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IDENTIFYING MARINE KEY BIODIVERSITY AREAS USING TRACKING DATA

Martin Stuart Beal

This thesis is submitted in partial fulfilment for the degree of PhD in

Behavioural Biology

2021

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DEDICATÓRIA

I don't know

Who does know?

Where to go

I don’t know

– Adam ‘MCA’ Yauch

To Mikey and Milo

and

all the future explorers and care-takers out there

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Palavras-chave:

Seguimento de animais; conservação marinha; áreas protegidas; key biodiversity areas

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Animal tracking; marine conservation; protected areas; key biodiversity areas

Categorias de Classificação da tese

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Chapter 3 – track2KBA: An R package for identifying important sites for biodiversity from tracking data”, published in *Methods in Ecology and Evolution* in September, 2021. 10.1111/2041-210X.13713

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Chapter 6 – Global political responsibility for the conservation of albatrosses and large petrels”, published in *Science Advances* in March, 2021. 10.1126/sciadv.abd7225

RESUMO

O impacto humano no ambiente marinho é substancial e crescente, causando uma preocupação pelo futuro de várias espécies marinhas. É necessário um leque de medidas para reduzir os impactos negativos, incluindo a implementação de áreas protegidas e a regulação das actividades humanas no mar. No entanto, para que os esforços sejam eficazes, precisamos de uma melhor compreensão da ecologia da biodiversidade marinha. O seguimento com recurso a dispositivos electrónicos revolucionou o estudo do comportamento e da ecologia dos animais marinhos, melhorando a capacidade de conservar os seus habitats. O foco central desta tese é a aplicação do seguimento de animais à ecologia e à conservação marinha. Apresentamos uma revisão bibliográfica, uma ferramenta de software, e análises espaciais para ilustrar as formas como os dados de seguimento têm e podem ser utilizados em estudos de conservação de espécies marinhas.

Para demonstrar como o seguimento de animais contribuiu na progressão do conhecimento sobre o comportamento e a ecologia das espécies marinhas, apresentamos exemplos da literatura relativos a avanços na compreensão da migração, da procura de alimento e seleção de habitat, e da navegação em megafauna marinha, desde aves marinhas a cetáceos.

Desenvolvemos uma ferramenta de software acessível, "track2KBA", na linguagem de programação R, que facilita a análise de dados de seguimento para identificar locais importantes para a conservação. Ilustrámos os passos de análise do software e fornecemos exemplos de como a ferramenta pode ser útil para analisar dados de seguimento de uma grande variedade de espécies, tanto no ambiente marinho como terrestre.

Analisámos dados GPS de 23 espécies de aves marinhas para avaliar a importância do seguimento de populações ao longo dos anos com o objetivo de identificar sítios de importância para essas espécies. Descobrimos que, quando um número suficiente de indivíduos é seguido, a amostra de dados recolhidos num único ano fornece frequentemente estimativas robustas da distribuição das populações.

Ao analisar os movimentos de 40 tartarugas-verdes fêmeas (*Chelonia mydas*) de uma população (importante ao nível global) na Guiné-Bissau, África Ocidental, avaliámos a qualidade de uma rede regional de áreas marinhas protegidas para a conservação de tartarugas ao longo das estações,em vários países. Verificámos que as tartarugas são espacialmente bem protegidas entre eventos de desova, menos protegidas durante a migração, e que a protecção dos locais de alimentação dependia do país para onde migravam.

Analisámos dados de seguimento de 39 espécies de albatrozes e espécies semelhantes (cagarras e pardelas) para quantificar, pela primeira vez, as áreas sob diferentes jurisdições, e a ligação entre elas, de que dependem estas aves marinhas severamente ameaçadas. Verificámos que estas aves passam 39% do seu tempo em áreas do alto-mar para além de jurisdições nacionais, e que através dos seus movimentos elas unem as jurisdições de numerosos países em todo o mundo, indicando a necessidade de uma cooperação internacional para que a sua conservação seja eficaz.

As análises de dados de seguimento de espécies individuais e de grupos de espécies apresentadas nesta tese representam aplicações inovadoras à escala local, regional e global. Este trabalho contribui directamente para a identificação de locais importantes para a biodiversidade, tais como as “marine Key Biodiverisity Areas”, e para o desenvolvimento de colaborações internacionais para a conservação da biodiversidade marinha tanto em águas nacionais como em alto mar.

ABSTRACT

The human footprint on the ocean environment is substantial and growing, causing widespread concern for the future of numerous marine species. Different measures are needed to reduce negative impacts, from establishing protected areas to regulating human activities at sea. For such efforts to be effective however, a sound understanding of the underlying ecology of marine biodiversity is needed. The tracking of animals using electronic devices has revolutionized our understanding of the behavior and ecology of marine animals and thereby improved our ability to effectively conserve them and their habitats. The central focus of this thesis is the application of animal tracking to marine ecology and conservation. Herein, we present a literature review, a software tool, and data analyses to illustrate ways in which tracking data have and can be used to inform the study and conservation of marine wildlife.

To demonstrate how animal tracking has helped advance our knowledge of the behavior and ecology of marine species, we present examples from the literature regarding the study of migration, foraging and habitat use, and navigation in marine megafauna, from seabirds to cetaceans.

We developed an accessible software tool, “track2KBA”, in the programming language R, which facilitates analyzing tracking data to identify important sites for conservation. We illustrate the package workflow, and provide examples of how the tool can be useful for analyzing tracking data from a wide variety of species and contexts, both in the marine and terrestrial realm.

We analyzed GPS tracking data from 23 species of seabirds to assess the relevance of tracking populations across years when identifying sites of importance. We found that, when enough individuals are tracked, tracking datasets collected in a single year often provide robust pictures of population distributions.

By analyzing the tracks of 40 female Green Turtles (*Chelonia mydas*) from a globally important nesting population in Guinea-Bissau, West Africa, we quantified how well a regional marine protected area network covers the turtles across seasons and countries. We found that turtles are spatially well-protected during the interesting period, less so during migration, and that protected area coverage at post-nesting foraging sites depended on the country turtles migrated to.

We analyzed tracking data from 39 species of albatrosses and large petrels to quantify, for the first time, the political areas and links between jurisdictions that these highly threatened seabirds depend on. We found that these birds spend 39% of their time in areas beyond national jurisdiction, and connect the jurisdictions of numerous countries around the world, necessitating international cooperation for their effective conservation.

The analyses of tracking data presented in this thesis represent novel applications at local, regional and global scales, concerning single species and groups of species. This work contributes directly to the identification of important sites for biodiversity, such as marine Key Biodiversity Areas, and to the development of international collaborations to conserve marine biodiversity in national waters and beyond.

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CHAPTER 1

GENERAL INTRODUCTION

The world's oceans are in a precarious state. Human activities, from coastal development to overfishing, are impacting marine ecosystems worldwide (United Nations, 2021). The current state of things is causing great concern for the future of life in the ocean, with potentially far-reaching effects for both human livelihoods and natural ecosystem function (Halpern et al., 2008). In 2021, the United Nations declared the start of the "Decade of. Ocean Science for Sustainable Development", to spur global action to improve our knowledge base of the marine environment and the life it supports, with the ultimate goal of promoting a responsible, sustainable, and healthy relationship between humankind and the ocean.

1.1 MARINE CONSERVATION

Nature conservation is the practice of understanding and managing processes that threaten the persistence of biological diversity, where 'biological diversity' (or 'biodiversity) is the countless ways lifeforms vary, from the genetic level to species and ecosystems (Roff et al., 2011; E. O. Wilson, 1988). Understanding what processes threaten biodiversity relies in large part on ecology, the study of organisms and their relationships to the environment. A central task of the field of conservation biology is then the application of ecological knowledge to the preservation (or sustainable use) of organisms and their environments (Roff et al., 2011; Soulé, 1985). In a world increasingly dominated by human life, modern conservation implies more than applied ecology, however, having grown into an interdisciplinary field with insight and participation from the social and political sciences, moral philosophy, civil society, and indigenous communities (Kareiva & Marvier, 2012; Mace, 2014). Nevertheless, a sound scientific understanding of marine ecology is key to ensuring a healthy ocean environment in the face of growing human pressures.

As we humans are land-based animals, our knowledge of the marine environment lags behind that of the terrestrial world (Roff et al., 2011). Due to the vastness of the ocean, which covers 70% of the world's surface, the oceans were long considered a global commons, unbounded in scale and home to inexhaustible resources (Roff et al., 2011). However, this historical assumption has begun to unravel, as the collective impact of humanity begins to reach even the furthest ends of the vast global ocean (Halpern et al., 2019). As early as the 19th century, international agreements among fishing nations were struck to address concerns about overfishing, such as the North Sea Fisheries Convention of 1882 (Reed, 2009). Throughout the 20th century, more and more people began to notice the negative impacts of human activities at sea, and pushed for action to protect the ocean environment. Initial efforts led to the adoption of international agreements to regulate certain human activities at sea, such as the establishment of the International Whaling Commission in 1946, as a result of the devastation of global whale populations in the 19th and early 20th centuries (C. W. Clark & Lamberson, 1982; Roff et al., 2011). Later, in 1982, the widespread adoption of the United Nations Convention on the Law of the Sea (UNCLOS) laid the international legal foundation for ocean resource management.

Despite decades of efforts to establish regulatory and policy instruments to manage human activities and their impacts at sea, the current consensus among marine scientists remains that the ocean environment and its constituent life is in peril (United Nations, 2021). This undesirable state of affairs implicates two shortfalls in our attempts to date: our protection and mitigation measures are inadequate in spatial, taxonomic or habitat coverage, and (or) are not effective enough (i.e, lacking in implementation and enforcement). A central pillar of conservation efforts globally is area-based protection, where sites are designated and managed with the explicit goal of separating some portion of biodiversity from processes that threaten their persistence (e.g., fishing/hunting) (Margules & Pressey, 2000).

Although the global spatial coverage of marine protected areas continues to increase, the conservation value of a number of established sites have come into question and there is a general lack of coverage in areas beyond national jurisdiction (hereafter referred to as the “high seas”), which represent nearly half of the earth’s surface (Devillers et al., 2015; Visconti et al., 2019). Ensuring that protected areas are placed where potential conservation benefits are maximized requires robust measuring and mapping of biodiversity elements (Margules & Pressey, 2000). Information on the spatiotemporal distributions of marine biodiversity is therefore crucial to the planning of protected areas and other area-based management measures, such as zoning regulations for extractive activities (e.g., fishing and mining) (Edgar et al., 2008; Wright et al., 2019).

In the past two decades, numerous approaches have been developed to quantify the potential importance of spatially explicit sites to the conservation of marine biodiversity. One such approach, named ‘Key Biodiversity Areas’, maps out sites of global or regional importance to the persistence of any macroscopic species (Edgar et al., 2008; IUCN, 2016). By identifying and delineating sites using a standardized set of quantitative criteria, important site networks (e.g., KBAs) represent a spatial layer of information on the importance of given areas to conservation, which can be useful for informing the placement of protected areas and in marine spatial planning exercises (Edgar et al., 2008).

1.2 ANIMAL TRACKING

The marine environment is a challenging system to study, as humans are terrestrial and vision-based animals, and most activity in the ocean happens below the surface or far from land (Hussey et al., 2015). The innovation of novel tools and techniques to study the marine environment has a long history, from underwater research stations to autonomous vehicles, and diving suits to deep-water submersibles (Clifton et al., 1970; Reed, 2009). One such technological advance has been the development of electronic sensors able to repeatedly record information about the movements, physiology, and surrounding environment of individual animals, collectively referred to as "biologging" or "biotelemetry" technology (Hussey et al., 2015; Ropert-Coudert & Wilson, 2005).

In 1969, the Craighead brothers, Frank and John, attached a locator device to an Elk cow (*Cervus canadensis*) in Yellowstone National Park, in the United States, and successfully tracked its movements via orbiting Nimbus satellites (Craighead et al., 1972). Later, in 1979, researchers from the National Oceanic and Atmospheric Association (NOAA) used a similar Nimbus tracking system to reveal the migratory route of a sea turtle named Dianne in the Gulf of Mexico, marking the first time satellites were used to monitor a marine species (Daniel, 1980). These and other similar studies revealed the immense potential in using electronic technologies to study wild animals at a distance, rather than only via visual and other short-range observation techniques, which are labor intensive and often impractical in the marine realm (Hussey et al., 2015). With the launch of the Argos-class satellites in the 1980s and the boom of miniaturized electronics in the 1990s, biologging entered a 'golden age', evidenced by the increasing number of scientific studies published on the subject each year. The focus of this thesis is on the use of electronic devices attached to animals to repeatedly relocate them over time, referred to as animal tracking, or simply "tracking". Tracking provides a spatiotemporal record of the movement trajectory of individual animals, referred to as "tracking data".

The technologies that make remote animal tracking possible are diverse, with new innovations occurring regularly (e.g., Ghaffarivardavagh et al., 2020). There are two principal ways to distinguish tracking devices, whether devices transmit or store the data, and how positions on the earth's surface are derived (Ropert-Coudert & Wilson, 2005). Transmitter devices send data on radio or sound waves via satellites, local relay and receiver stations, or the mobile telephone network, ultimately arriving to the researcher's computer. Archival data loggers, on the other hand, save on battery power by storing the sensor information locally, requiring recovery of the device to access the data and get the animal's spatial coordinates. Tracking devices derive geospatial positions via satellite triangulation (e.g., GPS), satellite-derived Doppler acceleration (e.g. ARGOS platform transmitter terminals [PTT]), ambient light levels (i.e., light-level geolocators [GLS]), and acoustic receivers (Cooke et al., 2004; Matley et al., 2021; Ropert-Coudert & Wilson, 2005). The positional accuracy of each geolocation method varies, which is inversely related to the power output needed to run the device, creating a trade-off between data precision and device size, weight and battery life (Ropert-Coudert & Wilson, 2005). The most common types of tracking devices used in the study of birds, sea turtles, and pinnipeds (the subjects of this thesis) are GPS, PTT, and GLS (ordered from high to low spatial precision).

1.3 TRACKING FOR CONSERVATION

The conservation promise of animal tracking has long been recognized, however the integration of information from animal tracking into policy-making and management processes has been varied (Allen & Singh, 2016; Fraser et al., 2018; Jeffers & Godley, 2016). In the marine realm, recent efforts have been made to integrate tracking data into regular processes of informing conservation efforts and assessing protection efficacy (D. C. Dunn et al., 2019; Hindell et al., 2020; B. G. Lascelles et al., 2016). With respect to area-based conservation, tracking data has already been used to identify ecologically important areas for a number of marine predator species (Dias et al., 2018; Hindell et al., 2020; B. G. Lascelles et al., 2016). Important sites derived from tracking information can be used to assess whether existing protected area networks encompass the important habitats animals rely on as they move (e.g., breeding and non-breeding areas), and to guide MPA design (Davies et al., 2021; J. M. Handley et al., 2020; Hindell et al., 2020). As tracking data accumulates in online repositories (e.g., Seabird Tracking Database [http://www.seabirdtracking.org/]), the potential impact of re-applying this existing information to inform conservation grows (Hays et al., 2019). Importantly, such post-hoc analysis can address questions which are often complementary to those inquiries which motivated the original data collection (Hays et al., 2019).

1.4 THESIS OVERVIEW & OBJECTIVES

The objective of this thesis is to contribute to the conservation of marine biodiversity, using animal tracking data as a principal tool. The specific aims were to, first, establish the relevance of animal tracking to the study of marine ecology (Chapter 2), then, to develop and test an analytical tool for applying tracking data to identifying important sites for biodiversity (Chapter 3). Then, through collaborations with marine ecologists and conservationists who have tracked marine species across the world, the objective was to analyze tracking data to inform conservation science at local, regional and global scales (Chapters 3, 4, 5, 6).

To do so, we executed a series of studies, organized in the following manner:

CHAPTER 2 – APPLICATIONS OF ANIMAL TRACKING TO THE STUDY OF THE BEHAVIOR AND ECOLOGY OF MARINE MEGAFAUNA

As conservation ultimately depends on a sound ecological foundation, in Chapter 2, I illustrate the utility animal tracking has had for studying marine ecology and animal behavior. I explore various tracking applications, showing how this tool has been used to improve understanding of the migrations, foraging behavior and habitat use, and navigational abilities of marine megafauna.

CHAPTER 3 – TRACK2KBA: AN R PACKAGE FOR IDENTIFYING IMPORTANT SITES FOR BIODIVERSITY FROM TRACKING DATA

The identification of important sites for conservation (e.g., Key Biodiversity Areas) relies on robust ecological data and analysis. In, Chapter 3, we introduce a novel software tool for analyzing tracking data, showing how the methods underlying the tool are useful for species and contexts beyond those for which they were originally designed, including species both in the terrestrial and marine realms.

CHAPTER 4 – QUANTIFYING ANNUAL SPATIAL CONSISTENCY IN BREEDING SEABIRDS: IS ONE YEAR OF TRACKING DATA SUFFICIENT FOR IDENTIFYING IMPORTANT SITES FOR CONSERVATION?

When estimating population-level spatial distributions, it is vital to consider what constitutes a robust sample of the wider population. In Chapter 4, we quantified the annual consistency in space use of 23 species of seabirds using tracking data. Analyzing annual consistency estimates, we assessed the relevance of multi-year sampling for the identification of important sites for seabird conservation at sea.

CHAPTER 5 – GREEN TURTLES HIGHLIGHT CONNECTIVITY ACROSS A REGIONAL MARINE PROTECTED AREA NETWORK IN WEST AFRICA

Regional protected area networks can, in theory, protect species that move over large distances by affording coverage of their disparate habitats. In Chapter 5, we used tracking data to quantify the degree to which a regional protected area network in West Africa covers the spatial distribution of a globally important population of Green Turtles (Chelonia mydas) across different seasons.

CHAPTER 6 – GLOBAL POLITICAL RESPONSIBILITY FOR THE CONSERVATION OF ALBATROSSES AND LARGE PETRELS

The conservation of far-ranging species requires international collaboration, as species often cross political borders and are thereby exposed to different regimes of environmental management. In Chapter 6, we identified quantitative links between countries which host albatrosses and large petrels (a highly threatened group of birds) during breeding, and other political areas (i.e., countries and fisheries management areas) the birds visit throughout the year.

