with both oceanographic variables became non-significant towards the highest values. While there was significant spatio-temporal variation in the presence of this species, this was not the case for abundance-given-presence. Again, differing from the presence models, herring density showed a significant (but weak) effect on the number of common dolphins detected: dolphin abundance reached a peak at NASC values between 65-70 (i.e. log-transformed value of approximately 4.2) (Figure 8B; Table 2B).

3.3.3 Presence of fin whales

The presence of fin whales increased linearly with increasing survey effort and decreased linearly with increasing sea state. The occurrence of this species showed significant spatial variation, with a higher probability of presence close to the southwestern coast and in the center and south of the eastern part of the study area. Environmental conditions did not show any significant effects, but the presence of fin whales was positively related to sprat density (Figure 9A; Table 2A).

3.3.4 Abundance-given-presence for fin whales

In the negative binomial models of the abundance of fin whales, only the effect of year was significant, with a decline in numbers over the last eight years of the study (Figure 9B; Table 2B).

3.3.5 Presence of all baleen whales

Similar to common dolphins, the occurrence of the "all baleen whales" category increased when more effort was applied and decreased as sea state increased. Mysticete species occurrence was highest in southwestern coastal areas and in the southeastern part of the study area. Their presence reached a maximum in 2015, although due to wide confidence intervals no significant trend is evident before 2014. Since 2015, the presence of baleen whales tended to decrease. Environmental conditions did not show any significant effect on the presence of baleen whales. Abundance of both prey species showed a positive linear effect on the presence of baleen whales, the effect being stronger in the case of sprat (deviance explained = 2.1% for sprat and 0.20% for herring) (Figure 10A; Table 2A).

3.3.6 Abundance-given-presence for all baleen whales

Based on the criteria described, two final models were selected to explain the abundance of baleen whales, due to their similar performance (Model A: 29.2% DE, 612.37 AIC; Model B: 29.3% DE, 613.41 AIC). Both models included the three detectability variables (sea state, visibility and effort). Although the statistical significance of their effects differed between the two models, visually their partial effects were similar: the number of whales tended to fall from sea state 1 to 4, and increased with both increasing visibility (in the range 3 (6-10km) to 4.7 (13-14km)) and increasing survey effort. While model A also included SST, indicating that the most favorable SST for the abundance of whales was the coldest (11.5°C), model B included herring density and suggested a weak influence of herring density (p= 0.053), with peak whale abundance at intermediate densities and a marked decline in whale abundance at the highest NASC values. There was no significant spatiotemporal variation (Figures 10B, C; Table 2B). Validation tests for every cetacean model indicated no problems. For further details about the model selection process for common dolphins, fin whales and all whales, see Supplementary Tables 4, 5.

4 Discussion

The starting point for this study was the expectation that the changing status of the Celtic herring stock as revealed by annual acoustic surveys, has consequences for predators (including cetaceans) feeding on herring. By using a combination of fisheries acoustic and cetacean visual data from scientific surveys, we were able to investigate this potential shift. Changes in the environmental conditions associated with the herring stock decline were observed and the drivers of the presence and abundance of common cetaceans in the area were investigated, considering the roles of both environmental conditions and fish density. This study highlights the importance of prey availability in the distribution of cetaceans, which may be especially important in areas with high fishing pressure.

4.1 Herring decline and associated changes in ecosystem components

The Celtic Sea herring stock has collapsed three times during the last six decades (Clarke and Egan, 2017), most recently since 2013 accordingly to NASC data and derivate indicators (TSN and SSB) (O'Donnell et al., 2020) or since 2012 as suggested by the most recent stock assessment results (ICES, 2021b). Since then, the stock has also concentrated towards the south-eastern coastal and offshore waters of the study area where the last of the large aggregations are present. Herring has not been detected along the south-western coast in recent years. Consequently, fishing effort has also shifted to this area, followed by the CSHAS surveys (O'Donnell et al., 2020).

The lack of herring off the west coast suggests that the already declining autumn-western spawning ground (Harma et al., 2012: Volkenandt et al., 2014) has all but disappeared. Negative effects of increasing SST have been observed on the Celtic herring autumn-spawning grounds, favoring winter spawning (Haegele and Schweigert, 1985; Harma et al., 2012), reducing size-at-age in the Celtic Sea herring (Lyashevska et al., 2020) and decreasing productivity in Baltic herring (Moyano et al., 2020). Irish waters have had a warming trend between 1850 and 2007 (Cannaby and Hüsrevolu, 2009), leading to concern about the future of this stock (e.g. Harma et al., 2012), given the upper limit of the optimal temperature range of the species around 14°C (Volkenandt et al.,