CHAPTER 2

APPLICATIONS OF ANIMAL TRACKING TO THE STUDY OF BEHAVIOR AND ECOLOGY OF MARINE MEGAFAUNA

Martin Beal

2.1 ABSTRACT

The use of miniature electronic devices to track the movements of wild animals has revealed numerous natural history phenomena and helped address long-standing questions in ecology. In the marine realm, the ‘golden era’ of tracking of the past three decades has led to the description of many novel behaviors, including migration routes and timings, foraging strategies, habitat use, and navigation strategies in a wide variety of species. I review selected examples from the vast literature on animal tracking to illustrate how the recent and ongoing expansion in the application of miniaturized tracking technologies has improved our understanding of natural behavioral variation in marine megafauna. I then discuss outstanding questions in the field of behavioral ecology that tracking devices and associated biologging tools may help unravel in the near future. I argue that tracking technologies have become an essential part of the toolkit of marine biologists, but that caution and planning is required to ensure that a balance is struck between animal welfare and knowledge gain.

2.2 INTRODUCTION

The use of animal-borne devices to record information about the movements, physiology, and environment of individual animals, termed “biologging” or “biotelemetry”, has long been touted as a revolutionizing technique for the studying the behavior and ecology of wild animals (Buechner et al., 1971). In the marine environment, where direct observation of animals is often impractical, biologging techniques have indeed provided many novel insights into the lives of previously mysterious species (Kooyman, 2004). Animal tracking in particular, the subset of biologging concerned with the relocation of free-ranging animals over time, has perhaps provided many novel and fundamental insights of the past few decades, capturing the imagination of researchers and the general public alike (Wilmers et al., 2015).

Animal tracking provides a simple piece of information long missing for most marine species: where are they and when? By unlocking the answers to these key questions, tracking allows us to begin asking the proximate question of “how?” and the ultimate question of “why?”. Understanding how and why animals move is the central task of the field of movement ecology, which postulates that movement is part of a feedback system, interacting with intrinsic (i.e., behavioral and physiological) and extrinsic (i.e., environmental) factors (Nathan, 2008). Placing patterns of movement in space and time, i.e., positional coordinates and time signatures, in the context of some known variables, such as remotely sensed environmental variables, can help elucidate the potential relationship between them.

Here, I review selected examples from the animal tracking literature with the aim of illustrating how this sampling technique has advanced knowledge of the behavior and ecology of marine animals. More specifically, I explore how tracking has been performed on a wide breadth of marine megafauna, thereby improving understanding of fundamental aspects of migration, foraging behavior and habitat selection, and navigation. I then discuss the directions in which the field is headed, and how future advances can continue to improve our knowledge of the behavioral ecology of marine life.

2.3 METHODS

I used Google Scholar and Microsoft Academic search engines to explore the breadth of primary literature related to animal tracking. I proceeded by first reading broad reviews on the subject of biologging and tracking, to get an understanding for how the field has changed and what the major questions were over time (Alerstam & Bäckman, 2018; I. L. Boyd et al., 2004; Buechner et al., 1971; Hays et al., 2016; Hussey et al., 2015; Lohmann et al., 2008; Matley et al., 2021; Ropert-Coudert & Wilson, 2005; Rutz & Hays, 2009; Wilmers et al., 2015). Based on these (and further) reviews, I chose to focus on migration, foraging behavior and habitat use, and navigation as these themes have appeared repeatedly as fields of study which have gained (or were expected to gain) from the animal tracking portion of the ‘biologging revolution’. When possible, I focused on more recent studies, to try and illustrate the ‘state of the field’, and I attempted to select studies from a wide breadth of marine megafauna taxa, although in some cases model systems are the same for different questions (e.g., sea turtles for migration and navigation).

2.4 ANIMAL BEHAVIOR THROUGH THE LENS OF TRACKING

2.4.1 Migration

One area of ecological study that has benefitted greatly from animal tracking technology is migration science. Migration, the relatively long-distance and periodic movement of animals, has fascinated humans for centuries (Alerstam et al., 2003). Although the migrations of some marine species had long been inferred from indirect evidence (e.g., whaling records), given that such movements often involve distances of hundreds to thousands of kilometers, studying them directly was highly impractical (Lockyer & Brown, 1981). Since the rapid development of miniaturized tracking devices in the 1990s, the characteristics of migration routes and the timings of departures and arrivals have been described in many species.

One of the most famous examples of a migratory feat uncovered by tracking is the migration of the Arctic Tern (*Sterna paradisaea*). Using 1.4-g light-level geolocators, birds from breeding sites in Greenland were tracked migrating to the Southern Ocean, with some reaching the antipodes of the earth before returning to Europe the following summer, marking this round trip of more than 80.000 km as the longest known migration of any animal (Egevang et al., 2010). Fascinating long-distance migrations have also been described in other marine animal groups, such as the trans-Pacific migrations of Leatherback Turtles (*Dermochelys coriacea*) and the ocean basin crossings of Basking Sharks (*Cetorhinus maximus*) (Benson et al., 2007; Gore et al., 2008).

By tracking different life-history subsets within populations, the role of intra-specific variation in the migrations of species has become apparent. For example, in Southern Elephant Seals (*Mirounga leonina*) breeding on the archipelago of South Georgia, satellite tracking data showed that female seals migrate up to 3000 km from their breeding beaches, while males remain largely resident (McConnell & Fedak, 1996). Similarly, the seasonal distributions of life-stage groups can differ. In Cory’s Shearwater (*Calonectris borealis*), long-term tracking of immature birds until they recruited into the breeding population at 8 or 9 years of age showed that while up to 17% of the adult population spends the non-breeding period in the North Atlantic, all immatures travel to overwintering grounds in the southern hemisphere (Campioni et al., 2019).

Understanding how migrating animals travel in order to handle the energetic and time costs of long distance migration has been a well-studied topic, particularly in terrestrial birds (Alerstam & Bäckman, 2018). Distinct movement strategies have been described, such as ‘move-and-forage’, whereby migrating animals feed during migratory movements, while other species fuel up prior to departure and make long non-stop flights to reach their destinations (Alerstam & Bäckman, 2018). Recent work has begun to shine light on the travel strategies used by marine migrants (Hays et al. 2016). By combining wet-dry immersion loggers with light-level geolocators, Bonnet-Lebrun et al (2021) showed that seabirds make frequent stops during migration, contrasting with the many non-stop fliers among terrestrial and wetland birds species. By satellite tracking Blue Whales (*Balaenoptera musculus*) over 10 years, Abrahms et al. (2019) showed how this species tracks developing phytoplankton blooms during migration in a manner analogous to terrestrial herbivores which track phenological “green waves” of new grass growth (Abrahms et al., 2019; Bischof et al., 2012; Shariatinajafabadi et al., 2014). Importantly, Abrahms et al. (2019) also found that Blue Whales likely rely on memory of locations which have been historically good on average, not the best locations in a given year, indicating a potential vulnerability to climate change-related shifts in productive sites.

2.4.2 Foraging and habitat selection

Foraging behavior is fundamental to the way animals maintain a positive energy balance, with consequences for individual fitness (Stephens & Krebs, 1986). The direct observation of foraging behavior in marine animals is challenging, as most species forage below the surface or far from shore. Tracking technology has been instrumental in gaining insights into where, when, and how marine animals search for food, and more generally in characterizing ‘habitat’ in the dynamic ocean environment (Wilmers et al., 2015).

Knowing where individuals choose to forage in relation to conspecifics is necessary to understanding the factors that determine search strategies and population-level space use. For example, Northern Gannets (*Morus bassanus*) tracked throughout the British Isles were found to segregate space by breeding colony, suggesting that density dependent competition and information exchange at colonies shape space use at the population level (Wakefield et al., 2013). Furthermore, tracking data has been used to explore how sexes can differ in their foraging strategies and habitat use. Sex-based differences in foraging behavior appear widespread in marine animals, with tracking efforts finding spatial segregation in species such as Scalloped Hammerhead Sharks (*Sphyrna lewini*) (Wells et al., 2018), Wandering

Albatrosses (*Diomedea exulans)* (Orgeret et al., 2021), and Antarctic Fur Seals (*Arctocephalus gazella)* (Jones et al., 2021). However, sex differences are not ubiquitous; for example, despite extreme sexual size dimorphism in Southern Sea Lions, Baylis et al. (2016) found minimal sex-based differences in foraging behavior and habitat. Further differences in foraging behavior have been identified between age-groups (i.e., immatures versus adults) (Fayet et al., 2015; Hazen et al., 2012). Residual differences in behavior explained by individual-level effects, termed "individual specialization", have also been increasingly reported in marine taxa (R. Phillips et al., 2017).

How animals search for food is a central aspect of foraging ecology, and has long been recognized in theoretical models of animal foraging (e.g., optimal foraging theory, Pyke, 1984). Over the past three decades, numerous studies on a wide variety of species have been devoted to exploring whether foraging search behavior follows general and simple mathematical rules (e.g., testing the "Levy flight/walk foraging hypothesis" and related random walk models), by analyzing empirical movements of tracked animals against model predictions (Viswanathan et al., 2008). This boon in research identified common movement patterns across an array of species, although the degree to which these commonalities represent the evolution of optimal search strategies has come into question, suggesting a need for a shift in paradigm (Pyke, 2015; Reynolds, 2015).

In the past two decades, new statistical and computational methods incorporating more biological realism into the analysis of animal movement have driven advances in the understanding of species distributions, such as individual- or agent-based models and inferential models (Pyke, 2015; Schick et al., 2008). Inferential models have become particularly popular, as by estimating the associations between animal movement decisions and remotely sensed environmental and/or physiological variables (e.g., measured via satellite or animal-borne sensors), they can be used to estimate the spatial distribution of species (Schick et al., 2008). Such inferential habitat modelling techniques based on tracking data have been widely used in the marine realm, where direct survey data often remains difficult to collect (Scales et al., 2017). With tracking data as key source of information about the 'used' environment, habitat models have been developed for a wide variety of species, including seabirds (Wakefield et al., 2017), pinnipeds (Arthur et al., 2017), sea turtles (Fujisaki et al., 2020), and sharks (Wells et al., 2018). A key output of such models is a prediction of habitat suitability beyond the observed locations of use, which has been applied to questions of niche segregation between and among species, and to inform spatial conservation and management planning (Scales et al., 2017; Wakefield et al., 2017).

2.4.3 Navigation

A major focus of inquiry regarding animal movement is how they navigate, or, in other words, how animals manage to chart a path to known (or unknown) destinations. Historically, studies of navigation were largely limited to captive animals, enabling close monitoring of their decision-making under experimental conditions (Åkesson et al., 2014). With tracking data, studies on what strategies and cues wild animals use to determine their travel directions and timings have proliferated. A central question is whether animal navigators use 'true navigation', i.e., a mental map and compass allowing for re-orientation *en route*, simple 'compass orientation', which only involves holding constant headings for set periods of time or distance, or something in between (Mouritsen, 2018).

Since the first successful satellite tracking of a migrating sea turtle in 1979, dozens of tracking studies have been performed on wild turtles investigating their mechanisms of orientation and navigation (Daniel, 1980; Lohmann et al., 2008). Many advances have been made, in part due to our ability to record the movement decisions of turtles in their natural environment. The environmental cues turtles use to orient themselves towards their foraging grounds or nesting beach have been tested extensively via displacement experiments, whereby animals are re-located and tracked as they navigate back to a known goal-area (Mouritsen, 2018). Displacement studies have found support for a number of orientation mechanisms in turtles, including natal imprinting of magnetic field properties (Luschi et al., 2007), olfactory signals driven by oceanic and wind currents (i.e., 'beaconing') (Åkesson et al., 2003), sunrise azimuth (Shimada et al., 2016), and landmarks (i.e., 'piloting') (Luschi et al., 2020). Recent work tracking Green Turtles (*Chelonia mydas*) indicates that the oceanic migrations made to reach foraging grounds after nesting are achievable using, in part, compass orientation rules (i.e., vector navigation) (Cerritelli et al., 2019, 2021; Hays et al., 2020). Therefore, the question as to whether turtles use 'true navigation' or not remains an open one.

In seabirds, homing movements to breeding sites are the most well-studied aspect of navigation, with tracking studies having been conducted on both displaced and free-ranging birds. A study by Padget et al. (2017) found that when the olfactory sense of free-foraging Scopoli's Shearwaters (*Calonectris diomedea*) was experimentally disturbed, the birds followed the coast more and wandered further astray during return flights to the colony compared to control and magnetically disturbed birds. This indicates that when available, visual landmarks close to home will be used, but that olfaction plays an important role in open sea orientation in this species. Olfaction has also been implicated as an important cue for finding food at sea, with tracking studies on Wandering Albatross, Cory's Shearwater and Scopoli's Shearwater finding patterns of foraging search consistent with the use of olfactory plumes produced by prey (Dell'Ariccia et al., 2014; Nevitt et al., 2008). Further, a displacement study by Padget et al. (2018) found that Manx Shearwaters (*Puffinus puffinus*) which had been experimentally exposed to shifted daylight hours behaved as if using the sun as a compass when orienting towards the breeding colony from the open sea.

Although many of the underlying bases of animal navigation remain a mystery, what has become clear is that animals utilize multiple mechanisms to reach their destinations, starting with a large-scale phase (e.g., geomagnetic compass), then a homing phase (e.g., combination of compass orientation and/or map cues, like landmarks or olfactory gradients), and finally a 'pin-pointing' phase to reach the destination (e.g., specific visual or olfactory cues, like a nest-burrow smell) (Mouritsen, 2018). The plethora of experimental and observational studies using tracking data to investigate questions of animal navigation has provided many answers but also opened up many new lines of inquiry (Guilford et al., 2011).

2.5 FUTURE DIRECTIONS

2.5.1 Equalizing tracking effort

The tracking of marine species has historically been biased towards large-bodied species and to richer, higher latitude, regions of the world, which means that our current perception of the diversity of migration, foraging, and navigation behavior in the marine realm is not comprehensive (Bernard et al., 2021; Wikelski et al., 2007). Therefore, a key advance in the coming decade will be the continued description of behaviors across un-tracked species and populations.

In a similar manner, early life cohorts have been tracked less than reproductive adults, due in part to complications related either to the need to re-capture individuals to recover data or to welfare concerns regarding the impact of devices on less robust and growing juveniles (Hays et al., 2016). Nevertheless, in order to unravel the roles of memory and learning on navigation, migration and foraging, understanding how naïve individuals behave relative to reproductive adults is essential. Fortunately, tracking devices are continually becoming smaller and lighter, and handling and attachment protocols are becoming increasingly optimized, making it possible to track sub-adult animals and thereby elucidate the ontogeny of movement behavior (see **Device effects** below) (Hazen et al., 2012; Williams et al., 2020). New tracking techniques are also under development, such as battery-less devices, which hold promise for tracking the movements of animals currently unknown to science (Ghaffarivardavagh et al. 2020).

2.5.2 Multi-sensor tracking

Although the spatio-temporal information provided by tracking devices has proved revolutionary to our understanding of natural behavior variation in marine megafauna, both the proximate mechanisms and ultimate explanation of many behaviors remain a mystery (Hays et al., 2016). The miniaturization of electronic devices has not proceed only for geolocation technology, but also to many other forms of biologging (Ropert-Coudert & Wilson, 2005). Through the remote measurement of body (or body-part) acceleration, physiological states (e.g., stomach temperature, heart rate), and camera footage, the biological and environmental context of tracking positions can be recorded. This allows for the estimation of energetic costs (and benefits) of particular movement decisions (Cooke et al., 2004). For example, using a combination of satellite tracking devices, depth recorders, mandible accelerometers, and video cameras, Adachi et al. (2021) showed that in order for female Northern Elephant seals to physiologically be able to forage on small mesopelagic fish, and thereby avoid predator-filled coastal habitats, they needed to spend 80-100% of their time foraging. In cases where the weight and size of additional loggers are still too great, models of physiological performance can be used. Estimates of field metabolic rates are now widely available for seabirds (R. E. Dunn et al., 2018), which can be combined with tracking data to inform models of population-level resource requirements and thereby the sensitivity of ecosystems to perturbation (e.g., via anthropogenic activities) (Cury et al., 2011).

2.5.3 Large-scale collaboration

An increasing trend in the world of animal tracking is for researchers to compile tracking data across international teams to address questions on a large scale. Recent such collaborations have provided novel insight into ecological trait variation across the distribution of single species (Frederiksen et al., 2012, 2016) and many species (Bonnet-Lebrun et al., 2021). This is an encouraging trend, as many questions regarding meta-population and community-level effects are best addressed at regional or global scales, such as how marine communities will respond to climate change (Hazen et al., 2013). Further, large-scale analyses can identify commonalities in the movements of widely differentiated species which may go undetected by single taxa studies (Brodie et al., 2018; Sequeira et al., 2018).

2.5.4 Device effects

As long as biologging devices have been used to monitor wild animals, negative effects resulting from handling or carrying devices have been reported (Gessaman & Nagy, 1988). This led to the widespread adoption of the so-called “3% rule”, which posits that three percent of the bodyweight of the study subject be the limit for device weight (Vandenabeele et al., 2012). However, recent work has shown that this simplistic rule ignores important aspects of how devices can cause discomfort and thereby alter behavior, such as via sub-optimal placement (Vandenabeele et al., 2014), lack of streamlining (Kay et al., 2019), and gravitational forces related to movement (R. P. Wilson et al., 2021). As the miniaturization of devices continues to advance, the potential for tracking ever-smaller species grows, making it more important than ever to consider how device design and attachment can be optimized to reduce deleterious effects (Holton et al., 2021; Ripperger et al., 2020; Wikelski et al., 2007). Using standard, informed metrics to monitor the behavioral and physiological responses of animals to handling and device-attachment can improve the assessments of the impact of biologging procedures (R. P. Wilson et al., 2018). With an enhanced understanding of device impacts, researchers and welfare committees alike will be better able to weigh the costs of attaching devices to wild animals against the benefits in terms of knowledge gain.

2.6 CONCLUDING REMARKS

Although animal tracking is but a subset of biologging, it is nonetheless an extensive field, with hundreds of papers published yearly on marine systems alone (Wilmers et al., 2015). Therefore, the summary I provide here of the literature on animal tracking and its contribution to animal behavior research is by no means comprehensive. Nevertheless, by exploring a variety of recent work across a wide diversity of marine megafauna I argue that animal tracking is providing key insights into central tenets of animal ecology, namely migration, foraging, and navigation. Although animal tracking has been in a ‘golden era’ for fifteen years, it shows no signs of slowing. Indeed, information on the spatiotemporal positions of individual animals will continue to be important for many ends, including monitoring the responses of animal populations to ongoing changes to climatic and seascape conditions, or to human activities at sea, such as fishing and energy production. Although tracking technologies have become an essential part of the toolkit of marine biologists, caution and consideration is required to ensure that a balance is struck between animal wellbeing and knowledge gain.

CHAPTER 3

TRACK2KBA: AN R PACKAGE FOR IDENTIFYING IMPORTANT SITES FOR BIODIVERSITY FROM TRACKING DATA

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3.1 ABSTRACT

Identifying important sites for biodiversity is vital for conservation and management. However, there is a lack of accessible, easily-applied tools that enable practitioners to delineate important sites for highly mobile species using established criteria. We introduce the R package ‘track2KBA’, a tool to identify important sites at the population level using tracking data from individual animals based on three key steps: (1) identifying individual core areas, (2) assessing population-level representativeness of the sample, and (3) quantifying spatial overlap among individuals and scaling up to the population. We describe package functionality and exemplify its application using tracking data from three taxa in contrasting environments: a seal, a marine turtle, and a migratory land bird. This tool facilitates the delineation of sites of ecological relevance for diverse taxa and provides output useful for assessing their importance to a population or species, as in the Key Biodiversity Area (KBA) Standard. As such, ‘track2KBA’ can contribute directly to conservation planning at global and regional levels.

3.2 INTRODUCTION

Site-based conservation is a key strategy for protecting biodiversity worldwide (Watson et al., 2014). However, to be effective, sites designated for protection must represent ecologically meaningful processes. Amid the rush to meet protected area coverage targets, there is a risk that governments protect spaces opportunistically where there are few competing interests, rather than where biodiversity is concentrated and at risk (Venter et al., 2018). Avoiding this scenario requires practical and accessible tools be made available to process ecological data for conservation planning.

One method for assessing the importance of a site for biodiversity is to use systematic criteria, such as those of the Key Biodiversity Area (KBA) Standard (IUCN, 2016). Under such criteria, ecological data are used to assess whether a site contributes significantly to the persistence of biodiversity, which is useful for conservation planning and the design and evaluation of protected areas networks (Boucher et al., 2014). However, delineating ecologically relevant boundaries for sites that can be assessed against such criteria remains challenging, particularly for highly mobile species in habitats that are spatially dynamic or otherwise hard to map directly. Although there are many tools available to analyze tracking data (Joo et al., 2020), bespoke tools that enable the use of tracking data to identify important sites for biodiversity are lacking.

We introduce the R package ‘track2KBA’, a tool for analyzing tracking data and deriving ecological information useful for (1) delineating important sites for local animal populations, and (2) assessing the importance of these sites against quantitative criteria of importance for regional or global biodiversity, such as the KBA Standard. The approach underlying ‘track2KBA’ was originally developed to identify marine Important Bird and Biodiversity Areas (mIBAs) for seabirds (B. G. Lascelles et al., 2016). Here, we exemplify applications of the method in three different taxa and environments: 1) Antarctic fur seals (*Arctocephalus gazella*) during the breeding season in the South Atlantic; 2) green sea turtles (*Chelonia mydas*) during the post-nesting period off the coast of West Africa, and 3) white storks (*Ciconia ciconia*) during migration between the breeding grounds in southern Europe and the wintering grounds in sub-Saharan Africa.

3.3 METHODS

3.3.1 Package overview

The R package ‘track2KBA’, based on the approach of Lascelles et al. 2016, has three key steps: (1) estimating individual core areas, (2) assessing sample representativeness, and (3) quantifying spatial overlap among individuals and scaling up to the population level. Four functions perform these key steps, and nine accessory functions are available for processing tracking data and plotting (Fig. 3.1, Table S1). See Supplementary Information S1 for a detailed description of the package workflow.

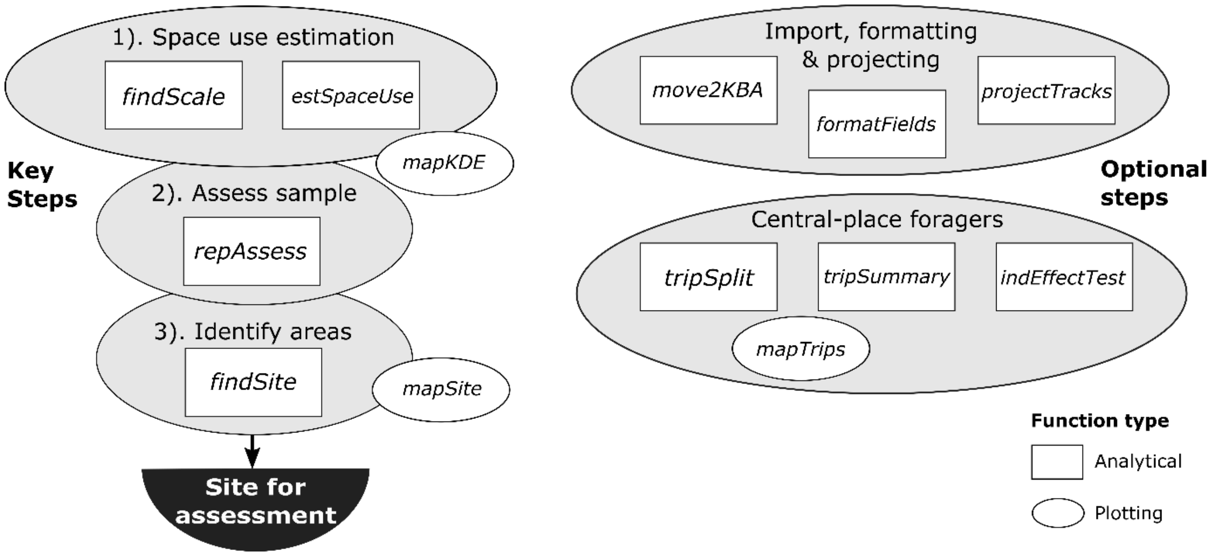

Fig. 3.1 Overview of ‘track2KBA’ R package workflow for identifying important areas from tracking data. ‘Key steps’ are the essential functions for identifying and delineating areas of importance for biodiversity while ‘Optional steps’ are case-dependent.

3.3.2 Identify individual core areas

In ‘track2KBA’, the space used during each independent tracking event is calculated using kernel density estimation (KDE). KDE is a non-parametric technique for deriving a probability surface, known as the utilization distribution (UD), from point data. When the input are animal locations regularly spaced in time, the UD represents the probability of an animal occurring in space (Worton, 1989). KDE was selected as the method to estimate space use given its accessibility and familiarity to a wide range of users, which facilitates the description and communication of the method to non-scientists, e.g., at policy fora (B. G. Lascelles et al., 2016).

UDs for several independent tracks can be derived using the function estSpaceUse. KDE requires the setting of a smoothing parameter (*h*, or ‘scale’ in package documentation) that affects kernel width and the resulting spatial estimate (Gitzen et al., 2006; see Supplementary Information S1B for details). When determining important sites for biodiversity, it is important that the results are not under- or over-smoothed, and that the *h* value reflects both the resolution of the available data (i.e., larger *h* for coarser data) and the ecology of the study species (B. G. Lascelles et al., 2016). The function findScale calculates several candidate *h* values, allowing the user to select the most appropriate for the study organism and objective (Supplementary Information S1B); for central-place foragers, the functions tripSplit and tripSummary may be used to derive metrics to facilitate comparison between candidate *h* values. Once an *h* value is selected, it is important to consider 1) the resolution of the spatial grid used for KDE and 2) the probability quantile that reflects the core areas of the track (‘UDLev’); 50% is a standard choice, but in some cases other values may be more appropriate (Dias et al., 2018).

3.3.3 Assess sample representativeness

Whether a tracking dataset is representative of the distribution of the source population is fundamental to identifying areas of importance for population persistence (B. G. Lascelles et al., 2016). Therefore, a vital step in the ‘track2KBA’ workflow is to assess the degree of representativeness of the tracked sample using the repAssess function (Supplementary Information S1C). repAssess iteratively selects sub-samples of individual tracks, averages them into a pooled UD and outlines a desired quantile (e.g., 50%), and then calculates the proportion of out-of-sample tracking locations within the resulting area (i.e., ‘inclusion rate’). A non-linear least squares regression is fitted to the relationship between sample size and inclusion rate to project this rate until its asymptote (i.e., the sample size which fully represents the source population distribution) and calculate the degree to which the tracked sample represents the space use of the wider population. The inclusion rate at the maximum sample size should approximate the specified UD quantile when the tracked sample is fully representative (Supplementary Information S1C). repAssess returns the percent representativeness, the estimated asymptote, and estimates of the sample sizes needed to achieve 70% and 95% representativeness.

3.3.4 Population-scaling and site delineation

The final step in the ‘track2KBA’ workflow is to delineate areas used by a substantial portion of the population, and produce quantitative information of site importance (Supplementary Information S1D). To delineate a candidate site, the function findSite calculates the proportion of individual core areas overlapping each grid cell and multiplies this by the proportional representativeness of the tracked sample. The result is a scaled estimate of the proportion of the source population that predictably uses each grid cell in the study region in the season of interest (Fig. S3.2). Potential important sites are then delineated by grouping together grid cells used by a threshold percentage of the source population (Fig. S3.2, Supplementary Information S1D). If the size of the source population is known or estimated, findSite multiplies the estimated proportion of the population using each grid cell by the population size to estimate the number of animals predictably using the candidate site; this is useful for assessing sites against standardized criteria, such as the KBA Standard (IUCN, 2016).

3.4 EXAMPLE APPLICATIONS

We analyze data from three species to illustrate how ‘track2KBA’ can be used to identify important sites for populations of mobile animals. We emphasize that sites identified here are illustrative examples, not proposed sites for conservation. See Supplementary Information S2 for a walk-through with code and Supplementary Information S3 for further details.

3.4.1 Antarctic fur seals

Using tracking data from Antarctic fur seals from Bird Island, South Georgia we illustrate a typical workflow for deriving important sites for a population and their preliminary assessment against global KBA criteria. An estimated 64,545 female seals breed at Bird Island (I. Boyd, 1993), amounting to 8% of the global adult population. Using data from 117 females tracked during the breeding season, we identify important at-sea sites for this population and assess whether they might meet global KBA criteria (i.e., areas used predictably by ≥ 1% of global population under ‘Demographic aggregations’ Criterion D1a; IUCN, 2016).

During the breeding season, female fur seals forage at sea and regularly return to suckle their pups on land. Using the function tripSplit, we split the tracking data into foraging trips, defines as periods of ≥ 12 h away from the colony at a distance of ≥ 5 km (Fig. 3.2A), and filtered out points falling within this radius (argument ‘rmNonTrip’). We then calculated trip characteristics using the function tripSummary, which showed that seals travelled a mean maximum distance of 114 km (max 296 km) and spent a median of 5.6 days (max 19.8 days) at sea per foraging trip. Next, we projected the tracks to a custom-centered equal-area projection with the function projectTracks, and estimated core areas (i.e., 50% UDs) for each individual seal using the function estSpaceUse with an *h* parameter value of 4.65 km (Fig. 2B). The *h* value was calculated using the function findScale and represents the log of the median foraging range (in km); this value was selected as it captured areas representing ecologically realistic estimates of the space in which individuals spent most of their time at sea (Fig. S3.1B). Using repAssess, we estimated the representativeness of this tracked sample for the distribution of the wider Bird Island population, obtaining a value of 96% (Fig. 3.2C).

Next, we provided the individual core areas, the representativeness estimate, and the population size estimate as input to the function findSite and delineated sites used by at least 10% of the population (i.e., the default threshold when representativeness > 90%; Fig. 3.2D, Fig. S3.2). We identified an area of 1,576 km^2 to the north-west of South Georgia used by up to 23.6% (16,787 seals) of the female population (Fig. 3.3A). This translates to an estimated

1.7-2% of the 700,000-1,000,000 fur seals globally (Hofmeyr, 2016) that predictably use the site during breeding, potentially meeting the criteria for a global KBA under Criterion D1.

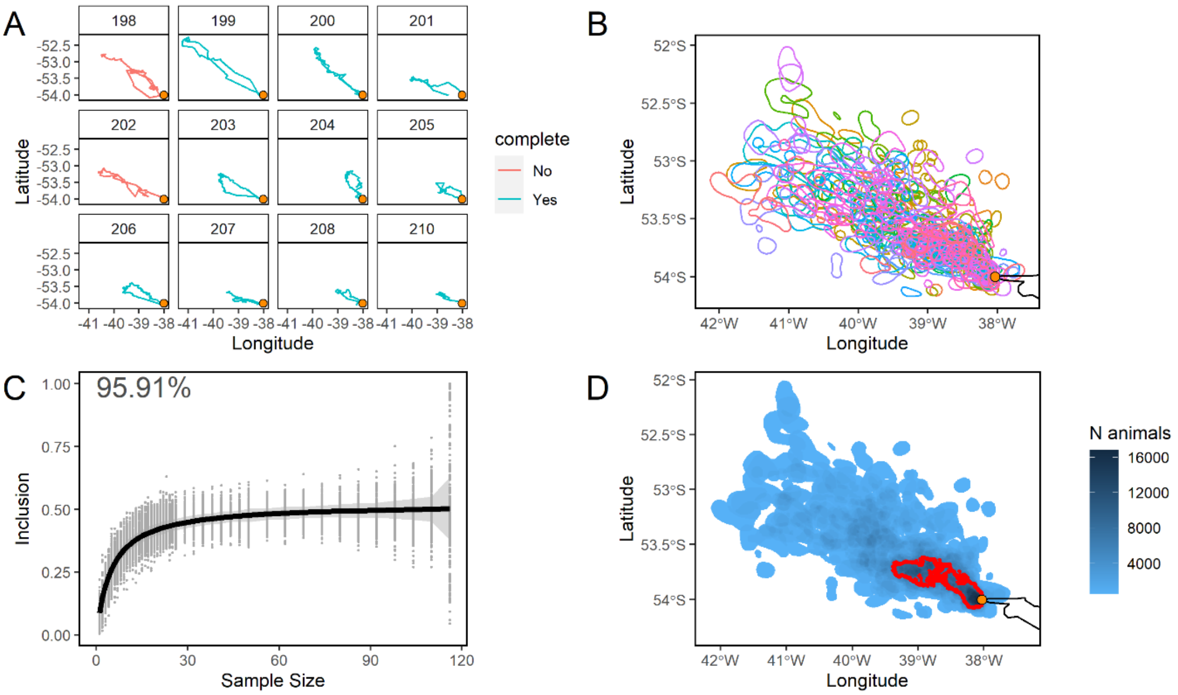

Fig. 3.2 Example 'track2kba' output from a tracking data set of Antarctic fur seals from South Georgia. (A) Using function tripSplit, data from each individual is split into foraging trips. (B) With the estSpaceUse function, the core areas are estimated for each individual, with colors representing individuals. (C) The degree to which the tracked sample (n=117) represents the distribution of the source population is estimated using the repAssess function. The sample was estimated to achieve 96% representativeness. (D) Using the findSite function, a conservative scaling up to the population is made based on the representativeness and the sample-derived pattern of overlap. Areas used by a threshold proportion of the population are delineated; here areas within the red border are used by at least 10% of the local population of fur seals.

3.4.2 Green turtles

To demonstrate the utility of the package for a marine species when not foraging from a central place, we analyzed tracking data from green turtles at Poilão Island in the Bijagós archipelago of Guinea-Bissau. Poilão hosts one of the largest rookeries in the Atlantic (P. Catry et al., 2009), with an estimated laying population of 18,573 females (Supplementary Information 3). After nesting, female green turtles disperse to foraging grounds where they feed and remain resident until the subsequent breeding event (Hamann et al., 2002). We used 'track2KBA' to identify core areas for 23 tracked females and assess the degree to which this sample captures the distribution of the adult female population during the post-nesting foraging period. For each individual, we estimated core areas (50% UD) using an *h* parameter of 2.18 km, which was the median of the reference bandwidth across individuals (Fig. S3.5A) and reflects an ecologically realistic scale for the species when foraging.

Due to the broad area over which turtles disperse in the post-nesting period, and the restricted scale of their movement when foraging, the sample achieved only 32% representativeness and is therefore not considered representative of the population-level distribution. Given the low level of representativeness, no important sites for the source population were delineated. We estimated that 98 turtles would need to be tracked in order to achieve 70% representativeness, a level at which delineating important sites at the population level is more feasible (B. G. Lascelles et al., 2016). Nonetheless, we found overlapping core areas among the tracked individuals, indicating that important sites may be identifiable for this population with further data collection (Fig. 3.3B).

3.4.3 White storks

We used data from the population of white storks in Portugal to exemplify a use-case in a migratory system. Of the 46,027 white storks in Portugal, an estimated 26,196 migrate to sub-Saharan Africa and back each year (see Supplementary Information S3). During migration, white storks often aggregate in large numbers at stopover sites to refuel (Arizaga et al., 2018). We used ‘track2KBA’ to identify important stopover sites for this population on migration to and from sub-Saharan Africa, using the GPS tracks of 76 individuals.

We estimated core areas (50% UD) for each individual using an *h* parameter of 7.5 km, which was determined as the median peak in the variance of the log First-Passage Time across individuals (Fig. S3.7A). This method identifies the spatial scale at which the birds are spending the most time (Fauchald & Tveraa, 2003), which on migration should represent stopover sites. The estimated representativeness of the sample for migratory Portuguese white storks was 96% (Fig. S3.7B).