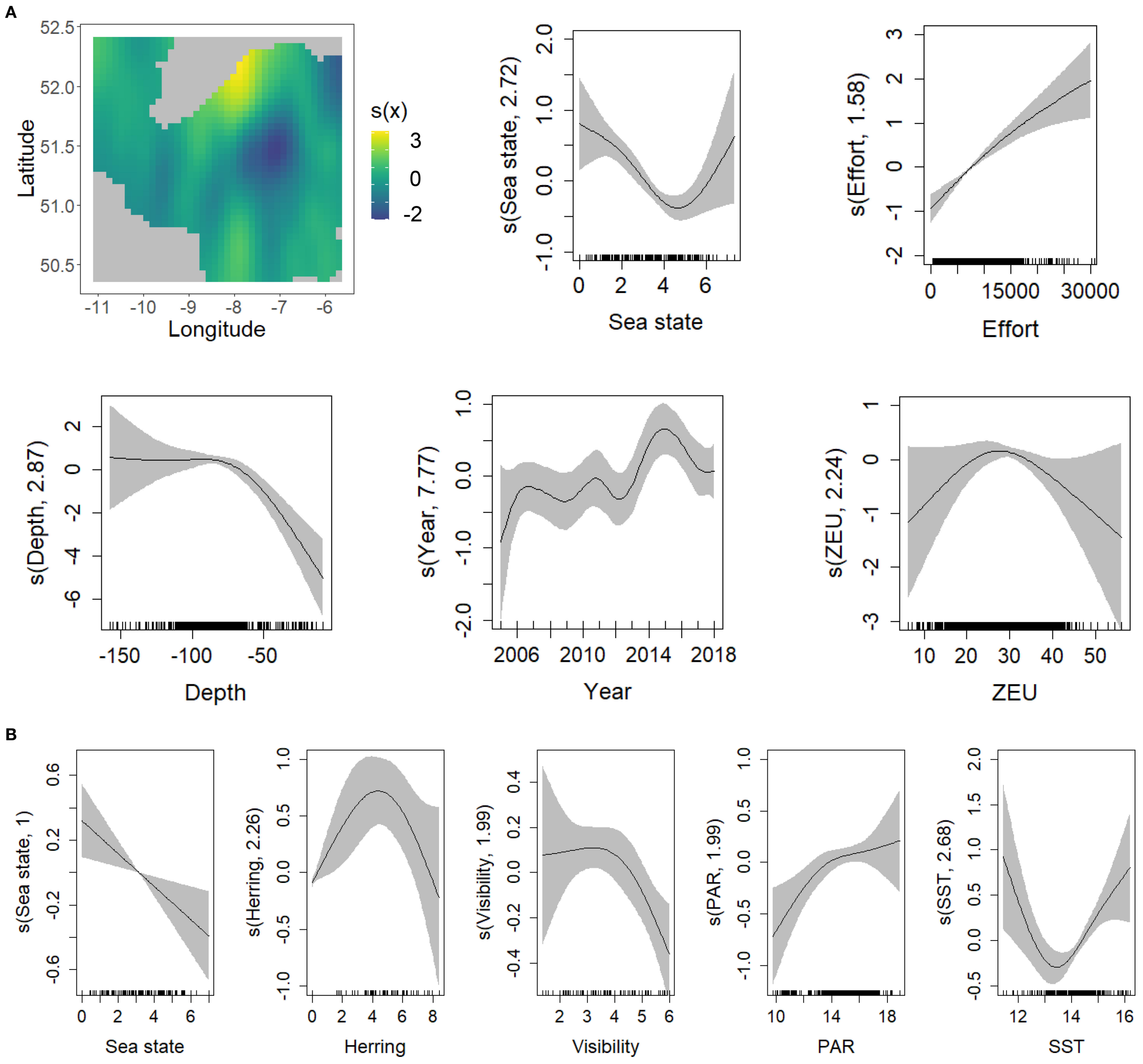

FIGURE 8
GAM smoothing curves for partial effects of the explanatory variables included in the final model of common dolphin presence **(A)** and abundance **(B)**. The grey shaded area of the smoother plots corresponds to the 95% confidence intervals around the effect. In the top left corner **(A)**, spatial variation in probability of presence of common dolphins is represented on a contour plot versus longitude (x axis) and latitude (y axis). (Note that the units on the Y axis of the smoother plots, and for colours on the contour plot, have not been transformed back to the original scale). ZEU (Euphotic Depth), PAR (Photosynthetically Available Radiation), SST (Sea Surface Temperature).

2014; Lyashevska et al., 2020). Although averaged SST in the study area did not increase significantly, it is clear from the oceanographic maps (Figure 4) that SST in the autumn spawning area did increase, which may support the hypothesis that the disappearance of the autumn-western spawning ground was also influenced by environmental change. However, other factors, such as the high fishing mortality, could have played a role as well.

Some fish stock collapses have been related to changes in environmental conditions which affect population parameters such as recruitment (e.g. Ottersen et al., 2010; Santos et al., 2012; Britten et al., 2016). In the Celtic Sea, no influence of changes in oceanographic conditions on herring distribution was found previous to the decline (Volkenandt et al., 2014). In contrast, our results from the data characterization suggested that some environmental changes could be associated with this herring decline, with SST increasing, CHL decreasing, and the ZEU extending deeper since 2013. These environmental changes were concentrated mainly in south-east and south-west coastal waters, the latter area coinciding with herring concentrations after the decline and the autumn spawning grounds (O'Sullivan et al., 2013). The prey models indicated that the probability of herring presence decreased for SSTs higher than 14°C. These models also showed an increasing trend of herring occurrence associated with increasing PAR (a primary productivity proxy), up to medium values of PAR

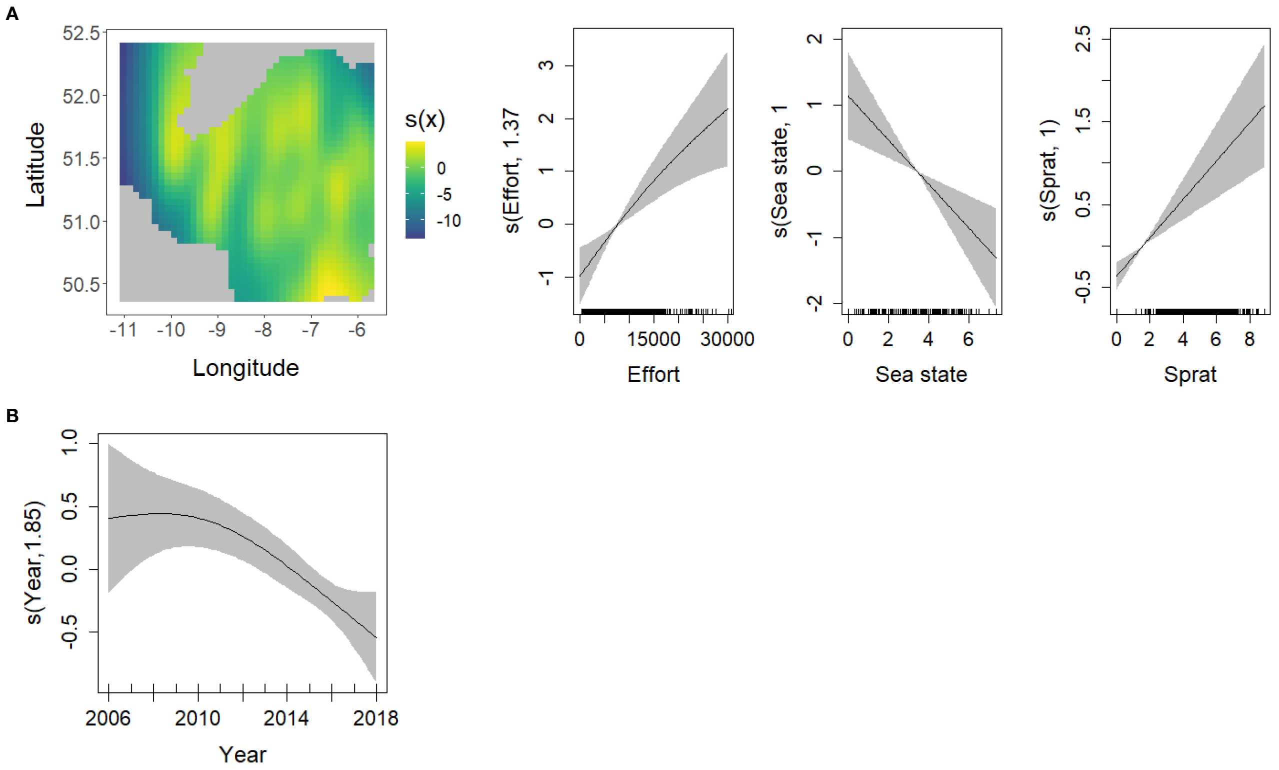

FIGURE 9
GAM smoothing curves fitted to partial effects of the explanatory variables included in the final model of fin whale presence **(A)** and abundance **(B)**. Grey shaded areas of the smoother plots correspond to the 95% confidence intervals around the main effect. On the left, the spatial variation in probability of presence of fin whale is represented on a contour plot of the longitude (x axis) and latitude (y axis). (Note that the units on the Y axis of the smoother plots and for colours on the contour plot, have not been transformed back to the original scale).

of 14. Herring presence also increased with higher values of logCHLSTD (at least within the mid-range of logCHLSTD values).

In contrast to herring, sprat biomass increased over the study period. Other studies have shown that herring and sprat respond differently to changes in environmental conditions (e.g. Hunter et al., 2019). The prey models revealed that the same variables that affected herring presence, also affect sprat but in different ways. Their acoustic density where they were present was driven by the static environmental variables (depth and distance to the coast) in the case of herring, and by the dynamic variables (PAR and SST) for sprat.

It might be expected that these changes in the Celtic Sea ecosystem would also affect predators of herring (Surma et al., 2018). No clear temporal association was evident between the time series of the relative abundance of cetaceans and prey density. First of all, absolute abundance of cetacean populations is unlikely to show an immediate response to changing prey abundance, even for preferred prey (any such changes would be slow due to the long generation times of cetaceans). It is more plausible that local abundance of cetaceans would track local abundance of important prey, but whether this could be detected depends on the extent of the change and on the scale at which it occurs, relative to the scale of the analysis. It should also be highlighted that the number of cetacean sightings was at the minimum values of the time series for all species, especially common dolphins, for which the number of sightings reached its lowest value in 2013, when the herring began to decline. Over the area, the distribution of the study species has showed similarities since 2013 when the highest relative abundances of cetaceans and herring were seen in the same two hot-spots. When humpback, minke and unidentified whales are considered together with fin whales, even though these rorqual species occurred at the herring hot-spots, their occurrence was also more widespread, consistent with differences in prey-predator associations among the rorqual species, as suggested by Volkenandt et al. (2015).

4.2 Drivers of the relative abundance and distribution of common dolphins in the study area

Brophy et al. (2009) found that herring and sprat were minor components of the diet of common dolphins (stranded and bycaught individuals) in the Celtic Sea. Despite this, our results indicated that where these dolphins were present, their local relative abundance increased as herring densities increased from low to medium values. In addition, the minimum number of common dolphins occurred in 2013, prior to the most recent herring decline. The positive effect of increasing herring density is however consistent with the previously reported preference of common

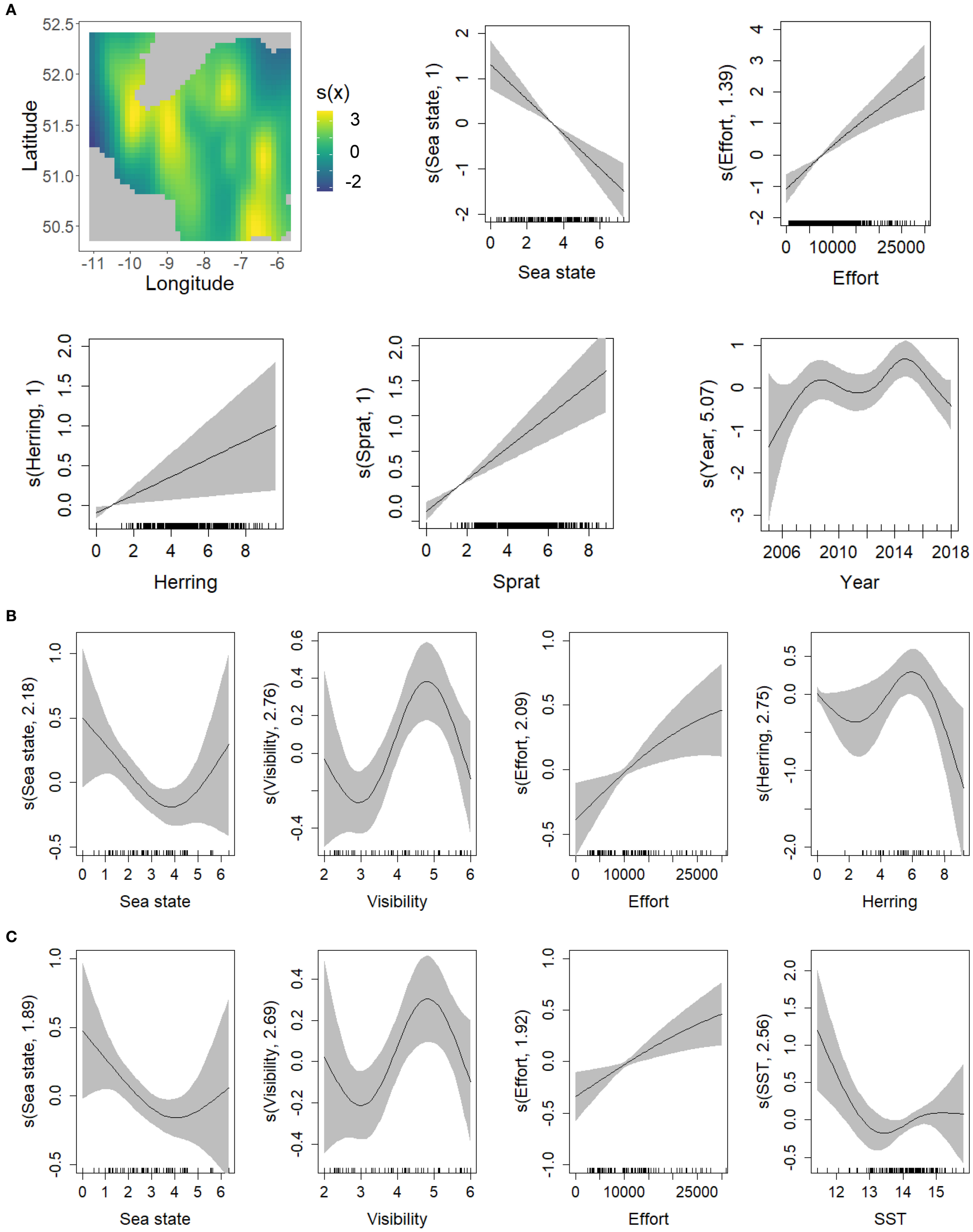

FIGURE 10
GAM smoothing curves for partial effects of the explanatory variables included in the final model of all baleen whale species presence **(A)** and abundance **(B, C)**. The grey shaded area corresponds to the 95% confidence intervals around the main effect. In the top left corner **(A)**, the spatial variation in probability of presence of whale species is represented on a contour plot of the longitude (x axis) and latitude (y axis). (Note that the units on the Y axis of the smoother plots and for colors on the contour plot, have not been transformed back to the original scale). SST (Sea Surface Temperature).

dolphins for energy-rich small pelagic species such as sardines, anchovies (*Engraulis encrasicolus*), mackerel (*Scomber scombrus*), sprat and herring, observed in several different regions and populations (e.g. Silva, 1999; Meynier et al., 2008; Pierce et al., 2008; Spitz et al., 2010; Santos et al., 2013). The apparent differences between our model results and what might have been expected from common dolphin diet, as described in the area by Brophy et al. (2009), could be due to high herring densities being associated with high prey availability generally - with the dolphins feeding on other prey species - or may indicate that the local importance of herring in common dolphin diet in recent years has been higher than was generally the case in the Celtic Sea.

Habitat use by common dolphins in the study area appears to be characterized by certain environmental conditions (bearing in mind that this possible preference may be secondary, related to the habitat preferences of their prey). Our results suggest that common dolphins were most likely to be present in coastal areas, in intermediate water depths (approximately 80 m) where the euphotic layer extends to around 30m. A preference for shallower or intermediate depths and coastal waters elsewhere has been related to prey distribution (Cañadas and Hammond, 2008; Silva et al., 2014; Tobeña et al., 2016; Milani and Vella, 2019).

Where common dolphins were present in the study area, they were more abundant in the coldest and the warmest waters registered during the study period, with lowest abundance in the range 12.5-14°C. Different theories about the relationships of this species with SST have been described elsewhere. For example, associations of common dolphins with warm waters have been observed in Irish and British waters (MacLeod et al., 2008: Robinson et al., 2010), while a thermal niche model suggested sea temperatures below 14°C were less suitable for common dolphins in the northeast Atlantic (Lambert et al., 2011). However, common dolphins may occur in colder waters due to high local productivity resulting from upwelling (Cañadas and Hammond, 2008; Correia et al., 2019). Local and seasonal upwelling events, highly variable in periodicity and magnitude, take place in Irish waters which affect the phytoplankton community and may have an effect on the food web, up to top predators (Raine et al., 1993; Edwards et al., 1996; O'Boyle et al., 2009).

In the present study, local abundance of common dolphins in the region increased towards areas with higher values of the primary production proxy PAR but the other primary production proxies used in the analysis (CHL and ZEU) did not have a significant effect. This apparent discrepancy could be explained by the time-lags associated with the effects of both proxies. The use of electromagnetic radiation as a source of energy for photosynthesis (PAR) needs time (Mõttus et al., 2012), and it also takes time for the effects to work their way through the food chain to top predators. Time-lags between CHL peaks and peaks of abundance of common dolphins have been already described, e.g. in the Azores (Tobeña et al., 2016). Evidently, caution is needed when interpreting effects inferred from statistical modelling of habitat preferences since the models are a fairly simplistic representation of what can be very complex processes.

4.3 Drivers of the relative abundance and distribution of whales in the study area

Baleen whales (rorquals) feed primarily on krill and small schooling fish such as herring and sprat, and occasionally on squids (Kawamura, 1980; Barros and Clarke, 2009). The diet composition varies among rorqual species as well as by area and season. The three rorqual species analyzed in this study have been shown to change their diet according to the season and location, related to prey availability (e.g. Witteveen et al., 2012; Víkingsson et al., 2014; Nøttestad et al., 2015; Aguilar and García-Vernet, 2018).