We delineated nine stopover sites, covering areas of between 19 km^2 and 1,150 km^2 in Spain and Morocco, used by at least 10% of the Portuguese population of migrating white storks. Of these sites, four are predictably used by up to 8,600 (2 sites), 9,600, and 11,580 storks, respectively representing 18.7%, 20.9%, and 25.2% of the total Portuguese population (i.e., migratory and resident birds) of white storks.

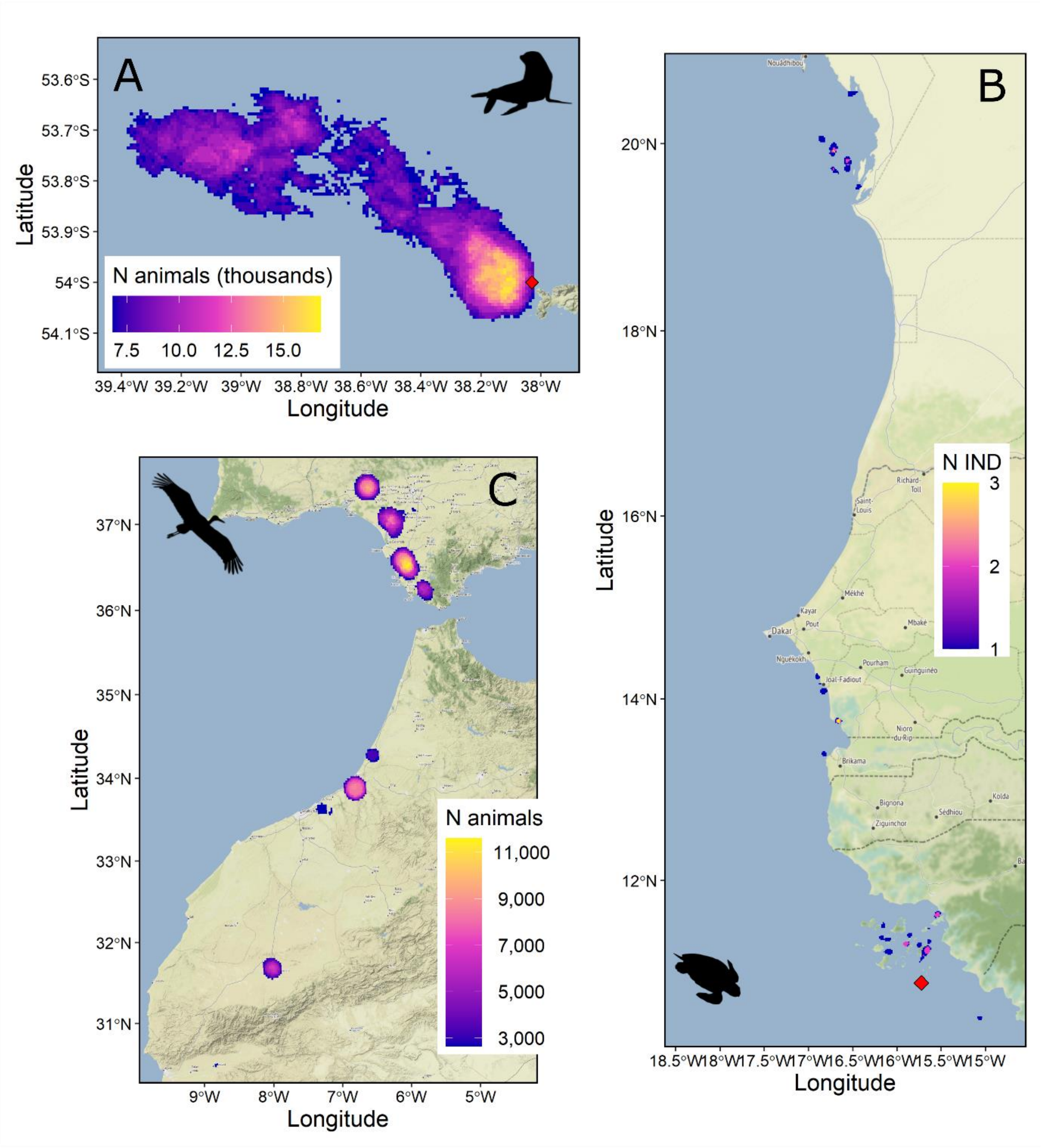

Fig. 3.3 Mapped results of ‘track2KBA’ tracking data analysis. (A) Areas used by at least 10% of the population of female Antarctic fur seals on Bird Island, South Georgia. (B) Areas used by female green turtles during post-nesting foraging in West Africa; areas shown reflect only overlap of the tracked individuals. (C) Stopover-sites used by 10% of white storks which migrate between Portugal and sub-Saharan Africa. Red diamonds signify the breeding colony or nesting beach.

3.5 CONCLUSION

Sites of importance for avian diversity (i.e., mIBAs) have been identified for seabirds across the world using this framework (Dias et al., 2018; B. G. Lascelles et al., 2016). Our example applications illustrate that, given a representative sample of the population-level distribution, this method can be used to identify important sites for species other than seabirds. ‘track2KBA’ facilitates application of the method across other vertebrate taxonomic groups, which could assist expansion of the taxonomic coverage of important areas and ultimately protected-area networks.

For formal assessment of sites against global criteria, as in the KBA Standard, users must consult with the relevant body and additional steps may be required, such as consulting with relevant stakeholders to ensure that site boundaries reflect the management landscape. Users are encouraged to provide feedback about possible extensions to package functionality that may facilitate yet broader implementation of ‘track2KBA’.

CHAPTER 4

QUANTIFYING ANNUAL SPATIAL CONSISTENCY IN BREEDING SEABIRDS: IS ONE YEAR OF TRACKING DATA SUFFICIENT FOR IDENTIFYING IMPORTANT SITES FOR CONSERVATION?

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4.1 ABSTRACT

Understanding the spatial distributions of animal populations is key to informing area-based conservation planning. Animal tracking data have recently afforded many novel insights into patterns of space use in numerous species. An important consideration, however, is how representative of the wider population is the sample of tracked animals. Additionally, it may be important to track animals in different years to capture changes in distribution at the population level in response to varying environmental conditions. Here, we estimate the degree of annual spatial consistency across 23 species of seabirds during the chick-rearing period to assess the relative importance of multi-year sampling for identifying important sites at sea. We found most species showed a similar degree of annual consistency in at-sea distributions, with no obvious relationship to taxonomy, foraging habitat, or latitude. We estimate that, on average, less than 10% of the multi-year core distribution of a population (7.9%; min: 2.6%, max 21.7%) may be outside an important site identified using tracking data from a single year. We show that for all species, the primary concern should be to track at least 10-15 individuals to get a representative estimate of distribution; however, in some cases tracking in several years provides substantial additional information on space use. This work shows that, during the chick-rearing period, most seabirds use very similar areas each year, and that core distributions and Key Biodiversity Areas can be identified from a single year of tracking data.

4.2 INTRODUCTION

The accurate estimation of the spatial distributions of animal populations is important for understanding patterns of resource use and demographic change, as well as for informing biodiversity conservation and management (Hays et al. 2019). The at-sea distribution of many species of marine megafauna have in recent decades been revealed using data derived from animal-borne tracking devices (Bernard et al., 2021; Hussey et al., 2015). To ensure that population-level inference and spatial management implementations are robust, it is vital to consider how representative a tracking dataset is of the movements of the untracked portion of the population across space and time (Shimada et al., 2020).

In the marine realm, tracking data have been used widely to inform conservation and management (Davies et al., 2021; Hays et al., 2019). Population-level spatial distributions derived from tracking data have contributed to assessments of the impacts of threats at sea, such as incidental mortality (bycatch) in fisheries, overfishing, and resource extraction (Clay et al., 2019; Garthe et al., 2017; Grémillet et al., 2016; Queiroz et al., 2019). Sites contributing to the global persistence of species, such as Key Biodiversity Areas (KBAs), can now be identified for an increasing diversity of marine taxa using new tracking data and novel analytical tools (Beal, Oppel, et al., 2021). It is important to consider, however, that if key sites for populations are identified using tracking samples that do not encompass natural variability in space use, the resulting borders may not adequately represent the wider area on which a population depends, potentially increasing exposure to risks outside the designated sites (Lovvorn et al., 2014).

The importance of tracking sufficient individuals to capture a stable picture of population-level space use has recently received considerable attention (Gutowsky et al., 2015; Shimada et al., 2020; Soanes et al., 2013). However, another aspect pertinent to assessing the representativeness of a tracking sample is the potential for a population to change distribution from year to year. A number of studies have investigated the importance of annual (among-year) variability in seabird foraging, and report both minimal and substantial shifts (Cerveira et al., 2020; Fromant et al., 2021; Meier et al., 2015; Osborne et al., 2020). Global standards for identifying important sites for biodiversity, such as the KBA Standard, account for annual variation by setting minimum thresholds for the number of years of distribution data required for the population in order to delineate important sites (three years for KBAs; KBA Standards and Appeals Committee, 2020). However, the relevance of such thresholds for different species and environmental contexts is uncertain. Given the substantial costs involved in tracking animals in remote locations, we need to understand the value of multi-year sampling for identifying stable sites of importance to ensure the optimal investment of limited research funds and effort (Canessa et al., 2015;

Williams et al., 2020). To date, few studies in the marine realm have compared annual consistency in population-level space use in multiple species, limiting our understanding of the relative importance of multi-year sampling for informing conservation planning (Arcos et al., 2012; Carpenter-Kling et al., 2020; Evans et al., 2021).

Here, we analyzed movement tracks from 23 seabird species during the chick-rearing period to investigate the importance of annual variability in space use. First, we quantified the spatial similarity between distributions in different years for each species to estimate the degree of consistency across years, and explored the potential of taxonomy, type of foraging habitat, and latitude for explaining inter-specific variation therein. We then performed iterative re-sampling procedures to further investigate the importance of sampling effects. First, we quantified the degree to which sampling in multiple years can provide a more comprehensive indication of the population distribution compared to a sample of the same size (in terms of the number of individuals tracked) from a single year. For several species with contrasting degrees of spatial consistency, we then simultaneously varied the number of tracks and the number of years per sub-sample to visualize the contribution of each sampling level to the population distribution. By analyzing tracking data from across the taxonomic diversity of seabirds, we provide insights into the general pattern in spatial consistency across years that is relevant for identifying core-use areas and important sites for seabirds at sea.

4.3 METHODS

4.3.1 Study species and data assembly

We compiled Global Positioning System (GPS) tracking data using several selection criteria to ensure comparability across species and sufficient sample sizes to allow for rigorous testing of sampling effects (**Table 4.1**). We only considered datasets if the following criteria were met: at least three years of GPS data from a minimum of 10 birds in each year, where all birds were tracked from the same breeding colony and during the same general breeding stage (i.e., chick-rearing). In total, we collated tracking data from the chick-rearing period for 23 species, representing 7 families and 4 orders of seabirds. For two species, Australasian Gannet (Morus serrator) and Little Penguin (Eudyptula minor), we had sufficient data from two different colonies; for all other species, we analyzed data from a single colony (**Table 4.1**). When producing population distributions (see Population distribution estimation below), we treated each species-colony dataset separately, then used the mean when comparing species-level metrics (e.g., annual overlap).

Table 4.1 Summary of GPS tracking data used in this study to analyze annual consistency in space use of seabirds. ‘*n* years’ indicates the number of years in which tracking data was collected, over a range of years (i.e., ‘Year range’). ‘*n* birds’ refers to the median number of individuals tracked per year and ‘*n* trips’ to the median number of foraging trips recorded per year, with the range shown in parentheses.

Common name	Scientific name	Family	Breeding site	Year range	*n* years	*n* birds	*n* trips
Common Murre	*Uria aalge*	Alcidae	Colonsay, Scotland	2011-2014	3	12 (10 - 16)	35 (21 - 45)
Thick-billed Murre	*Uria lomvia*	Alcidae	Coats Island, Nunavut	2010-2019	5	55 (18 - 55)	136 (45 - 252)
Black-legged Kittiwake	*Rissa tridactyla*	Laridae	Bempton Cliffs, Humberside	2010-2015	4	14 (13 - 16)	34 (22 - 44)
Wandering Albatross	*Diomedea exulans*	Diomedeidae	Bird Island, South Georgia	2002-2019	5	25 (11 - 34)	30 (12 - 40)
Laysan Albatross	*Phoebastria immutabilis*	Diomedeidae	Midway Island, Hawaii	2013-2018	4	11 (10 - 25)	12 (11 - 27)
Black-footed Albatross	*Phoebastria nigripes*	Diomedeidae	Midway Island, Hawaii	2013-2018	3	13 (12 - 23)	13 (13 - 26)
Buller's Albatross	*Thalassarche bulleri*	Diomedeidae	The Snares, New Zealand	2008-2011	4	20 (11 - 23)	20 (11 - 27)
Grey-headed Albatross	*Thalassarche chrysostoma*	Diomedeidae	Bird Island, South Georgia	2009-2020	4	28 (24 - 30)	29 (25 - 33)
Black-browed Albatross	*Thalassarche melanophris*	Diomedeidae	Bird Island, South Georgia	2009-2020	5	27 (24 - 30)	33 (29 - 59)
Cory's Shearwater	*Calonectris borealis*	Procellariidae	Selvagem Grande, Madeira	2009-2018	6	25 (12 - 41)	35 (22 - 89)
Cape Verde Shearwater	*Calonectris edwardsii*	Procellariidae	Raso Islet, Cabo Verde	2015-2019	4	28 (12 - 34)	149 (102 - 160)
Streaked Shearwater	*Calonectris leucomelas*	Procellariidae	Awashima Island, Niigata	2013-2016	4	40 (26 - 42)	211 (129 - 243)
Common Diving-Petrel	*Pelecanoides urinatrix*	Procellariidae	Kanowna Island, Victoria	2017-2020	4	13 (11 - 38)	25 (13 - 76)
Westland Petrel	*Procellaria westlandica*	Procellariidae	Punakaiki, New Zealand	2012-2017	3	14 (12 - 16)	20 (18 - 26)
Little Penguin	*Eudyptula minor*	Spheniscidae	Gabo Island, Victoria	2011-2016	5	28 (20 - 52)	32 (21 - 54)
Little Penguin	*Eudyptula minor*	Spheniscidae	London Bridge, Victoria	2011-2015	5	27 (10 - 43)	34 (11 - 77)
Chinstrap Penguin	*Pygoscelis antarcticus*	Spheniscidae	King George Island, South Shetland	2006-2014	3	18 (11 - 19)	18 (11 - 19)
European Shag	*Gulosus aristotelis*	Phalacrocoracidae	Isle of May, Scotland	2003-2014	6	22 (10 - 33)	198 (22 - 314)
Pelagic Cormorant	*Urile pelagicus*	Phalacrocoracidae	Middleton Island, Alaska	2006-2018	4	20 (14 - 22)	166 (84 - 273)
Northern Gannet	*Morus bassanus*	Sulidae	Bass Rock, Scotland	2015-2019	5	21 (13 - 31)	109 (34 - 139)
Australasian Gannet	*Morus serrator*	Sulidae	Point Danger, Victoria	2012-2018	4	20 (10 - 28)	36 (10 - 56)
Australasian Gannet	*Morus serrator*	Sulidae	Pope's Eye, Victoria	2011-2015	4	19 (14 - 38)	94 (19 - 179)
Masked Booby	*Sula dactylatra*	Sulidae	Dog Island, Anguilla	2014-2016	3	22 (19 - 68)	87 (69 - 137)
Brown Booby	*Sula leucogaster*	Sulidae	Dog Island, Anguilla	2012-2015	4	29 (19 - 41)	127 (67 - 189)
Red-footed Booby	*Sula sula*	Sulidae	Europa Island, Scattered Islands	2003-2013	4	23 (11 - 37)	29 (11 - 116)

Our goal was to analyze the distributions of each species during chick-rearing as this is the time of year when seabirds are most spatially restricted and therefore when area-based management measures can be particularly effective (Oppel et al. 2018); consequently, tracking data collected during chick-rearing are often used to identify priority areas for conservation (Dias et al., 2018; J. Handley et al., 2021; Heerah et al., 2019). Although all datasets were from adults during chick-rearing, the relative timing in terms of the age of the chick (i.e., whether adults were brooding chicks or not) differed in some cases between species (see Table S4.2 for breeding-stage coverage). Nevertheless, for 104 out of 106 annual datasets (98%), tracking was initiated during the early part (i.e., first half) of the chick-rearing period.

4.3.2 Tracking data standardization

We cleaned and filtered tracking datasets for each species and study colony to improve comparability. First, we excluded all duplicate locations, and any that were pre- or post-deployment. Next, we applied speed filters, with thresholds set to include only biologically realistic travel speeds (Table S1). Then, we split tracks from individual birds into discrete foraging trips, using the R package track2KBA (Beal, Oppel, et al., 2021), which we defined as periods of a minimum duration spent outside a spatial buffer around the breeding colony, to ensure GPS locations were excluded from periods spent resting on land or rafting just by the colony. We set the radius of colony buffers for each species by considering the scale of foraging trips (Table S1). To further standardize comparisons and reduce the effect of prolonged tracking of some species and not others, we only analyzed data from trips initiated within the first 2 weeks of device deployment for each individual bird.

Tracking data were originally collected at varying sampling intervals (Fig. S4.1), so we regularized data to a 10 min interval for most species using linear interpolation, to improve comparability. Although many datasets were of a higher temporal resolution, we used a standard 10 min interval to ensure that no dataset had a ratio of interpolated to raw points higher than 2:1. The exceptions were European Shag (Gulosus aristotelis) and Pelagic Cormorant (Urile pelagicus), for which interpolation to 10 min would result in too few location estimates (< 10) for kernel density estimation for more than 5% of foraging trips; hence to avoid losing information from short trips, we instead interpolated data for these species to 5 min intervals. Interpolation was performed using the R package adehabitatLT (Calenge, 2006).

4.3.3 Population distribution estimation

To estimate space use, we used kernel density estimation (KDE) to derive utilization distributions (UD) for each foraging trip, a method often used when analyzing tracking data to inform conservation (Beal, Oppel, et al., 2021; B. G. Lascelles et al., 2016; Soanes et al., 2016). Determining an appropriate smoothing parameter, or bandwidth, is an important step in KDE, as it determines the scale at which the data points are smoothed. When comparing species that move at similar scales, authors often recommend using the same parameter value, to avoid introducing differences that would be an artifact of the parameter values alone (Carneiro et al., 2020). However, the movement scales of the species in this study ranged from <5 km to >700 km in terms of maximum range from the colony. Therefore, applying a standard smoothing value across species would either over-smooth data at a scale larger than the maximum range, or under-smooth the data and result in no overlapping use-areas. To achieve a similar degree of smoothing for each species, and thereby make overlap estimates comparable, we calculated the reference smoothing parameter (href), which reflects the number of positions and their spatial variance in the X and Y directions and is a typical smoother used for identifying important sites for biodiversity (Beal, Oppel, et al., 2021). We then fitted a second-order polynomial function between smoothing value and species rank, ordered by foraging range (calculated as the median of the maximum range for each foraging track). Next, for species whose *href* values deviated more than 5 km from the value predicted by the model, the prediction was used instead of the actual values to set the smoothing parameter systematically, i.e., related to the movement range of each species (Fig. S2). To assess whether the parameter selection process imposed a pattern on the results, we visually inspected estimates of among-year consistency against smoothing-parameter values for each species and identified no apparent relationship (Fig S3).

For each species and colony, we produced annual population distributions by averaging together, with equal weighting, the trip UDs from all birds tracked in each year. If multiple trips were available for each individual, we randomly selected a single trip UD per individual and year. This process was re-iterated in each analysis to maximize usage of available information while accounting for potential pseudoreplication (see Overlap analyses for details; Lascelles et al., 2016). We then generated multi-year reference distributions (hereafter the ‘reference distribution’) for each species by averaging together the distributions from single years. We averaged across single-year distributions, rather than estimate utilization distributions from the collated multi-year dataset to avoid years with higher sample sizes contributing disproportionately to the shape of the reference distribution (**Fig. 4.1**).

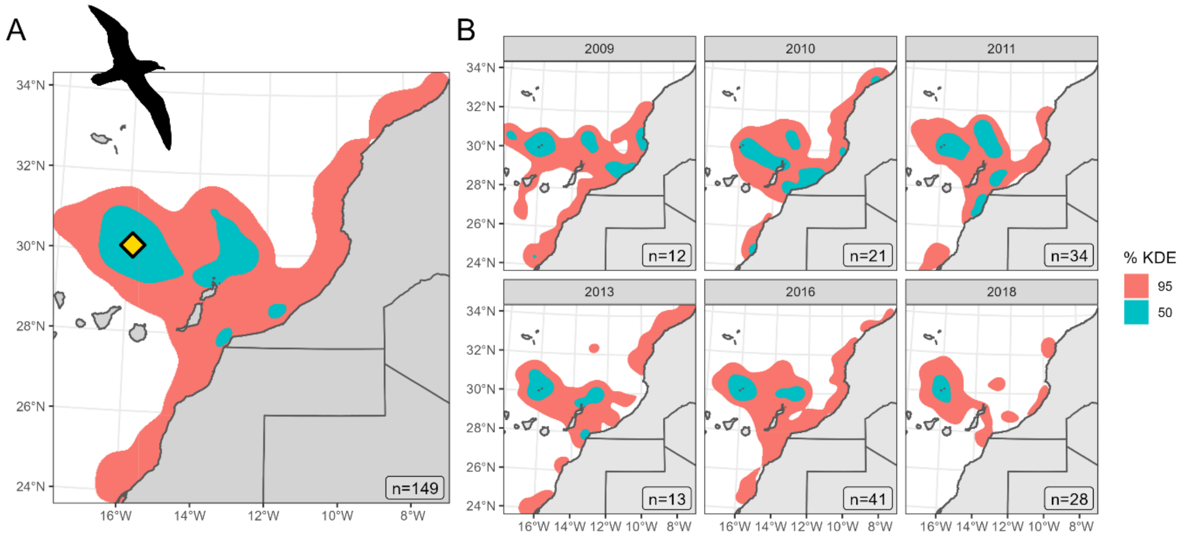

Fig. 4.1 Utilization distributions (UDs; % kernel density estimations) of Cory's Shearwaters from Selvagem Grande Island, Portugal (yellow diamond) tracked during the chick-rearing period in different years, (A) all years combined, and (B) years separate. The multi-year reference distribution (A) is the average of the single-year UDs, based on a single trip from each bird regardless of deployment durations. Each single-year distribution is the average of the UDs of individual birds. Values in the bottom left-hand corner represent the number of birds tracked in each case. This visualization represents one iteration of the re-sampling process used to avoid pseudoreplication while maximizing use of available data.

4.3.4 Overlap analyses

Annual consistency

To estimate the degree of annual consistency in space use for each species, we calculated the spatial overlap between all pairwise combinations of single-year distributions. Overlap was calculated using the Bhattacharyya's Affinity (BA) and Volume of Intersection (VI) indices, which provide probabilistic measures of UD similarity (Fieberg & Kochanny, 2005). We report the BA index for the main analysis, and used the VI results to test the sensitivity of the absolute estimate of consistency for each species, and the relative differences between species to the index type.

To make full use of each dataset, the trip UDs contributing to each single-year distribution were randomly re-sampled across 100 iterations and pairwise annual overlap calculated, which ensured that all trips by a given individual were included in the simulation, but only a single trip per individual for each iteration. For datasets with fewer than 50 possible trip UD combinations, the number of iterations was capped and unique sets of UDs were ensured in each iteration (e.g., with only 1 trip per bird, only 1 iteration was run). We then calculated the mean annual overlap across all iterations, and visualized overlap against several factors potentially related to inter-specific differences in spatial consistency: taxonomic family, foraging habitat, and foraging latitude (based on the mean of all at-sea locations). Based on visual inspection of the spatial distribution of foraging trips in relation to bathymetry, we classified the predominant foraging habitat of each population as either 'shelf', 'oceanic' or 'mixed' (see Supplement for details and Table S4.1 for classification).

Single-year vs. multi-year sampling

To test whether sampling across years provides more robust estimates of population distributions than sampling in a single year, we compared the spatial coverage of multi-year reference distributions with samples of equal size drawn from varying numbers of years. We randomly sub-sampled *n* trip UDs from one, two, or three years, and averaged them to form a sample distribution. The number *n* was determined by the smallest sample size in any given year (*m*) for that species and population, and was set at *m*-2 to cover the possible combinations for all datasets (i.e., if the smallest year-sample was $m = 10$, then $n = 8$ tracks were used). We then calculated the percentage of the respective UD areas of the reference distribution that was covered by the 50% and 95% sample UDs. In this case, we calculated simple spatial overlap instead of probability indices to ensure the effect sizes were interpretable in terms of area (rather than probability). Distributions were generated and overlap calculated over 100 iterations, wherein trip UDs were randomly re-sampled at each iteration.

Next, we tested whether the percent coverage of the reference distribution differed between samples drawn from one year, compared with samples from two or three years using ANOVAs. We report the model effect size (i.e., difference in the percentage of the reference distribution covered) for species-years, which represents the potential spatial information gained by spreading sampling effort across multiple years.

Number of tracks vs. number of years

The importance of tracking enough birds to gain a representative picture of the population-level distribution is well recognized (Thaxter et al., 2017). Here, we simultaneously varied the sample size (i.e., number of birds tracked) and the number of years from which the sample was collected to illustrate the relative importance of each sampling level. We used the same procedure as in *Single-year vs. multi-year sampling* to calculate percentage overlap between sample and reference distributions, and iterated the process 100 times at each sample size to include different trip UD combinations. We visualized this relationship for each species to provide guidance on the value of information gained by tracking birds for several years compared to tracking more birds in a single year.

We present three examples from species which showed contrasting degrees of consistency and provide the results for the other species in the Supplement.

4.4 RESULTS

4.4.1 Annual consistency

Estimates of annual consistency as measured by BA overlap among single-year distributions were high, ranging from a grand mean of 0.56 (SD 0.27) for Common Diving Petrel (Pelecanoides urinatrix) to 0.93 (SD 0.02) for Chinstrap Penguin (Pygoscelis antarcticus) (**Fig. 4.2**). Overlap values as calculated using the VI index were lower, ranging from 0.35 (SD 0.22) to 0.74 (SD 0.06) (Fig. S4), although relative differences between species were very similar between the indices, with a significant positive correlation in species ranks as ordered by mean overlap (Spearman rank correlation: S = 60, rho = 0.97, p=<0.001, Fig. S3).

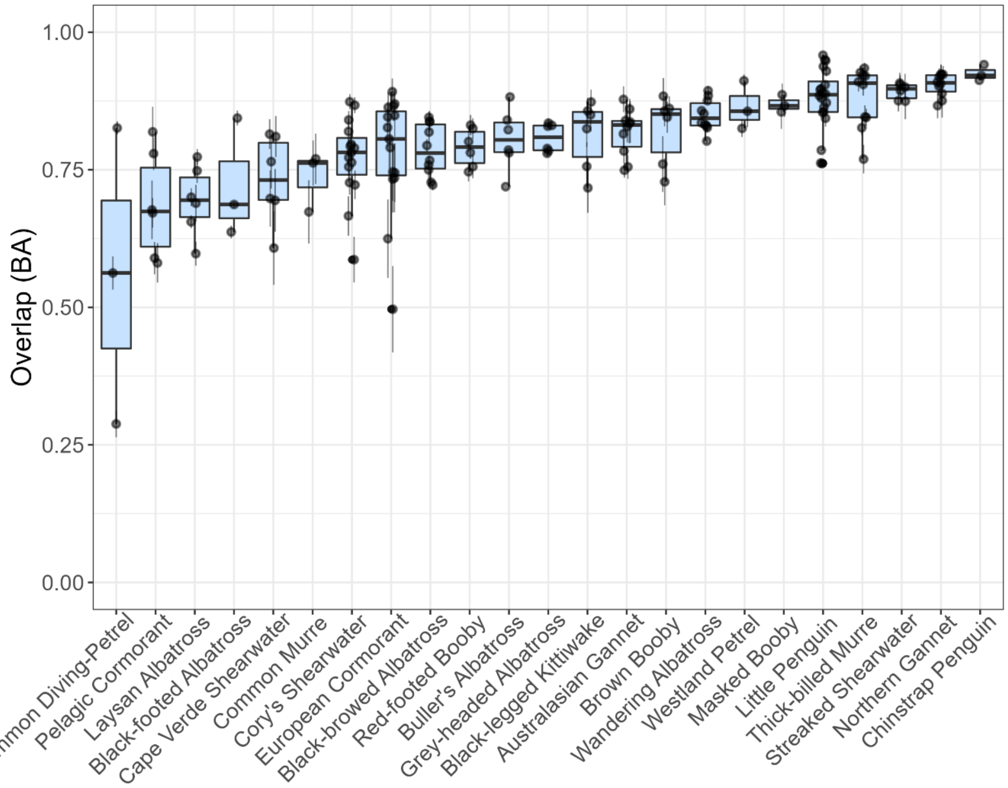

Fig. 4.2 Annual spatial consistency of 23 species of seabirds during the chick-rearing period. Consistency was estimated as the degree of spatial overlap between pairwise combinations of single-year distributions using the Bhattacharyya's Affinity (BA) index. Species were ranked according to their mean level of annual consistency. Boxes represent the distribution of overlaps calculated across all pairwise combinations of years. Dots represent the mean overlap (and lines the standard deviation) calculated across 20 iterations of re-sampling each pairwise comparison, in each of which a single

foraging trip was selected per individual to derive the population distribution for each year. Values for Little Penguin and Australasian Gannet are based on tracking data from two populations.

Despite apparent differences among families in terms of consistency, in general, within-family variation was greater than between-family variation, indicating the main differences were among and within species. There was no obvious sorting of families in terms of consistency in relation to the predominant foraging habitat of the species within each family (**Fig. 4.3**A). Similarly, variation in consistency among species did not appear to be related to foraging latitude (**Fig. 4.3**B).

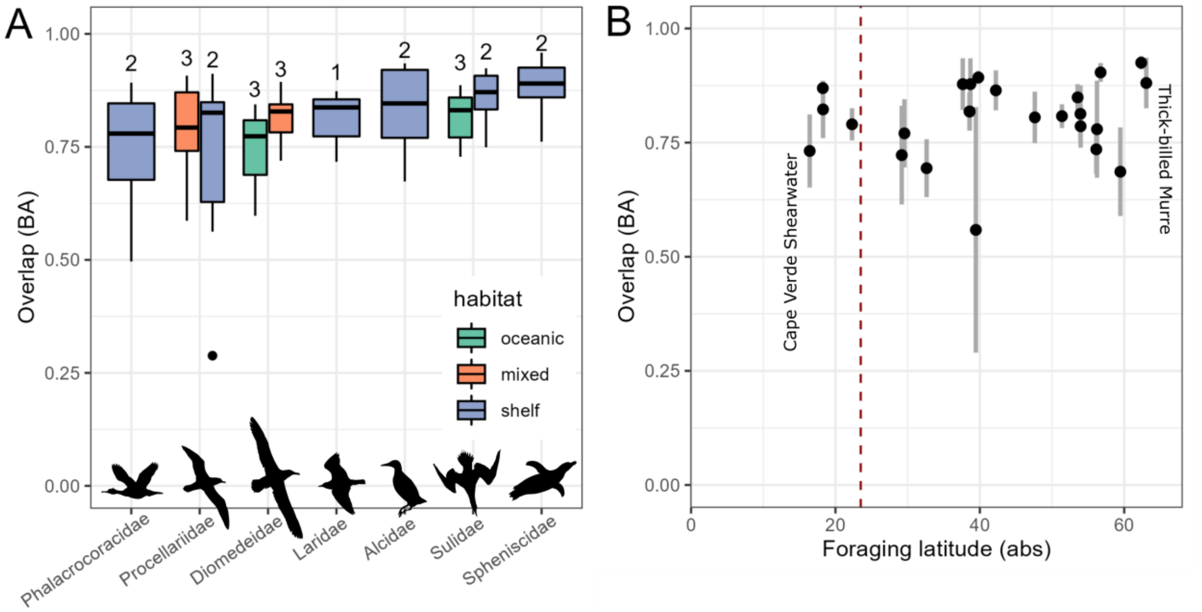

Fig. 4.3 Overlap (Bhattacharyya's Affinity; BA) indices in relation to (A) family and predominant foraging habitat (of the populations in our sample), and (B) mean foraging latitude. Box height in (A) relates to the variation within and between species in each family, with the number of species indicated above the box. In (B), the error bars and the red dashed line signify the standard deviation of consistency across years, and the Tropic parallel (i.e., 23.5°), respectively.

4.4.2 Single-year vs. multi-year sampling

We tested whether distributions derived from samples of the same number of individuals drawn from a single year or multiple years differed in the per cent coverage of the multi-year reference distribution. We found that multi-year sample distributions covered a significantly higher percentage of reference distributions in 17 and 16 species (74% and 70%, n =23 species) for 95% and 50% UD areas, respectively (**Fig. 4.4**). For 95% sample UDs, the mean difference in coverage was 6.3% and ranged from 2.4% in Chinstrap Penguins to 17.7% in Common Diving Petrels, and for 50% sample UDs, the mean difference in coverage was 7.9%, and ranged from 2.6% in Black-footed Albatross to 21.7%

in Common Diving Petrels. Three species, Wandering Albatross (*Diomedea exulans*), Common Murre (*Uria aalge*), and Streaked Shearwater (*Calonectris leucomelas*) showed no significant difference in coverage between single-year and multi-year samples for either 95% or 50% sample UDs, whereas in six other species, Laysan Albatross (Phoebastria immutabilis), Buller's Albatross (*Thalassarche bulleri*), Chinstrap Penguin (*Pygoscelis antarcticus*), Westland Petrel (*Procellaria westlandica*), Masked Booby (*Sula dacytlatra*) and Red-footed Booby (S. sula), there were differences either in the 95% or the 50% sample UDs (**Fig. 4.4**).