The results of the models showed a positive effect of sprat density on the presence of both rorqual species groups analyzed (i.e. fin whales and all baleen whales). Sprat density was one of the two factors that affected the local abundance of these whale species where they were present (although the nature of the relationship was not as expected: baleen whales were more abundant at intermediate herring densities). Herring density had a weak (compared to the effect of sprat density) but significantly positive effect on the presence of the all baleen whales group. Fin whale presence was not affected by herring density.

The differences found between the two groups (i.e. fin whales and all baleen whales) suggest that minke, humpback and/or other unidentified whale species may have relied more on herring than was the case for fin whales. Previous research using stable isotope composition of skin samples suggested differences in the diet of fin and humpback whales in the study area, with krill being more important in the diet of fin whales, while small herring and large sprat were more important for humpback whales (Ryan et al., 2013a). Evidence of fin whales feeding on krill in offshore waters off the west of our study area (i.e. Porcupine Seabight) was also found by Baines et al. (2017). Fin whales were the most frequently sighted and abundant baleen whale species in the study area and, based on this information the least likely to be affected by changes in herring abundance; the effect of herring abundance on the presence of the all baleen whales group is thus most likely due to effects on the other rorqual species present. Evidently, it would be useful to have information on krill density in the study area.

Results from the models showed a significant decrease in the abundance of fin whales where they were present since 2013 (although there was no significant change in the proportion of presence records), agreeing with the decrease in the total number of sightings of this species reported in Irish inshore waters during April to August, from 517 sightings in 2008 to 190 in 2018 by Whooley (2019), which is also consistent with unpublished data held by IWDG (Simon Berrow and Dave Wall, Personal observation, 12th August 2019). No clear trend was observed from the time series on the number of sightings divided by effort of fin whales in the study area. Note that the annual average sightings rate is a function of both the proportion of presences and the abundance where the animals are present. Our models showed no effect of herring density on fin whales but there was a direct relationship with sprat (i.e. fin whales presence increased with higher sprat density).

Of the environmental factors considered, only SST showed an effect on the abundance of the baleen whale group in the study area. Baleen whales in general seemed to be more abundant in the coldest areas and, as also seen in common dolphins, less numerous in temperatures from 12.5 to 14°C. This raises the question of whether the lower abundance of cetaceans in this SST range is a direct effect of SST or an indirect consequence of its effect on fish abundance (as discussed in the previous section).

4.4 Limitations

Multiannual ecosystem surveys, such as the CSHAS, in principle can overcome the common limitations such as the lack of spatio-temporal consistency and lack of simultaneously recorded data from different taxa or ecosystem variables (Torres et al., 2008). However, the data refer to a specific time of year (October) and in a specific area, so that effects with a time-lag of less than one year and events which occur in surrounding waters are hidden from the study. Moreover, in most real world situations prey availability in the moment and area where a sighted cetacean is feeding is hard to measure, and it is therefore difficult to determine whether foraging choices are truly opportunistic (Torres et al., 2008; Santos et al., 2013), and consequently, we cannot be sure how cetaceans perceive prey availability. The fine-scale resolution of the available acoustic raw data (NASC, 1.85km) allowed the interpretation of prey-predator associations. However, even though NASC was used as a proxy of fish abundance, it should be kept in mind that NASC measures the acoustic density of the fish, which may also be affected by other factors such as the size of the species or migration behavior which might influence their target strength (Simmonds and Maclennan, 2007).Visual data on cetaceans have some unavoidable limitations, including the use of multiple observers with different levels of experience contributing to long-term datasets and detection bias since sightings are only possible when the animals are at the surface. In the present study, an additional issue was the use of a different platform during very poor weather (i.e. when the weather was rougher the observers needed to come down from the crow's nest to the bridge). Because this change in platform height was associated with rougher weather, we expect that most of the effect of this change will have been included in the explanatory variable sea state. Although fishery surveys typically following a transect-based design which in principle enables the estimation of marine mammal abundance through distance sampling (Buckland et al., 1993), the CSHAS design did not follow the requirements (e.g. two observer platforms would be needed). Consequently, we could not calculate a detection function nor estimate the proportion of animals not seen due to being underwater (g(0)), even though it was possible to model the effects of environmental conditions on sightings detection probability. Thus, the number of sighted cetaceans per km on effort, is at best a measure of relative abundance of cetaceans.

The results of the models might be improved by accounting for additional variables that affect the detection probability of cetaceans, such as swell, glare, precipitation, etc. This information was not consistently recorded throughout the study period and could not be used. The resolution of fin and baleen whale models could be improved by using a larger number of observations of these species, such as might become available if the work continues for several more years. Moreover, testing the effects of other variables such as NAO, intensity of the currents and the wind, and considering time-lagged effects of variables, could contribute to achieve a better understating of how environmental variables affect the relative abundance and distribution of cetaceans.

It is important to point out that even though we had 14 years of data to fit the GAMs, with larger number of observations it is preferable to divide data into "model fitting" and "model testing" components. Predictions derived from the former can be tested against the latter, thus allowing a genuine hypothesis test. Results from GAMs (or indeed other kinds of statistical models) fitted to entire datasets are best viewed as descriptive, representing a hypothesis that still needs to be tested. Statistical correlation cannot be used to prove the existence of cause-effect relationships.

Better understanding of the system studied is essential to allow correct interpretation of the results. For example, complementary studies of the feeding ecology of the cetaceans based on stable isotope analysis of tissue samples would be useful.

5 Conclusions

The Celtic Sea herring stock suffered a marked decline since 2013. From then, the stock has concentrated during October towards the south-eastern coastal and southern offshore Irish waters within the Celtic Sea ecoregion. In the same period sprat density increased, the sea surface temperature increased, chlorophyll concentration decreased and the euphotic zone extended to greater depths. The models for herring and sprat support the idea that these species have different environmental relationships.

The factors influencing the probability of presence and relative abundance of the cetaceans differed between species. The presence of common dolphins was related to depth while, where they were present, their abundance was related to SST and herring density. Fin whales were more likely to be present where there was a higher density of sprat, while when all whale species were considered, there was also an effect of herring density. Where present, abundance of all whale species was related to warmer sea surface waters and herring density.

The results obtained provide valuable information about the functioning of the Celtic Sea ecosystem and the distribution and feeding ecology of cetaceans, as well as describing changes associated with the decline of the herring stock. They are potentially relevant for the implementation of the MSFD, specifically of the Descriptors 1, 3 and 4 (Biodiversity, Population of commercial fish species and Food webs, respectively). In addition, understanding the complex and dynamic relationships among different ecosystem components (predators, prey and the environment) can inform the implementation of Ecosystem-Based Management. Lastly, the work highlights the benefits of carrying out integrative surveys in which information about different ecosystem components is gathered simultaneously.

Data availability statement

The data analyzed in this study is subject to the following licenses/restrictions: The raw datasets of fish and cetacean species analyzed for this study are subject to data requests to the Marine Institute and the

Irish Whale and Dolphin Group. Requests to access these datasets should be directed to corresponding author and co-authors, https://www.marine.ie/marine-institute-request-digital-data, https://iwdg.ie/access-to-iwdg-sighting-and-stranding-data/.

Ethics statement

Ethical review and approval was not required for the animal study because this research is based on data from observations (cetaceans sightings and acoustic fisheries data) without applying any techniques that might disturb the animals.

Author contributions

SB and AF-B designed the research. CO'D, SB, DW, VV, MG, and AF-B collected data. AF-B and GP analyzed the data. All the authors contributed to the study with ideas and knowledge and to write up 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.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2023.1033758/full#supplementary-material

References

Aguilar, A., and García-Vernet, R. (2018). "Fin whale: balaenoptera physalus," in *Encyclopedia of marine mammals* (London: Academic Press), 368–371.

Anderson, D. R., and Burnham, K. P. (2002). Avoiding pitfalls when using information-theoretic methods. *J. Wildlife Manage.* 66 (3), 912–918. doi: 10.2307/3803155

Anderwald, P., Evans, P. G. H., Dyer, R., Dale, A., Wright, P. J., and Hoelzel, A. R. (2012). Spatial scale and environmental determinants in minke whale habitat use and foraging. *Mar. Ecol. Prog. Ser.* 450, 259–274. doi: 10.3354/meps09573

Baines, M., Reichelt, M., and Griffin, D. (2017). An autumn aggregation of fin (Balaenoptera physalus) and blue whales (B. musculus) in the porcupine seabight, southwest of Ireland. *Deep-Sea Res. Part II: Topical Stud. Oceanography* 141, 168–177. doi: 10.1016/j.dsr2.2017.03.007

Barros, N. B., and Clarke, M. R. (2009). "Diet," in *Encyclopedia of marine mammals* (London: Academic Press), 311–316.

Barlow, J. (2015). Inferring trackline detection probabilities, g (0), for cetaceans from apparent densities in different survey conditions. *Mar. Mammal Sci.* 31 (3), 923–943. doi: 10.1111/mms.12205

Britten, G. L., Dowd, M., and Worm, B. (2016). Changing recruitment capacity in global fish stocks. *Proc. Natl. Acad. Sci.* 113 (1), 134–139. doi: 10.1073/pnas.1504709112

Brophy, J. T., Murphy, S., and Rogan, E. (2009). The diet and feeding ecology of the short-beaked common dolphin (Delphinus delphis) in the northeast Atlantic. *Reports of the International Whaling Commission, SC/61/SM 14.*

Brunel, T., and Dickey-collas, M. (2010). Effects of temperature and population density on von bertalanffy growth parameters in Atlantic herring: a macro-ecological analysis. *Mar. Ecol. Prog. Ser.* 405, 15–28. doi: 10.3354/meps08491

Buckland, S. T., Anderson, D. R., Burnham, K. P., and Laake, J. L. (1993). *Distance sampling: estimating abundance of biological populations* (London: Chapman and Hall), 446.

Cannaby, H., and Hüsrevolu, Y. S. (2009). The influence of low-frequency variability and long-term trends in north Atlantic sea surface temperature on irish waters. *ICES J. Mar. Sci.* 66 (7), 1480–1489. doi: 10.1093/icesjms/fsp062

Cañadas, A., and Hammond, P. S. (2008). Abundance and habitat preferences of the short-beaked common dolphin delphinus delphis in the southwestern Mediterranean: implications for conservation. *Endangered Species Res.* 4 (3), 309–331. doi: 10.3354/esr00073

Cardinale, M., Cardinale, M., Casini, M., Arrhenius, F., and Håkansson, N. (2003). Diel spatial distribution and feeding activity of herring (Clupea harengus) and sprat (Sprattus sprattus) in the Baltic Sea. *Aquat. Living Resour.* 16 (3), 283–292. doi: 10.1016/S0990-7440(03)00007-X

Carvalho, N., Keatinge, M., and Guillen Garcia, J. *EUR 28359 EN* (Luxembourg: Publications Office of the European Union). doi: 10.2760/911768

Castro, J., Couto, A., Borges, F. O., Cid, A., Laborde, M. I., and Pearson, H. C. (2020). Oceanographic determinants of the abundance of common dolphins (Delphinus delphis) in the south of Portugal. *Oceans* 1 (3), 165–173. doi: 10.3390/oceans1030012

Clarke, M., and Egan, A. (2017). Good luck or good governance? the recovery of celtic Sea herring. *Mar. Policy* 78 (September 2016), 163–170. doi: 10.1016/j.marpol.2016.10.025

Correia, A. M., Gil, Á., Valente, R., Rosso, M., Pierce, G. J., and Sousa-pinto, I. (2019). Distribution and habitat modelling of common dolphins (Delphinus delphis) in the eastern north Atlantic. *J. Mar. Biol. Assoc. United Kingdom* 99, 1443–1457. doi: 10.1017/S0025315419000249

Council Directive 92/43/EEC (1992). Of 21 may 1992 on the conservation of natural habitats and of wild fauna and flora. OJ l 206/7. *Off. J. Eur. Union* L206, 7–50.

Cragg, J. G. (1971). Some statistical models for limited dependent variables with application to the demand for durable goods. *Econometrica* 39, 829–844. doi: 10.2307/1909582

CSHMAC (2018). “Report no MSC026,” in *Marine stewardship council full re-assessment public certification report for the CSHMAC (Celtic Sea herring management advisory committee) celtic Sea herring fishery, SAI global.*

Derville, S., Torres, L. G., Iovan, C., and Garrigue, C. (2018). Finding the right fit: comparative cetacean distribution models using multiple data sources and statistical approaches. *Diversity Distributions* 24), 1657–1673. doi: 10.1111/ddi.12782

Directive 2008/56/EC (2008). Of the European parliament and of the council of 17 June 2008 establishing a framework for community action in the field of marine environmental policy (Marine strategy framework directive). OJ l 164/19. *Off. J. Eur. Union* L164, 19–40.

Edwards, A., Jones, K., Graham, J. M., Griffiths, C. R., MacDougall, N., Patching, J., et al. (1996). Transient coastal upwelling and water circulation in bantry bay, a ria on the south-west coast of Ireland. *Estuarine Coast. Shelf Sci.* 42 (2), 213–230. doi: 10.1006/ecss.1996.0016

Engelhard, G. H., Peck, M. A., Rindorf, A., Smout, C. S., van Deurs, M., Raab, K., et al. (2014). Forage fish, their fisheries, and their predators: who drives whom? *ICES J. Mar. Sci.* 71 (1), 90–104. doi: 10.1093/icesjms/fst087

Eurostat (2020) *Fish catch 2019*. Available at: https://ec.europa.eu/eurostat/web/products-eurostat-news/-/edn-20201016-3 (Accessed 13 November 2021).

ESRI (2011). *ArcGIS desktop: release 10* (Redlands, CA: Environmental Systems Research Institute).

ESRI (2016). *ArcGIS desktop: release 10.4* (Redlands, CA: Environmental Systems Research Institute Ì).

Forney, K. (2000). Environmental models of cetacean abundance: reducing uncertainty in population trends. *Conserv. Biol.* 14, 1271–1286. doi: 10.1046/j.1523-1739.2000.99412.x

Gannier, A. (2002). Summer distribution of fin whales (Balaenoptera physalus) in the northwestern Mediterranean marine mammals sanctuary. *Rev. d'Ecologie (La Terre la Vie)* 57 (2), 135–150. doi: 10.3406/revec.2002.2390

Gerritsen, H. D., and Lordan, C. (2014). *Atlas of commercial fisheries around Ireland* (Ireland: Marine Insitute), 59. Available at: http://hdl.handle.net/10793/958.

González García, L., Pierce, G. J., Autret, E., and Torres-Palenzuela, J. M. (2018). Multi-scale habitat preference analyses for azorean blue whales. *PloS One* 13 (9), e0201786. doi: 10.1371/journal.pone.0201786

Haegele, C. W., and Schweigert, J. F. (1985). Session 2: spawning, development, and survival of early life stages of herring distribution and characteristics herring spawning grounds and description of spawning behavior. *Can. J. Fisheries Aquat. Sci.* 42, 39–55. doi: 10.1139/f85-261

Harma, C., Brophy, D., Minto, C., and Clarke, M. (2012). The rise and fall of autumn-spawning herring (Clupea harengus l.) in the celtic Sea between 1959 and 2009: temporal trends in spawning component diversity. *Fisheries Res.* 121–122, 31–42. doi: 10.1016/j.fishres.2012.01.005

Hunter, A., Speirs, D. C., and Heath, M. R. (2019). Population density and temperature correlate with long-term trends in somatic growth rates and maturation schedules of herring and sprat. *PloS One* 14 (3). doi: 10.1371/journal.pone.0212176

ICES (2017). “Sprat (Sprattus sprattus) in subarea 6 and divisions 7.a–c and 7.f–k (West of Scotland, southern celtic seas),” in *Report of the ICES advisory committee 2017*, vol. 2017. (ICES Advice). doi: 10.17895/ices.pub.3258

ICES (2018a). “Herring (Clupea harengus) in divisions 7.a south of 52°30'N, 7.g–h, and 7.j–k (Irish Sea, celtic Sea, and southwest of Ireland),” in *Report of the ICES advisory committee 2018*, vol. 2018. (ICES Advice). doi: 10.17895/ices.pub.4475/

ICES (2018b). *'Report of the workshop on integrated trend analysis in support to integrated ecosystem assessment (WKINTRA)',* (Hamburg, Germany: ICES CM 2018/IEASG) 14, 21.