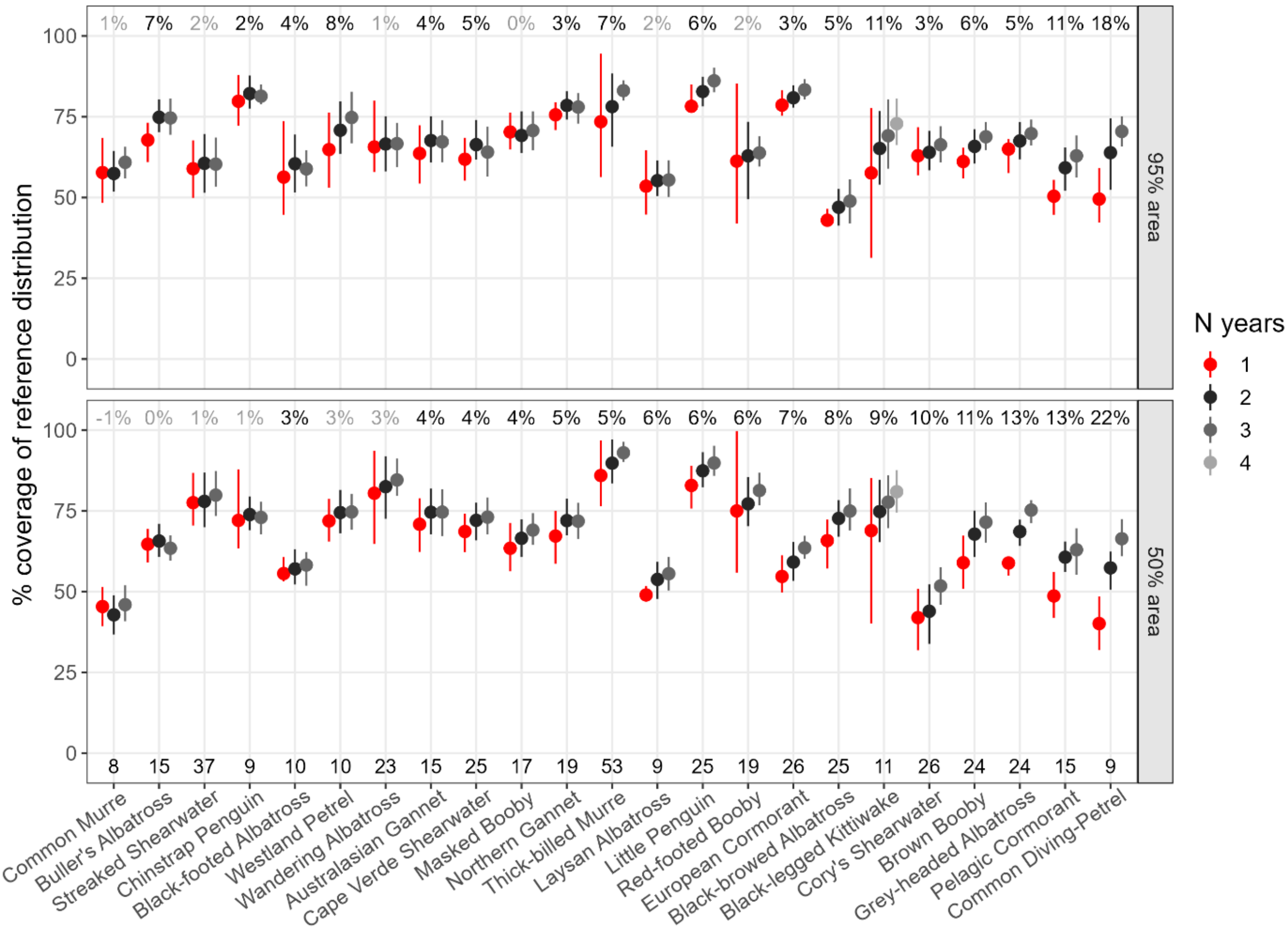

Fig. 4.4 Difference in coverage of multi-year population distributions by sample distributions derived from differing numbers of years. Species were ranked according to the difference in coverage between a multi- and a single-year sample. Panels correspond to the coverage for 95% and 50% utilization distributions. A fixed number of trip utilization distributions, indicated by the number above the x-axis, was re-sampled 20 times. In each run, a sample distribution was derived by averaging trip distributions and then overlapped with a reference distribution based on all years of tracking data. ANOVAs were used to test whether sample distributions from a single year differed in the per cent coverage

compared to samples drawn from multiple years; significant differences are indicated in bold text at the top of each panel where the value indicates the maximum effect size.

4.4.3 Number of tracks vs. number of years

For all 23 species, increasing the number of birds tracked increased the per cent coverage of the multi-year reference distribution. Increasing the number of years in which the population was tracked varied in importance, adding spatial information in some species (in addition to that gained by tracking more birds), but without an obvious gain in others (Fig. S5-S25). For many species, the apparent relationship between sample size and per cent coverage approached an asymptote, indicating that the maximum sample size captured a large portion of the population-level spatial distribution. This is visualized for three species with varying degrees of consistency to show the value of information gained by sampling multiple years: Common Diving Petrel, Grey-headed Albatross (*T. chrysostoma*), and Northern Gannet (*M. bassanus*) (**Fig. 4.5**). As suggested by the estimates of average consistency of overlap between years (**Fig. 4.2**), the relative importance of sampling across years differed among species, with the benefit of multi-year samples most apparent for Common Diving Petrels, and negligible for Northern Gannets (**Fig. 4.5**).

4.5 DISCUSSION

We used tracking data collected in multiple years to estimate the spatial consistency of 23 seabird species of 7 families during the chick-rearing period, and assess its value for identifying important sites at the population level. Most species showed a similar degree of consistency in their distributions, and the differences did not appear to be explained by taxonomy, foraging habitat, or latitude. Although tracking in multiple years provided more robust estimates of spatial distributions of some populations, in many cases, it was sufficient to track a large sample in a single year to provide a similar level of information. These conclusions are highly relevant for project managers planning the allocation of limited research funds to estimating seabird distributions to inform their conservation, and to conservationists involved in the development and implementation of standardized criteria for identification of important sites at sea.

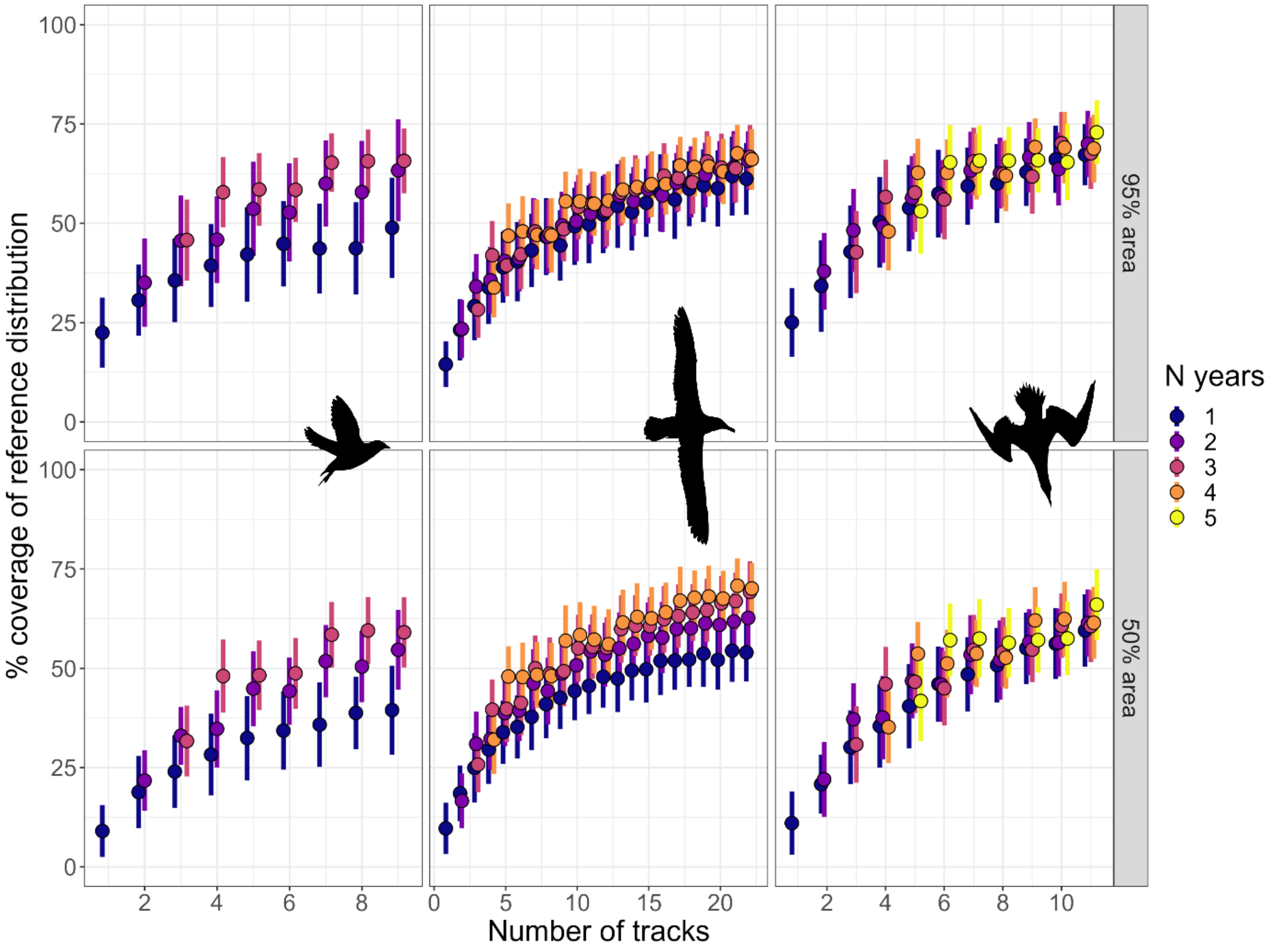

Fig. 4.5 Sampling effects on estimation of population-level distributions for three species of seabirds (left to right: Common Diving-Petrel, Grey-headed Albatross, Northern Gannet). By re-sampling the number of tracks (i.e., one per bird) and the number of years from which tracks were selected, the functional relationship between sample size and annual sampling was estimated for each species. The process of re-sampling tracks was iterated 100 times, and in each iteration the percentage to which the 95% (top row) and 50% (bottom row) probability areas of the resulting sample distribution covered the same quantile areas of a multi-year reference distribution was calculated. Reference distributions were the average of all single-year distributions for each species. Points signify the mean spatial coverage across iterations, and bars denote the standard deviation.

4.5.1 Is it sufficient to track seabirds in a single year?

For the majority of species in our study, tracking in two or three years provided significant increases in the spatial coverage of areas used by the population, suggesting that multi-year tracking efforts are often worthwhile. However, the additional area identified by tracking a population across years, was larger by <5% than those identified using a single year of data in 10 and 12 species out of 23 (as measured by the 50% UD and 95% UD, respectively). We also showed that the number of individuals tracked has a large effect on the estimation of population-level distributions, in accordance with several previous studies (Gutowsky et al., 2015; Soanes et al., 2013; Thaxter et al., 2017). Therefore, even for species or populations with low annual consistency in space use, the primary concern should be to track enough individuals – not necessarily in multiple years - to represent the distribution of the population.

4.5.2 Scale

The spatial distributions of marine species, and their prey, are often affected by climatic cycles, such as the El Niño-Southern Oscillation of the tropical Pacific which operates on a period of 2 to 10 years (Ballance et al., 2006; Philander, 1983). Therefore, it is possible that the timescales over which we had tracking data for our study populations, which ranged from 3 to 6 years, were insufficient to fully capture distributional changes in response to environmental cycles. However, other studies on comparable timescales have identified shifts in space use at the population level in response to oceanographic changes (Evans et al., 2021; Osborne et al., 2020). Indeed, a dataset we analyzed here was used recently to illustrate the effects of a marine heatwave on breeding success and at-sea distributions, explaining the low consistency we report for Common Diving Petrels (Fromant et al., 2021). This case illustrates how tracking over just a few years can provide important information about the areas used during stressful climatic events. In contrast, for Black-legged Kittiwakes, we found small changes in space use across four years for a population in England, over the same period that a population in the Gulf of Alaska largely shifted their distribution to new areas in response to a local heatwave (Osborne et al., 2020). These contrasting patterns within the same species suggest that the spatial consistency of populations may vary more due to local environmental conditions than taxonomy or general foraging behavior.

Spatial scale is a key parameter in analyses of spatial overlap (Winner et al., 2018). We determined the appropriate scales of analysis using a standard approach recommended for identifying important sites for biodiversity, adapted to ensure comparability among species (Beal, Oppel, et al., 2021). For investigations with a focus on ecology or local environmental changes, different analytical scales may be needed to uncover subtle shifts in space use at the population level (Evans et al., 2021; Warwick-Evans et al., 2016). In such cases, long-term monitoring may be needed to identify links between at-sea distribution, environmental conditions, and demographic responses (Ventura et al., 2021). Indeed, as tracking studies begin to extend over decadal time-scales, they are revealing the responses of populations to long term climatic changes (B. Clark et al., 2021; Weimerskirch et al., 2014). However, although such long-term monitoring is clearly desirable, the reality is that research is usually constrained both practically and financially. As such, it is often necessary to implement pragmatic approaches to tracking such as those explored here.

4.5.3 Three-year rule

As area-based management tools are increasingly integrated into global marine conservation policy (De Santo, 2018), the criteria used to designate sites as important for biodiversity are becoming standardized across countries and taxa (e.g., the KBA programme). Our results for seabirds suggest that setting standard thresholds of the number of years of distribution data needed to identify sites may offer little advantage in many cases, particularly where a representative sample of individuals has been tracked in a single year. Given the high expense involved in tracking marine animals in remote locations, the requirement to track a population in three years may be impracticable, and ultimately to the detriment of conservation if important sites might otherwise have been identified from data in a single year. Although standard thresholds (e.g., the KBA ‘three-year rule’) encourage temporal robustness of sites, perhaps more flexible solutions would be preferable to ensure that sites are identified where they are needed, not just in countries where there is funding for long-term studies. For example, instead of strict thresholds, site identification guidelines could incorporate estimates of the representativeness of tracking samples at the population level, or the vulnerability of a site to extreme weather events such as heatwaves (Beal, Oppel, et al., 2021; Shimada et al., 2020).

4.5.4 Recommendations for future studies

We analyzed tracking data from seabirds collected during the chick-rearing phase; therefore, an obvious extension of this work would be to analyze distributions during other phases, including the pre-laying, incubation and non-breeding periods, when the movements of many species are less constrained (R. Phillips et al., 2017). Globally, tracking effort in seabirds is biased towards large-bodied, high latitude species during the breeding season (Bernard et al., 2021; Mott & Clarke, 2018). Therefore, it is also important to include under-studied taxa, such as gadfly petrels (genera Pterodroma and Pseudobulweria), storm petrels, and terns, in future analyses of area and habitat use, and its consistency in seabirds. As more tracking data become available for other species, life-history classes and stages of the annual cycle, it should be possible to apply more robust analyses such as phylogenetically independent contrasts, and to examine ecological drivers, seasonality in movement patterns, and the effects of sex, age, status and other intrinsic factors (Carneiro et al., 2020; Jovani et al., 2016; R. Phillips et al., 2017).

4.6 CONCLUSION

Whether a sample of tracked individuals is representative of the wider population is a fundamental consideration in animal tracking studies and to inform spatial planning. We provide evidence that large samples of tracking data collected in a single year can be sufficient to represent population-level distributions of diverse seabird taxa during chick-rearing over the short term. However, when the space use of a population is suspected to vary, e.g., during extreme climatic events, multi-year samples may help reveal other areas used only if conditions are marginal. These results have relevance for application of tracking data to the identification of robust important sites for the conservation of seabirds, which can be useful in the assessment of space-based threats at sea and protected area designation.

CHAPTER 5

GREEN TURTLES HIGHLIGHT CONNECTIVITY ACROSS A REGIONAL MARINE PROTECTED AREA NETWORK IN WEST AFRICA

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5.1 ABSTRACT

Networks of marine protected areas (MPAs) are invaluable for the protection of species with high dispersal capacity, yet connectivity within networks and the spatial coverage of species distributions are poorly understood. We demonstrate here the connectivity across the regional network of MPAs in West Africa (RAMPAO), mediated by the largest green turtle population in the Eastern Atlantic. We used satellite tracking to unravel the spatial distribution of green turtles nesting in the João Vieira - Poilão MPA, within the Bijagós Archipelago, Guinea-Bissau, throughout internesting, migration, and foraging, and quantified the MPA coverage during each of these critical periods. We found that this population connects at least six RAMPAO MPAs, and calculated that 94.8% (SD 0.1%, range: 46% - 100%) of tracking positions fell within MPA limits during internesting and 72.7% (SD 45.4%, n=28, range: 2% - 100%) during foraging. We identified novel foraging areas for this population and found variable migratory strategies, involving resident turtles foraging at 40-90 km from their breeding site (n=12), movements of 300-400 km to MPAs in The Gambia and Senegal (n=10), and movements of >1000km to an MPA in Mauritania (n=13). Migration corridors with high turtle passage were located along the littoral from the outer Bijagós Archipelago to The Gambia, off the city of Dakar in Senegal, and the littoral of Mauritania south of the Banc d'Arguin, and 21% of these high passage areas fell within the MPA network. Some foraging areas (e.g., in the Bijagós) and important migration areas (e.g., Cap Vert peninsula, Senegal) described here are currently unprotected. These results are therefore relevant to any considerations of MPA extension or establishment within the regional network, which would contribute towards meeting the Convention on Biological Diversity targets for national marine protected area estate coverage. By documenting biological connectivity across RAMPAO, this study represents an important example of the relevance of international protected area networks for green turtle conservation and for wider conservation action at a regional scale.

5.2 INTRODUCTION

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

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

To protect these critical ecosystems and conserve their biodiversity, several MPAs were established in the region, most from the year 2000 onwards (Failler et al., 2020), followed by the creation of a regional network of MPAs in 2007 called RAMPAO (from the French ‘Réseau Régional d'Aires Marines Protégées en Afrique de l'Ouest’). The RAMPAO network extends across seven West African nations: Cabo-Verde, Mauritania, Senegal, The Gambia, Guinea-Bissau, Guinea, and Sierra Leone (https://rampao.org/). Although the existence of migratory species and shared resources were considered in the establishment of RAMPAO, to date, there is scant empirical evidence that the MPA network contributes to the connectivity of any particular animal population (Godley et al., 2010). The green turtle is a marine migratory species of conservation concern, well represented in the region, which hosts a nesting population among the top six worldwide (SWOT, 2011), with over 25,000 clutches laid annually (Patrício et al., 2019). The core-nesting site is Poilão Island, within the João Vieira - Poilão Marine National Park (JVPMNP), an MPA within the RAMPAO, located in the Bijagós Archipelago of Guinea-Bissau (P. Catry et al., 2009; Patrício et al., 2019). A previous study tracked the post-breeding migrations of four green turtles from Poilão Island to the National Park of the Banc d’Arguin in Mauritania (PNBA), also in RAMPAO, *ca.* 1000 km north of Poilão(Godley et al., 2010). This was the first indication of biological connectivity within this network, but sample size was limited, and recent research suggested that this population may migrate to different locations after breeding (Patrício et al., 2019), thus requiring further tracking to elucidate the full seasonal distribution.