ICES (2019). *'EU request for advice on a monitoring TAC for herring in ICES divisions 7 . a south of 52 ° 30 ' n , 7 . g – h , and 7 . j – k', in report of the ICES advisory committee 2019* Vol. 2019 (ICES Advice). doi: 10.17895/ices.advice.5614

ICES (2020a). *Herring (Clupea harengus) in divisions 7.a south of 52°30'N, 7.g–h, and 7.j–k (Irish Sea, celtic Sea, and southwest of Ireland)* Vol. 2020 (Report of the ICES Advisory Committee). doi: 10.17895/ices.advice.5944

ICES (2020b). *Herring assessment working group for the area south of 62° n (HAWG)* Vol. 2 (ICES Scientific Reports), 1151. doi: 10.17895/ices.pub.6105

ICES (2021a). *Herring (Clupea harengus) in divisions 7.a south of 52°30'N, 7.g-h, and 7.j-k (Irish Sea, celtic Sea, and southwest of Ireland)* (ICES Advisory Committee). doi: 10.17895/ices.advice.7773

ICES (2021b). *Herring assessment working group for the area south of 62° n (HAWG)* Vol. 3 (ICES Scientific Reports), 779. doi: 10.17895/ices.pub.8214

IFAW (2000). *Logger 2000 software* (London: International Fund for Animal Welfare).

Kawamura, A. (1980). A review of food of balaenopterid whales. *Sci. Rep. Whales Res. Inst.* 32), 155–197.

Lambert, E., MacLeod, C. D., Hall, K., Brereton, T., Dunn, T. E., Wall, D., et al. (2011). Quantifying likely cetacean range shifts in response to global climatic change: implications for conservation strategies in a changing world. *Endangered Species Res.* 15 (3), 205–222. doi: 10.3354/esr00376

Lambert, C., Mannocci, L., Lehodey, P., and Ridoux, V. (2014). Predicting cetacean habitats from their energetic needs and the distribution of their prey in two contrasted tropical regions. *PloS One* 9 (8), e0105958. doi: 10.1371/journal.pone.0105958

Lambert, C., Authier, M., Doray, M., Dore, G., and Ridoux, V. (2018). Hide and seek in the bay of Biscay {[/amp]]mdash; a functional investigation of marine megafauna and small pelagic fish interactions. *ICES J. Mar. Sci.* 76 (1), 113–123. doi: 10.1093/icesjms/fsy143

Lyashevska, O., Harma, C., Minto, C., Clarke, M., and Brophy, D. (2020). Long-term trends in herring growth primarily linked to temperature by gradient boosting regression trees. *Ecol. Inf.* 60 (April), 101154. doi: 10.1016/j.ecoinf.2020.101154

MacLeod, C. D. (2013). *An introduction to using GIS in marine biology* (Glasgow: Pictish Beast Publications).

Macleod, K., Fairbairns, R., Gill, A., Fairbairns, B., Gordon, J., Blair-Myers, C., et al. (2004). Seasonal distribution of minke whales balaenoptera acutorostrata in relation to physiography and prey off the isle of mull, Scotland. *Mar. Ecol. Prog. Ser.* 277, 263–274. doi: 10.3354/meps277263

MacLeod, C. D., Weir, C. R., Santos, M. B., and Dunn, T. E. (2008). Temperature-based summer habitat partitioning between white-beaked and common dolphins around the united kingdom and republic of Ireland. *J. Mar. Biol. Assoc. United Kingdom* 88 (6), 1193–1198. doi: 10.1017/S002531540800074X

Marine Institute (2013). *The stock book 2013: annual review of fish stocks in 2013 with management advice for 2014* (Rinville, Oranmore, Ireland: Marine Institute).

Meynier, L., Pusineri, C., Spitz, J., Santos, M. B., Pierce, G. J., Ridoux, V., et al. (2008). Intraspecific dietary variation in the short-beaked common dolphin delphinus delphis in the bay of Biscay: importance of fat fish. *Mar. Ecol. Prog. Ser.* 354, 277–287. doi: 10.3354/meps07246

Milani, C., and Vella, A. (2019). Abundance , distribution and diet of the common dolphin , delphinus delphis , in the northern Aegean Sea (Greece). *Aquatic Conserv: Mar. Freshw. Ecosyst.* 1–11. doi: 10.1002/aqc.3081

Molloy, J. (2006). *The herring fisheries of Ireland 1900–2005: biology, research, development and assessment* (Rinville, Oranmore, Ireland: Marine Institute).

Mõttus, M., Sulev, M., Baret, F., Lopez-Lozano, R., and Reinart, A. (2012). “Photosynthetically active radiation: measurement and modeling,” in *Encyclopedia of sustainability science and technology*. Ed. Meyers, (New York, NY: Springer). doi: 10.1007/978-1-4614-5806-7_451

Moyano, M., Illing, B., Polte, P., Kotterba, P., Zablotski, Y., Gröhsler, T., et al. (2020). Linking individual physiological indicators to the productivity of fish populations: a case study of Atlantic herring. *Ecol. Indic.* 113, 106146. doi: 10.1016/j.ecolind.2020.106146

Nøttestad, L., Krafft, B. A., Anthonypillai, V., Bernasconi, M., and Langård, L. (2015). Recent changes in distribution and relative abundance of cetaceans in the Norwegian Sea and their relationship with potential prey. *Front. Ecol. Evol.* 2 (83). doi: 10.7557/3.2713

O'Boyle, S., McDermott, G., and Wilkes, R. (2009). Dissolved oxygen levels in estuarine and coastal waters around Ireland. *Mar. Pollut. Bull.* 58 (11), 1657–1663. doi: 10.1016/j.marpolbul.2009.07.002

O'Brien, J., Berrow, S., McGrath, D., and Evans, P. (2009). Cetaceans in irish waters: a review of recent research. *Biol. Environ.* 109 (2), 63–88. doi: 10.3318/BIOE.2009.109.2.63

O'Donnell, C., Mullins, E., Lynch, D., Lyons, K., Keogh, N., Callaghan, S. O., et al. (2018). *Celtic Sea herring acoustic survey cruise report 2018, 8-28 October 2018* Vol. 2018 (Marine Institute).

O'Donnell, C., Mullins, E., Lyons, K., Connaughton, P., and Perez Tadeo, M. (2020). *Celtic Sea herring acoustic survey cruise report 2020, 4-24 October 2020* Vol. 2020 (Marine Institute).

O'Sullivan, D., O'Keeffe, E., Berry, A., Tully, O., and Clarke, M. (2013). An inventory of Irish herring spawning grounds. *Irish Fisheries Bull.* 42, 38.

Ottersen, G., Kim, S., Huse, G., Polovina, J., and Stenseth, N. C. (2010). Major pathways by which climate may force marine fish populations. *J. Mar. Syst.* 79, 343–360. doi: 10.1016/j.jmarsys.2008.12.013

Palialexis, A., Connor, D., Damalas, D., Gonzalvo, J., Micu, D., Mitchel, I., et al. (2019). *Indicators for status assessment of species, relevant to MSFD biodiversity descriptor* (Luxembourg: EUR 29820 EN, Publications Office of the European Union). doi: 10.2760/282667

Pendleton, D. E., Sullivan, P. J., Brown, M. W., Cole, T. V.N., Good, C. P., Mayo, C. A., et al. (2012). Weekly predictions of north Atlantic right whale eubalaena glacialis habitat reveal influence of prey abundance and seasonality of habitat preferences. *Endangered species Res.* 18, 147–161. doi: 10.3354/esr00433

Piatt, J. F., Methven, D. A., Burger, A. E., McLagan, R. L., Mercer, V., Creelman, E., et al. (1989). Baleen whales and their prey in a coastal environment. *Can. J. Zoology* 67 (6), 1523–1530. doi: 10.1139/z89-217

Pierce, G. J., Santos, M. B., Reid, R. J.O., Patterson, I. A.P.O., and Ross, H. M.O. (2004). Diet of minke whales in Scottish (UK) waters with notes on strandings of this species in Scotland 1992-2002. *Mar. Biol. Assoc. United Kingdom* 84, 1241–1244. doi: 10.1017/S0025315404010732h

Pierce, G. J., Santos, M. B., Murphy, S., Learmonth, J. A., Zuur, A. F., Rogan, E., et al. (2008). Bioaccumulation of persistent organic pollutants in female common dolphins (Delphinus delphis) and harbour porpoises (Phocoena phocoena) from western European seas: geographical trends, causal factors and effects on reproduction and mortality. *Environ. Pollut.* 153 (2), 401–415. doi: 10.1016/j.envpol.2007.08.019

Pikitch, E. K., Santora, C., Babcock, E. A., Bakun, A., Bonfil, R., Conover, D. O., et al. (2004). Ecosystem-based fishery management. *Science* 305 (5682), 346–347. doi: 10.1126/science.1098222

Pingree, R. D. (1980). Chapter 13. physical oceanography of the celtic Sea and English channel. *Elsevier Oceanography Ser.* 24, 415–465. doi: 10.1016/S0422-9894(08)71358-8

Pingree, R. D., Mardell, G. T., Holligan, P. M., Griffiths, D. K., and Smithers, J. (1982). Celtic Sea and armorican current structure and the vertical distributions of temperature and chlorophyll. *Continental Shelf Res.* 1 (1), 99–116. doi: 10.1016/0278-4343(82)90033-4

Prieto, R., Tobeña, M., and Silva, M. A. (2017). Habitat preferences of baleen whales in a mid-latitude habitat. *Deep-Sea Res. Part II: Topical Stud. Oceanography* 141 (August 2016), 155–167. doi: 10.1016/j.dsr2.2016.07.015

Pusineri, C., Magnin, V., Meynier, L., Spitz, J., Hassani, S., Ridoux, V., et al. (2007). Food and feeding ecology of the common dolphin (Delphinus delphis) in the oceanic northeast Atlantic and comparison with its diet in neritic areas. *Mar. Mammal Sci.* 23 (1), 30–47. doi: 10.1111/j.1748-7692.2006.00088.x

Raine, R., Whelan, D., Conway, N., Joyce, B., Moloney, M., Hoey, M. J., et al. (1993). "The oceanography of southwest Ireland: current research activities," in *Lough beltra 1989-1991: proceedings of the R.V. lough beltra workshop, dalkey, 30th and 31st January 1992*. Eds. M. Gillooly and P. Byrne (Dublin: Fisheries Research Centre).

Ramp, C., Delarue, J., Palsb, P. J., Sears, R., and Hammond, P. S. (2015). Adapting to a warmer ocean {{/amp]]mdash; seasonal shift of baleen whale movements over three decades. *PLoS ONE* 10 (3), e0121374. doi: 10.1371/journal.pone.0121374

R Core Team (2018). R: a language and environment for statistical computing. *R Foundation Stat. Computing* (Vienna, Austria). Available at: https://www.R-project.org/.

Rijnsdorp, A. D., Peck, M. A., Engelhard, G. H., Mo, C., and Pinnegar, J. K. (2009). Resolving the effect of climate change on fish populations. *ICES J. Mar. Sci.* 66, 1570–1583. doi: 10.1093/icesjms/fsp056

Robinson, K. P., Eisfeld, S. M., Costa, M., and Simmonds, M. P. (2010). Short-beaked common dolphin (Delphinus delphis) occurrence in the Moray firth, north-east Scotland. *Mar. Biodiversity Records* 3. doi: 10.1017/S1755267210000448

Ryan, C., Berrow, S., McHugh, B., O'Donnell, C., Trueman, C. N., O'Connor, I., et al. (2013a). Prey preferences of sympatric fin (Balaenoptera physalus) and humpback (Megaptera novaeangliae) whales revealed by stable isotope mixing models. *Mar. Mammal Sci.* 30, 1–17. doi: 10.1111/mms.12034

Ryan, C., Whooley, P., Berrow, S., Barnes, C., Masset, N., Strietman, W. J., et al. (2015). A longitudinal study of humpback whales in Irish waters. *Mar. Biol. Assoc. United Kingdom* 96, 1–7. doi: 10.1017/S0025315414002033

Ryan, C., McHugh, B., McHugh, B., Trueman, C. N., Sabin, R., Deaville, R., Harrod, C., et al. (2013b). Stable isotope analysis of baleen reveals resource partitioning among sympatric rorquals and population structure in fin whales. *Mar. Ecol. Prog. Ser.* 479, 251–261. doi: 10.3354/meps10231

Saavedra, C., Pierce, G. J., Gago, J., Jusufovski, D., Cabrero, Á., Cerviño, S., et al. (2017). Factors driving patterns and trends in strandings of small cetaceans. *Mar. Biol.* 164 (8), 481. doi: 10.1007/s00227-017-3200-3

Santos, M. B., German, I., Correia, D., Read, F. L., Cedeira, J. M., Caldas, M., et al. (2012). Cycles, trends, and residual variation in the Iberian sardine (Sardina pilchardus) recruitment series and their relationship with the environment. *ICES J. Mar. Sci.* 69 (5), 739–750. doi: 10.1093/icesjms/fsr186

Santos, M. B., González-Quirós, R., Riveiro, I., Cabanas, J. M., Porteiro, C., Pierce, G. J., et al. (2013). Long-term variation in common dolphin diet in relation to prey abundance. *Mar. Ecol. Prog. Ser.* 481, 249–268. doi: 10.3354/meps10233

Santos, M. B., and Pierce, G. J. (2015). Marine mammals and good environmental status: science, policy and society; challenges and opportunities. *Hydrobiologia* 750, 13–41. doi: 10.1007/s10750-014-2164-2

Santos, M. B., Saavedra, C., and Pierce, G. J. (2014). Quantifying the predation on sardine and hake by cetaceans in the Atlantic waters of the Iberian peninsula. *Deep-Sea Res. Part II* 106, 232–244. doi: 10.1016/j.dsr2.2013.09.040

Scientific, Technical and Economic Committee for Fisheries (STECF) (2019). *The 2019 annual economic report on the EU fishing fleet (STECF 19-06)*.