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

5.3 METHODS

5.3.1 Satellite Tag Deployment

We equipped 45 nesting green turtles with satellite tracking devices from 2018 to 2020 at the João-Vieira Poilão Marine National Park (JVPMNP, **Fig. 5.1**), in the Bijagós Archipelago, Guinea-Bissau (hereafter “Bijagós”). The park includes four main islands (João Vieira, Cavalos, Meio and Poilão) and an islet (Cabras) where green turtle nesting occurs, with Poilão hosting the great majority of the nests (Patrício et al., 2019). Satellite tags were deployed in Poilão (n=43) and Meio (n=2). The green turtle nesting season at these rookeries extends from July to November (P. Catry et al., 2009), and we deployed tags throughout the season to maximize our chances of obtaining sufficient data from the seasonal periods of internesting, migration, and post-nesting foraging. We used two models of Platform Transmitter Terminal (PTT) devices; SPOT-375B from Wildlife Computers, Seattle, Washington (n = 19, 2018), which transmit Argos locations, and F6G - 376B from Lotek, Havelock North, New Zealand (n = 11, 2019; n = 15, 2020), which transmit both Argos and Fast GPS (hereafter 'FGPS') location information via the Argos satellite system. Both tag types were set to transmit a position every 15s. For details on attachment protocol, see Supplemental Methods.

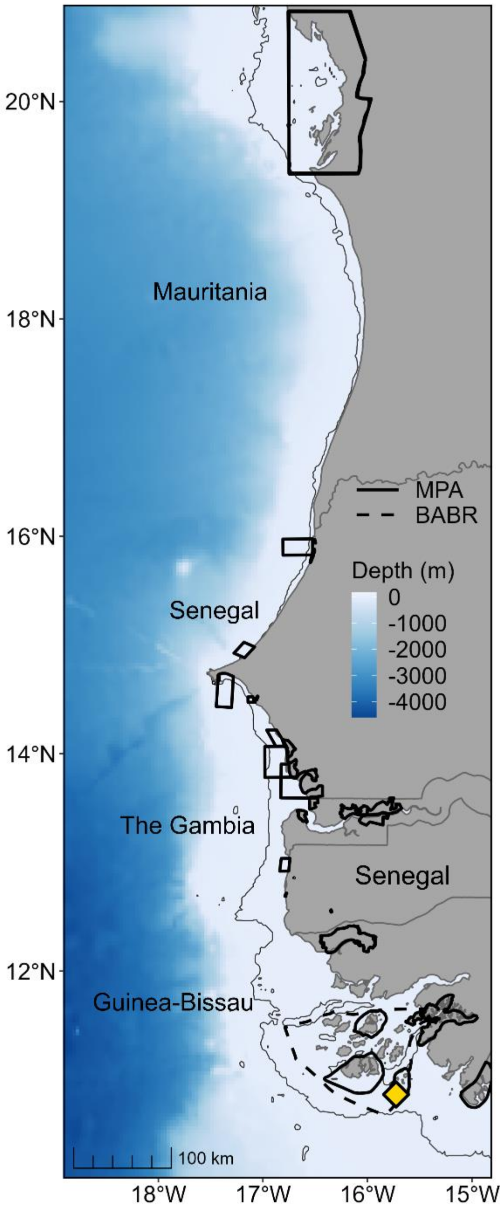

Fig. 5.1 Map of West Africa from the north of Guinea in the south to Mauritania in the north. Solid black polygons show the limits of existing marine protected areas (MPAs). Dashed black line shows the limit of the UNESCO Bolama-Bijagós Archipelago Biosphere Reserve. Yellow diamond indicates

the main nesting site of the study population of green turtles (*Chelonia mydas*); Poilão Island. The bathymetry is shown in a scale of blue, and a thin grey line is the 15 m depth contour.

5.3.2 Ethics Statement

Research permits were granted by the Instituto da Biodiversidade e das Áreas Protegidas, Dr. Alfredo Simão da Silva (IBAP), of Guinea-Bissau. Fieldwork protocols involving sea turtles followed recommended guidelines (NMFS-SFC, 2008), to enhance efficiency and reduce possible disturbance to the turtles, and were conducted by trained personnel, in collaboration with national authorities for biodiversity management.

5.3.3 Tracking Data Filtering

We split tracking data into the behaviorally distinct seasonal periods of internesting, migration, and post-nesting foraging (hereafter "foraging") based on close inspection of individual tracks (Fig. S1). As no animals migrated south or west, we defined migration tracks as those that travelled north of the Bijagós (i.e., 11.6° N) and defined the start of migration as directional and persistent movements at least 10 km from the nesting islands. The 10 km buffer was selected as this is approximately the range in which the turtles spend most time during inter-nesting (**Fig. 5.2**), so most tracking positions outside this area are clearly distinguishable as migratory movements. Turtles which did not have a least 10 days of localized movements (indicating foraging behavior) before device failure were not considered for foraging period analysis (n=10). Next, we filtered the raw tracking data to remove positions with high spatial error. For Argos PTT data we retained only positions with a quality index of 1, 2 or 3, while for FGPS data we retained positions fixed with 6 or more satellites and used a data-driven speed and angle filter (Shimada et al., 2012) to remove biologically unrealistic positions. A total of 28.2% of positions were retained after quality filtering. We used the raw, filtered positions for subsequent analysis, as a sensitivity test showed that interpolation of the data to a regular time interval had little effect on the final outcome (Table S5.1). For each seasonal period, we retained only individuals with at least 10 tracking locations for analysis.

5.3.4 Spatial Analysis

MPA coverage of internesting and foraging periods

To estimate how the spatial distribution of adult females during the internesting and foraging periods falls in relation to marine protected areas, we downloaded MPA spatial polygons from the Protected Planet database (UNEP-WCMC 2021) and calculated: (1) the number of tracked turtles visiting MPAs, and (2) the percentage of tracking positions falling within MPA borders. The average percentage of positions within MPAs was calculated first per individual then across individuals to give an estimate at the population level. The breeding site is located within the UNESCO Bolama-Bijagós Archipelago Biosphere Reserve (BABR, **Fig. 5.1**). Despite the current lack of any management regulations specific to this reserve area, we additionally assessed the proportion of locations within the BABR limits to demonstrate the potential benefits if protection measures were introduced.

To assess whether the spatial error of tracking positions affected our calculations regarding MPA coverage, we performed a sensitivity analysis comparing results using only PTT data (which tend to have higher error) against only FGPS data. For the turtles transmitting both PTT and FGPS positions during internesting (n = 21) and foraging (n = 20) respectively, we compared the percentage of points within and outside MPAs separately for each geolocation method. We found little difference in the percentage of positions within MPAs between the geolocation methods, suggesting our filters removed positions with large enough error to affect MPA overlap (Table S5.2).

Home range and core-use areas

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

Migration corridors

To estimate migration routes for each turtle and identify population-level high-passage corridors, we used dynamic Brownian bridge movement models (dBBMM). Brownian bridge movement models estimate the probability of occurrence of animals in space during the tracking period by using a conditional random walk to approximate potential movement paths connecting tracking positions, while taking into account the time gaps between them. Brownian bridge models are able to handle irregular sampling intervals and incorporate positional errors into the occurrence estimation. dBBMMs extend classic Brownian bridge models by detecting behavioral changes within “moving windows” along the movement path and dynamically assigning appropriate Brownian motion variance values (σ2m) to the random walk procedure. This allows for more accurate estimations of occurrence over lengthy tracking periods, during which the movement behavior of animals may change (Kranstauber et al., 2012).

Following Buechley et al. (Buechley et al., 2018), we estimated migratory corridors for the adult female green turtle population by calculating the percentage of migration routes (i.e., tracked turtles) overlapping across a gridded surface. A 'migration route' was defined as the 95% occurrence probability as estimated by the dBBMM, fitted using filtered locations and their estimated horizontal spatial error for each individual turtle. To estimate the Brownian motion variance, we used a sliding window of seven locations with a margin of three locations. We used a grid cell resolution of 10 x 10 km, which is large enough to identify similar route selection among the turtles, while remaining of relevance for informing spatial protection measures, such as MPA border extension or temporal fisheries restrictions in RAMPAO, where MPAs cover a median of 200 km^2 (range 0.5 – 12,006 km^2). Finally, we identified "high-passage corridors" as grid cells visited by at least 25% of the turtles which migrated north of the Bijagós after nesting (n=18). We then calculated the percentage of high passage cells falling within established MPAs.

5.4 RESULTS

We obtained spatial data from 44 of the 45 tagged individuals. Not all 44 turtles contributed data for the three seasonal periods analyzed, due to premature device failure and resident foraging behavior (i.e., no migratory period; Table S3.3, Fig. S3.1). After filtering, we retained for analysis the tracks of 40 individuals during internesting (88.9%, n=45), 18 individuals during migration (48.9%, n=45), and 35 during foraging (77.8%, n=45). In total, we analyzed 4,358 tracking days, with each individual tracked between 15 - 332 days (mean 99 days ± SD 73 days). Mean curved-carapace-length of tagged turtles was 98.5 cm (SD 8.9 cm, range: 78.0 – 121.5), with no significant differences in curved-carapace-length between years (ANOVA: F1,42 = 0.383, p = 0.540).

The green turtles tracked in this study were distributed between 10.5° N and 20.5° N, an area within which there are 28 MPAs (**Fig. 5.1**, Table S5.4).

5.4.1 MPA coverage and home ranges during internesting

Tracking during the internesting period extended from August to early December (Fig. S3.1). We found that the 95% home ranges and 50% core-use areas of individual turtles during internesting were highly concentrated around the nesting islands (**Fig. 5.2**). The spatial distribution of breeding females was well covered by MPAs during internesting, with all 40 individuals using MPAs and a mean of 94.8% (SD 0.1%, range: 46% - 100%) of tracking positions falling within MPAs. The mean percent coverage increased to 99.5% (SD 0.01%) of positions when considering the limits of the BABR.

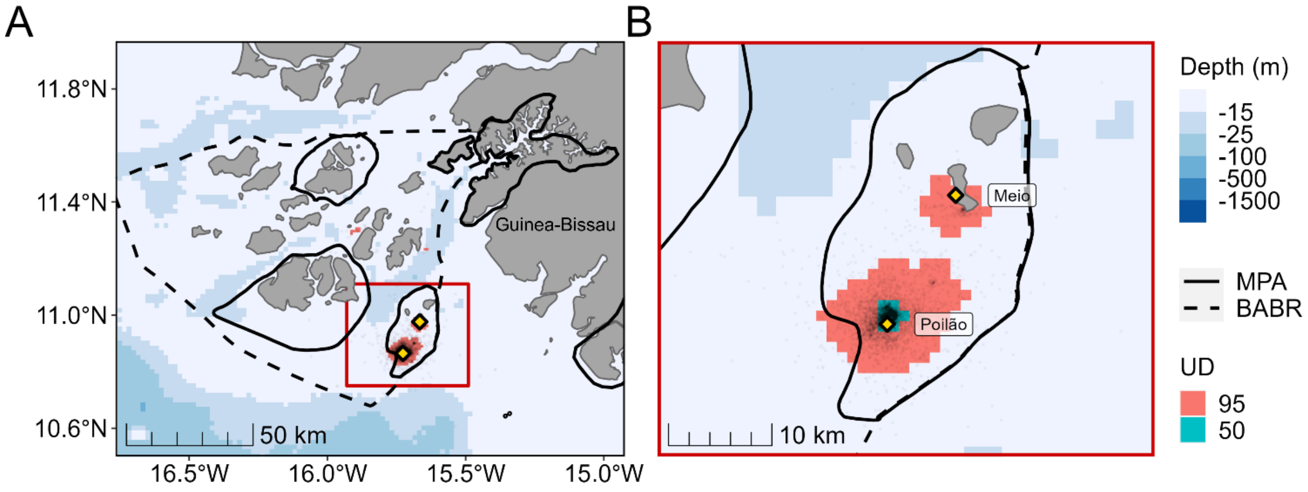

Fig. 5.2 Distribution of 40 female green turtles (*Chelonia mydas*) tracked during internesting. Solid black polygons show the limits of existing marine protected areas (MPAs). The 95% (red) and 50% (blue-green) utilization distribution areas are shown, respectively signifying the population-level home range and core-use areas during internesting. The bold solid lines indicate the locations of existing marine protected areas (MPAs) and the dashed line shows the extent of the Bolama-Bijagós Archipelago Biosphere Reserve (BABR).

5.4.2 Migration corridors

The migration period of the tracked turtles extended from September to December (Fig. S3.1). The routes of the 18 individuals which migrated north of the Bijagós followed the shoreline for the most part, with some individuals travelling several hundred kilometers offshore (**Fig. 5.3**). The areas of highest migration route concentration were used by 61% (11 individuals) of migrating turtles. With 25% of turtles (i.e., 5 individuals) set as a minimum threshold to define high-passage migration corridors, we identified three main coastal stretches as particularly important: the littoral from the outer Bijagós to The Gambia, off the city of Dakar in Senegal, and the littoral of Mauritania south of the Banc d'Arguin (**Fig. 5.3**). We calculated that RAMPAO MPAs overlapped 18 of the 84 (21%) high-passage corridor cells identified in our analysis. If the BABR area was included, the coverage rose to 30 of 84 (36%) of high-passage cells.

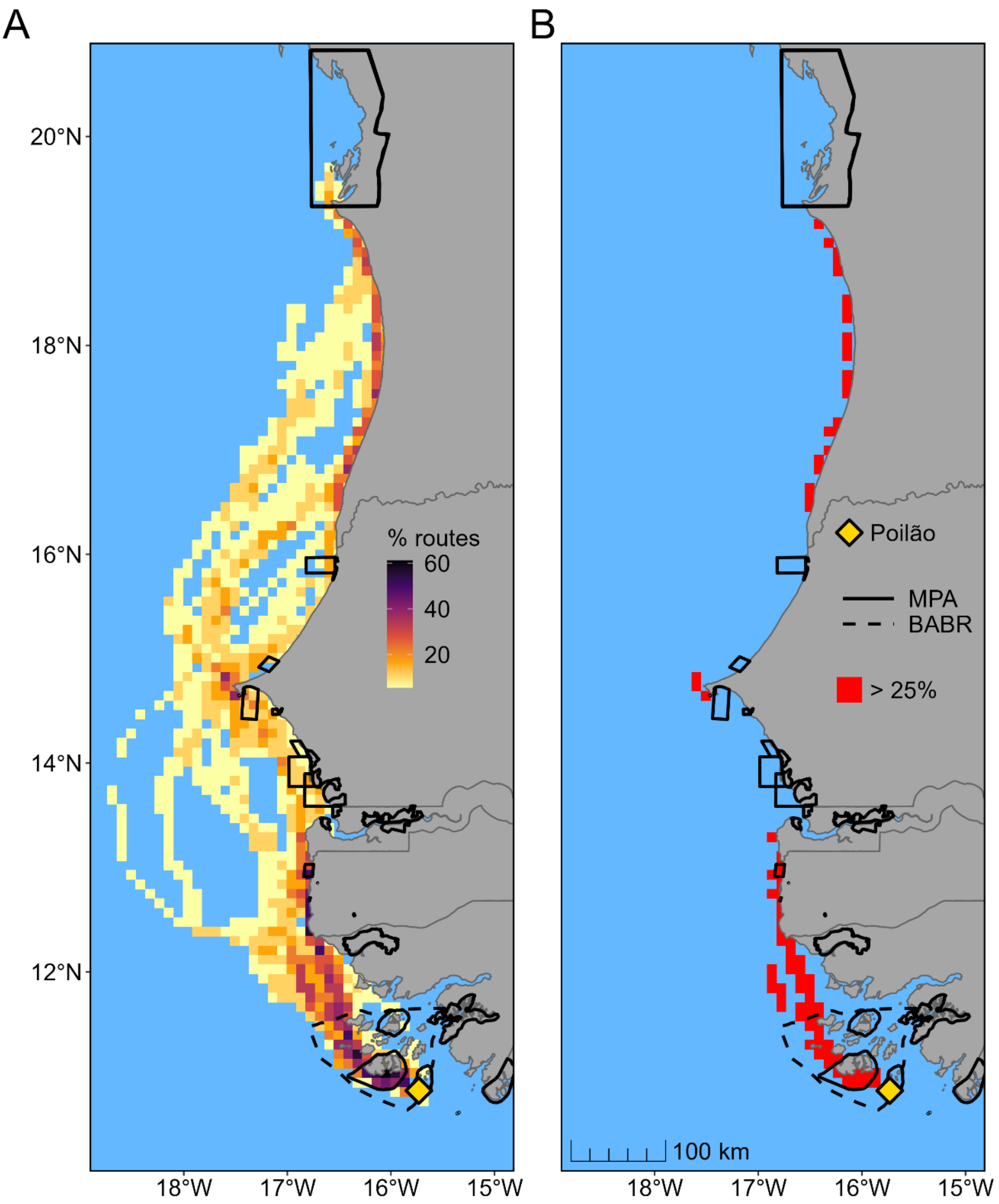

Fig. 5.3 Migration routes of 18 female green turtles (*Chelonia mydas*) travelling from the nesting island in Guinea-Bissau (i.e., Poilão Island) to foraging areas in Senegal, The Gambia or Mauritania. (A) Percentage of overlapping migration routes, defined as 95% probability areas estimated using dynamic Brownian bridge movement models. (B) Identified high-passage corridors, defined as grid cells used by at least 25% of migrating turtles. Black solid and dotted lines represent existing conservation areas in the region. Only movements extending north of the Bijagós Archipelago (i.e., 11.6 N latitude) were considered as migration routes.

5.4.3 Foraging areas, MPA coverage and home ranges during foraging

The nesting population of Poilão and Meio displayed variable migratory strategies, with 34.2%, of the turtles remaining resident in the Bolama-Bijagós region, foraging at 40-90 km from the breeding sites, 28.6% migrating 300-400 km to The Gambia and Senegal, and 37.1% migrating >1000 km to the north of Mauritania (n=35). A single turtle relocated ca. 80km southeast of Poilão Island. The turtles analyzed here engaged in foraging behavior (i.e., localized movements) for a range of 10 to 288 days (Table S5.3 and Fig.S5.1) before device failure, and no turtle that migrated north of the Bijagós (i.e. non-resident) stopped to foraged within the archipelago.