Silva, M. A. (1999). Diet of common dolphins, delphinus delphis, off the Portuguese continental coast. *Mar. Biol. Assoc. United Kingdom* 79, 531–540. doi: 10.1017/S0025315498000654

Silva, M. A., Prieto, R., Cascão, I., Seabra, M. I., Machete, M., Mark, F., et al. (2014). Spatial and temporal distribution of cetaceans in the mid-Atlantic waters around the Azores. *Mar. Biol. Res.* 10 (2), 123–137. doi: 10.1080/17451000.2013.793814

Simmonds, J. E., and Maclennan, D. N. (2005). "Fisheries acoustics: theory and practice: second edition," in *Fisheries acoustics: theory and practice: second edition*, 1–252. doi: 10.1002/9780470995303

Spitz, J., Mourocq, E., Leauté, J.-P., Quéro, J.-C., and Ridoux, V. (2010). Prey selection by the common dolphin: fulfilling high energy requirements with high quality food. *J. Exp. Mar. Biol. Ecol.* 390, 73–77. doi: 10.1016/j.jembe.2010.05.010

Spitz, J., Ridoux, V., Trites, A. W., Laran, S., and Authier, M. (2018). Prey consumption by cetaceans reveals the importance of energy-rich food webs in the bay of Biscay. *Prog. Oceanography* 166, 148–158. doi: 10.1016/j.pocean.2017.09.013

Scientific, Technical and Economic Committee for Fisheries (STECF) (2019). *The 2019 Annual Economic Report on the EU Fishing Fleet (STECF 19-06)*, N. Carvalho, M. Keatinge and J. Guillen Garcia editor(s), EUR 28359 EN, Publications Office of the European Union, Luxembourg. doi: 10.2760/911768

Surma, S., Pitcher, T. J., Kumar, R., Varkey, D., Pakhomov, A., Lam, M. E., et al. (2018). Herring supports northeast pacific predators and fisheries : insights from ecosystem modelling and management strategy evaluation. *PloS One* 13 (7), e01. doi: 10.1371/journal.pone.0196307

Tobeña, M., Prieto, R., Machete, M., and Silva, M. A. (2016). Modeling the potential distribution and richness of cetaceans in the Azores from fisheries observer program data. *Front. Mar. Sci.* 3, 202. doi: 10.3389/fmars.2016.00202

Torres, L. G., Read, A. J., and Halpin, P. (2008). Fine-scale habitat modeling of a top predator: do prey data improve predictive capacity? *Ecol. Appl.* 18 (7), 1702–1717. doi: 10.1890/07-1455.1

Trenkel, V. M., Pinnegar, J. K., Dawson, W. A., and Buit du Tidd, M. H. A. N. (2005). Spatial and temporal structure of predator-prey relationships in the celtic Sea fish community. *Mar. Ecol. Prog. Ser.* 299, 257–268. doi: 10.3354/meps299257

Víkingsson, G. A., Elvarsson, B. T., Ólafsdóttir, D., Sigurjónsson, J., Chosson, V., and Galan, A. (2014). Recent changes in the diet composition of common minke whales (Balaenoptera acutorostrata) in icelandic waters. a consequence of climate change? *Mar. Biol. Res.* 10 (2), 138–152. doi: 10.1080/17451000.2013.793812

Virgili, A., Authier, M., Boisseau, O., Cañadas, A., Claridge, D., Cole, T., et al. (2019). Combining multiple visual surveys to model the habitat of deep-diving cetaceans at the basin scale: Large-scale modelling of deep-diving cetacean habitats. *Global Ecol. Biogeography* 28 (3), 300–314. doi: 10.1111/geb.12850

Visser, F., Hartman, K. L., Pierce, G. J., Valavanis, V. D., and Huisman, J. (2011). Timing of migratory baleen whales at the azores in relation to the north atlantic spring bloom. *Mar. Ecol. Prog. Ser.* 440 (June 2015), 267–279. doi: 10.3354/meps09349

Volkenandt, M., Berrow, S., O'Connor, I., Guarini, J., and O'Donnell, C. (2014). Prespawing herring distribution in the Irish celtic Sea between 2005 and 2012. *ICES J. Mar. Sci.* 72, 498–507. doi: 10.1093/icesjms/fsu143

Volkenandt, M., O'Connor, I., Guarini, J., Berrow, S., and O'Donnell, C. (2015). Fine-scale spatial association between baleen whales and forage fish in the celtic Sea. *Can. J. Fisheries Aquat. Sci.* 73 (2), 197–204. doi: 10.1139/cjfas-2015-0073

Wall, D., Murray, C., O'Brien, J., Kavanagh, L., Ryan, C., Glanville, B., et al. (2013). *Atlas of the distribution and relative abundance of marine mammals in Irish offshore Waters : 2005 – 2011* (The Irish Whale and Dolphin Group).

Whooley, P. (2019). 2019: sightings to September. *Flukes* 2, 4–5.

Whooley, P., and Berrow, S. (2019). Bowhead whale (Balaena mysticetus Linnaeus), a cetacean species new to Irish waters. *Irish Naturalists J.* 36, 169–172.

Whooley, P., Berrow, S., and Barnes, C. (2011). Photo-identification of fin whales (Balaenoptera physalus l.) off the south coast of Ireland. *Mar. Biodiversity Records* 4 (e8). doi: 10.1017/S1755267210001119

Winters, G. H., and Wheeler, J. P. (1996). Environmental and phenotypic factors affecting the reproductive cycle of Atlantic herring. *ICES J. Mar. Sci.* 53, 73–88. doi: 10.1006/jmsc.1996.0007

Witteveen, B. H., Worthy, G. A.J., Foy, R. J., and Wynne, K. M. (2012). Modeling the diet of humpback whales: an approach using stable carbon and nitrogen isotopes in a Bayesian mixing model. *Mar. Mammal Sci.* 28 (3), E233–E250. doi: 10.1111/j.1748-7692.2011.00508.x

Wood, S. N. (2006). On confidence intervals for generalized additive models based on penalized regression splines. *Aust. New Z. J. Stat.* 48, 445–464. doi: 10.1111/j.1467-842X.2006.00450.x

Wood, S. (2013) *Mgcv: mixed GAM computation vehicle with GCV/AIC/ REML smoothness estimation.* Available at: http://cran.r-project.org/web/packages/mgcv/index.htm.

Zerbini, A. N., Friday, N. A., Palacios, D. M., Waite, J. M., Ressler, P. H., and Rone, B. K. (2016). Baleen whale abundance and distribution in relation to environmental variables and prey density in the Eastern Bering Sea. *Deep-Sea Res. II* 134, 312–330. doi: 10.1016/j.dsr2.2015.11.002

Zuur, A. F., Ieno, E. N., and Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* 1, 3–14. doi: 10.1111/j.2041-210X.2009.00001.x

Zuur, A. F., Ieno, E. N., and Smith, G. M. (2007). *Analysing ecological data* (New York, NY: Springer).

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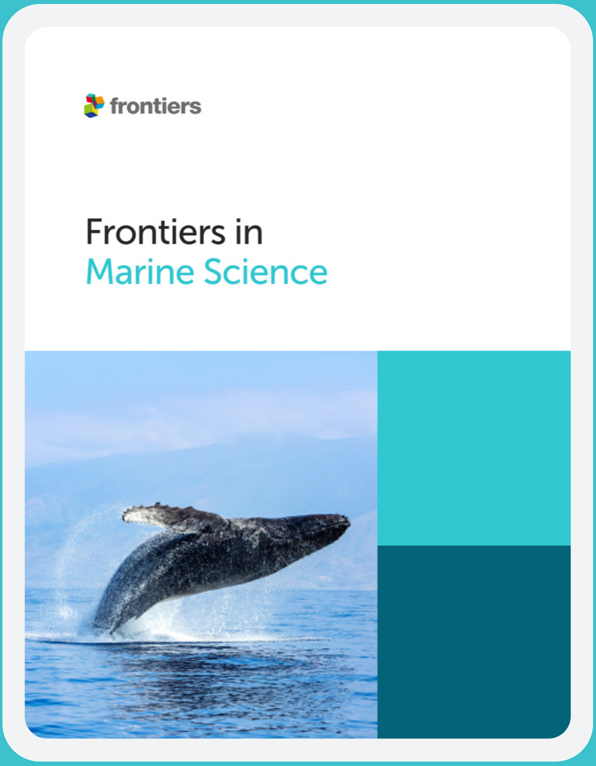

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