Table 5.1 Coverage of adult female turtles during the post-nesting foraging period in West Africa by marine protected areas (MPA). 'Group' refers either to a calculation for all turtles (i.e., Overall) or subsets split by foraging destinations. Mean estimates are shown with ± standard deviation.

Group	All tracked turtles		Turtles using MPAs		
	n turtles	mean % positions inside MPAs	n turtles	% turtles using MPAs	mean % of positions inside MPAs
Bijagos	12	7.0 ± 13.6	7	58.3	12.0 ± 16.3
Senegal/The Gambia	10	75.5 ± 37.9	9	90.0	83.9 ± 28.7
Mauritania	13	93.3 ± 16.5	13	100	93.3 ± 16.5
Overall	35	58.1 ± 45.4	29	82.9	72.7 ± 38.9

The 95% home ranges and 50% core-use areas of individual turtles during the foraging period were more dispersed than during internesting (**Fig. 5.4**). During the foraging period, we found lower MPA coverage than during the internesting, with 28 of 35 individuals (80.0%) using MPAs at some point (**Table 5.1**). Of the individuals using MPAs, a mean of 72.7% (SD 38.8%, range: 2% - 100%) of their tracking positions fell within protected area borders. Disaggregating this result by foraging destination, a mean of 93.3% (SD 16.5%) of positions from turtles which migrated to Mauritania fell within MPAs, 83.9% (SD 28.7%) of positions of those which travelled to The Gambia and Senegal, and 12.0% (SD 16.3%) for turtles which remained in the wider Bijagós region (**Table 5.1**, **Fig. 5.4**). With the BABR included in the coverage calculation, the percentage of tracking positions occurring within all conservation areas for post-nesting turtles in the Bijagós increased to 96.3% (SD 0.08%).

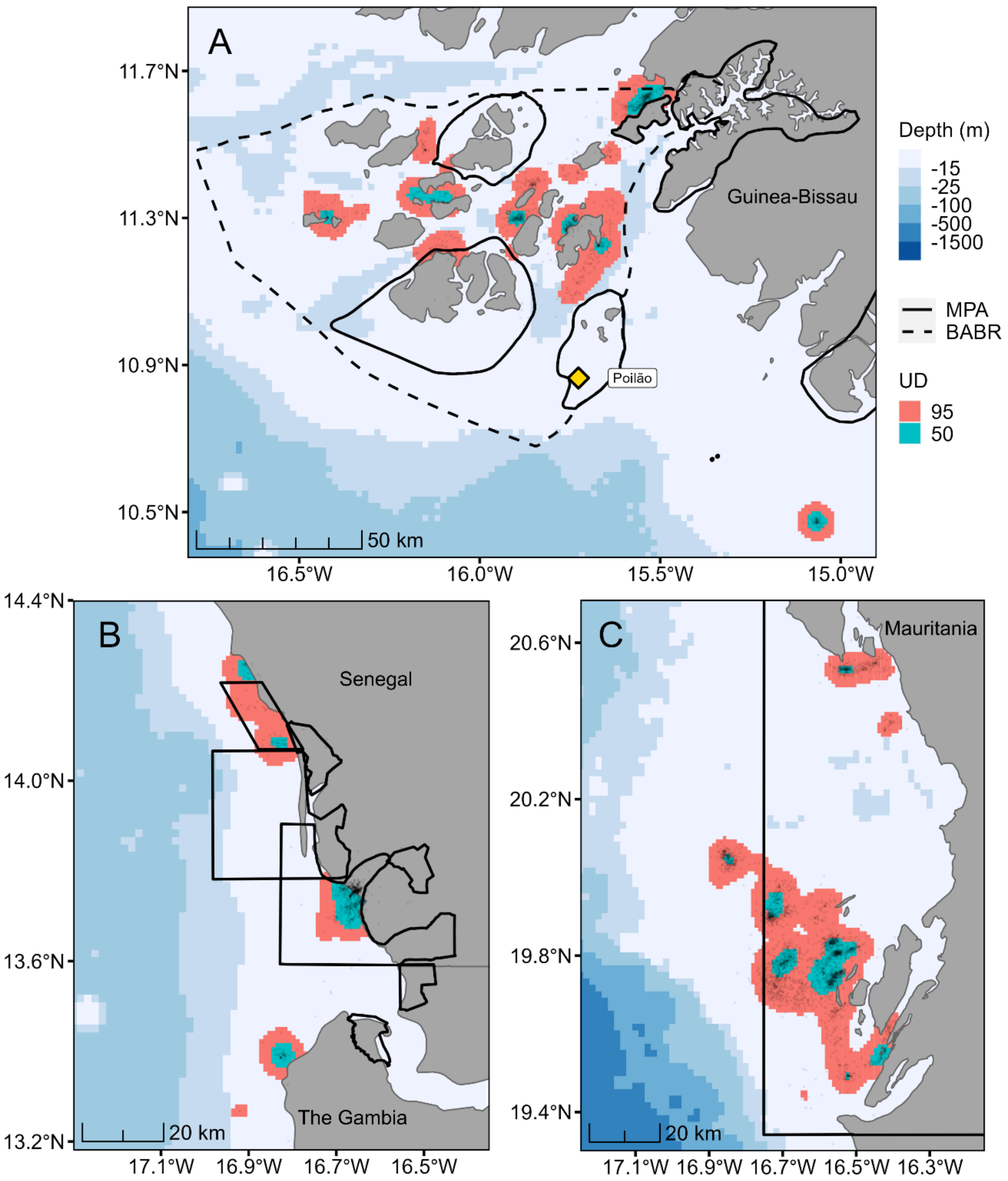

Fig. 5.4. Distribution of 35 female green turtles (Chelonia mydas) tracked during the post-nesting foraging period in (A) the Bijagós Archipelago of Guinea-Bissau, (B) the Saloum and Gambia river deltas of Senegal and The Gambia and (C) the Bay of Arguin in Mauritania. Black dots represent tracking locations, and the underlying colored areas represent the 95% (pink) and 50% (blue-green) utilization distribution areas, respectively signifying the population-level home range and core-use areas during foraging. The bold solid lines indicate the location of existing marine protected areas (MPAs) and the dashed line shows the extent of the BABR nature reserve.

5.5 DISCUSSION

Assessing the seasonal distributions of migratory species is a key step to informing marine spatial planning and to identifying opportunities for cross-regional collaboration for conservation (Beal, Dias, et al., 2021). By analyzing the movements of reproductive female green turtles across three seasonal periods, we provide novel information on the spatial distribution of this globally significant rookery, which is highly relevant to regional conservation and management efforts. Using tracking data, we identified multiple post-nesting migratory strategies, novel foraging sites, and high-density migration corridors. We then quantified the spatial coverage of seasonally important areas by the West Africa MPA network, RAMPAO. Our findings highlight the biological relevance of the RAMPAO, and its importance for the conservation of this charismatic species and wider biodiversity in the region. We provide recommendations for MPA managers, to improve both the protection coverage and knowledge of this important population.

5.5.1 MPA coverage during the internesting period

During the internesting period, breeding females concentrated near the nesting beaches, remaining within the limits of the João Vieira – Poilão Marine National Park (JVPMNP). This supports findings by Godley et al., (2010), based on the internesting movements of seven turtles tracked in 2001. Indeed, the protection of this globally significant rookery was one of the main motivations for the creation of this MPA (Catry et al., 2002, **Table 5.2**), but conservation efforts are mostly concentrated on the terrestrial phase (i.e. nesting and egg incubation), particularly at Poilão Island. Illegal fishing is known to occur inside the MPA (186 seized fishing boats from 2011 to 2019) with fishers mostly from neighboring countries (ca. 62%, Senegal, Guinea, Ghana, Sierra Leone), where marine turtles have commercial value (notably not the case in Guinea-Bissau (Barbosa et al., 2018; P. Catry et al., 2018). Still, marine surveillance at the JVPMNP and enforcement of fines, contribute to deter most illegal activities, and enhance protection during the nesting season.

Small home ranges and high MPA coverage during internesting were also found among hawksbill turtles from the Solomon Islands, West Pacific, spending 98.5% of their internesting time within the Arnavon Community Marine Park (Hamilton et al., 2021), and from the Dominican Republic, Caribbean Sea, with 82.7% of their internesting time within the Del Este National Park (Revuelta et al., 2015). Further studies reported restricted home ranges during the internesting period among loggerhead (Schofield et al., 2010) and green turtles (Shimada et al., 2021; Snape et al., 2018). Thus, implementing relevant measures around rookeries of conservation value (e.g. protected areas, fishing restrictions) may be a good strategy to protect vulnerable populations during internesting (Dryden et al., 2008).

Table 5.2 Summary of relevant management characteristics of five marine protected areas (MPAs) of the West Africa MPA network (RAMPAO), used by the green turtle population breeding in the Bijagós Archipelago, Guinea-Bissau.

MPA name	**Country**	**Area (ha)**	**MPA goals**	**Fishing regulations**	**Who can fish in the MPA?**	**Main types of fishing gear used**	**Active surveillance program?**	**Initiatives in the MPA and adjacent areas relevant for marine turtle conservation**	**Sea turtle species present**	**Important benthic habitats**
Parc National Du Banc D'Arguin	Mauritania	1,170,000	Maintain productivity of ecosystems Preserve endangered and migratory species Contribute to development of local populations	Only traditional sailing boats allowed, hired or owned by Imraguen fishers Prohibited: fishing at night, blocking channels, traps on mudflats or channels Sesonal fishing restrictions and monthly biological rests in place Some areas closed to all fishing activities	Residents in the park	Mullet net (mesh size 56-60mm), meagre net (min. mesh size 20 - 26cm), melloussa net (min. mesh size: 14 - 18cm), sole net (min. mesh size 50mm) Traps, lines and handlines	yes	Local Imraguen fishers are engaged in in water surveys of sea turtles for research and conservation	*Chelonia mydas*, *Caretta caretta*	Seagrass (*Cymodocea*, *Halodule*, *Zoostera*), Area of intertidal meadows ~ 1000 km^2
Joal-Fadiouth	Senegal	17,400	Biodiversity conservation Enhancement of fishing yields Socioeconomic growth for local populations	Areas with specific regulations with biological rest periods Prohibited: fishing at night, scuba dive, purse seine, beach seine, gillnet and longlines	Residents native to Fadiouth	Up to 5 km from the coast: line and hook or fishing rod Beyond 5 km from the coast: large mesh nets (100 mm)	yes	Awareness campaigns among priests, imans and fishers and law enforcement halted the sale of turtle meat in local markets Fishers take tourists to watch turtles	*Chelonia mydas*	Seagrass (*Cymodocea*, *Halodule*)
Parc National du Delta du Saloum	Senegal	76,000	Protection of marine ecosystems and natural resources	Prohibited: gillnets and monofilament nets	Redidents on the park perimeter	Line and hook or fishing rod	yes	Communication and awareness campaigns for fishers, law enforcement with offense reports, funding of reconversion activities	*Chelonia mydas*, *Lepidochelys olivacea*, *Caretta caretta*	Seagrass (*Cymodocea*, *Halodule*, *Zoostera*)
Orango National Park	Guinea-Bissau	158,235	Protection of biodiversity and ecosystems Promote the sustainable use of natural resources for socioeconomic growth of local populations	Four no-take zones, in chanels between islands. Prohibited: monofilament nets, fishing camps by non-resident fishers, bottom trawl, catching rays and sharks, fishing techiniques blocking channels	Residents and licensed recreational fishers	Gill net (max. 28 mm mesh size) and cast net ('ramanga') Traditional harpoon ('Canhaco') Fishing trap ('Impande') Line fishing (max. 500 hooks/ no. 7, 8)	yes	Community members are engaged in marine turtle monitoring activities and marine monitoring activities for awareness	*Chelonia mydas*, *Eretmochelys imbricata*, *Dermochelys coriacea*, *Lepidochelys olivacea*	uncharacterized
National Marine Park of João Vieira Poilão	Guinea-Bissau	49,500	Protection of biodiversity and ecosystems Conservation of sea turtles and colonial shorebirds Enhancement of Bijagó cultural heritage Regeneration of fish stocks Ecotourism development	No take zone 11,000 ha Prohibited: monofilament nets, big nets to catch sharks or other big fish, fish transshipment Max. engine power: 15 - 40 hp	Residents from Canhabaque and licensed recreational fishers	Hook traps (max. 500 hooks / no.7) Gill net (max. 3 bands / max. mesh size 30mm) and cast net Line fishing (hooks no.7, 8)	yes	Community members are engaged in marine turtle monitoring activities and marine monitoring activities for awareness	*Chelonia mydas*, *Eretmochelys imbricata*	uncharacterized

5.5.2 Migration corridors

MPA coverage during the migration period was relatively low (21%), with a large portion of coverage provided by the Orango National Park (ONP), located near the nesting islands in the Bijagós. It seems intuitive that turtles may follow a similar path at the onset of migration, as they are leaving from the same location and can potentially be using the same environmental cues, such as ocean currents, to orient themselves (Åkesson et al., 2014). Yet some individuals diverted this corridor, and other populations display highly dispersed post-nesting migratory paths (Hays et al., 2014). Nevertheless, high-passage migratory corridors near the nesting beach have been found in several marine turtle populations, as well as near foraging locations (Hamilton et al., 2021; Pendoley et al., 2014; Santos et al., 2021; Stokes et al., 2015), suggesting these areas can be a good choice to implement conservation measures.

The majority of the turtles that migrated to Mauritania converged around the Cap-Vert Peninsula (where the city of Dakar is situated). This prominent promontory acts as a migratory bottleneck (sensu Bayly et al., 2018), funneling huge numbers of migratory seabird, which are compelled by the promontory to approach the shore (Dubois et al., 2009; Paiva et al., 2015; Péron & Grémillet, 2013). Given our findings, combined with the apparent importance of this site for other taxa, increasing spatial protection here may have a broad impact on biodiversity in the region. The National Park of the Madeleine Islands is a terrestrial only protected area located just offshore of the peninsula, in an area of high turtle passage, suggesting that extension of the limits of the park to the marine zone would increase protection coverage for migrating green turtles. There are currently processes ongoing to validate the limits of a new MPA in the southern bay of the Cap-Vert Peninsula, which our results could inform by providing information on where migrating turtles may best benefit from additional spatial protection (Barbosa et al., 2018; P. Catry et al., 2018). As migration is restricted to a well-defined period of the year (Alerstam & Bäckman, 2018; Santos et al., 2021; September to December in our study), migratory bottlenecks are seasonal and therefore temporal measures in these areas could be effective. This could take the form of implementing seasonal, spatially explicit bans on fishing practices that cause turtle bycatch.

5.5.3 MPA coverage of foraging grounds and connectivity across the RAMPAO

We found that after nesting, females had three distinct migratory strategies, with some turtles remaining nearly resident in the Bijagós and others performing short or long migrations to foraging grounds in other parts of West Africa. Non-migratory green turtles have also been reported from the Cocos Keeling Islands, in the eastern Indian Ocean (Whiting et al., 2008), and a similar pattern of near-residency and migration was observed among green turtles from the Chagos Archipelago, in the Indian Ocean (Hays et al., 2014).

We found that this nesting population from the Bijagós connects at least five RAMPAO MPAs, across three countries, which have a marine area with fishing regulations and active marine surveillance programs (**Table 5.2**). Overall, the MPA coverage of foraging areas was good (over 70%), but it varied greatly between the foraging regions. At the Bay of Arguin, in Mauritania, most of the foraging occurred within the Banc d'Arguin National Park (PNBA). In Senegal, a very high proportion of the foraging period was spent within the limits of either the Saloum Delta National Park (SDNP) or the Joal Fadiouth MPA (JFMPA). Some turtles foraged around the Bijol Islands of The Gambia, where green turtle nesting is also known to occur (Barnett et al., 2004), and although these islands are part of the Reserve of the Tanji Bijol Island Banks, this MPA does not currently include a marine area. Extending the limits of this reserve to include nearshore waters would enhance protection of both the turtles which nest on the Bijol Islands during internesting, as well as turtles from the Bijagós during foraging. In the Bijagós, the majority of turtles foraged outside MPAs (88%, n=12), but within the limits of the UNESCO Bolama-Bijagós Archipelago Biosphere Reserve (BABR, 98.1%). Notably, the BABR also hosts foraging aggregations of immature green turtles (Monteiro et al., 2021), therefore, creating and implementing relevant regulations within the BABR would greatly enhance the protection of green turtles in West Africa.

Foraging habitats were not uniformly distributed along the West African coast, which may indicate that food resources are patchy. The PNBA of Mauritania, and the SDNP and JF MPA of Senegal, have vast seagrass meadows (Cunha & Araújo, 2009). As seagrass is one of the preferred food sources of green turtles (Moran & Bjorndal, 2007), the distribution of this resource could in part explain the locations of turtle foraging areas. However, although Cunha and Araújo (2009) found seagrass along the coast from the south of the Bay of Arguin to Nouakchott, Mauritania, none of the turtles we tracked foraged in this area, suggesting that other factors influence their choice of foraging area. Additionally, in the Bijagós seagrass is scarce (Campredon & Catry, 2016), although more benthic surveys are needed for a thorough characterization. Macroalgae potentially contribute to the diet of green turtles in the Bijagós, however to future diet studies are needed to investigate this possibility.

5.6 FINAL CONSIDERATIONS

Identifying green turtles as a common conservation target for several of the RAMPAO MPAs can motivate and inform collaboration. We recommend that stakeholders from each interested country define together standard monitoring parameters for systematic data collection to increase the knowledge of this globally important population, and reinforce information exchange to support conservation actions and management. Additionally, for a complete picture of the MPA coverage and connectivity of this breeding population, future research should address the spatial distribution of reproductive males. Spatial analyses should also extend to other taxa, to maximize effective MPA design encompassing key ecosystems and a broad range of species of ecological and conservation value.

This study unequivocally demonstrates the importance of an established MPA network, the RAMPAO, for the conservation of a marine migratory species. Ongoing research indicates that connectivity across the RAMPAO is also established by migratory coastal waders (Rocha pers comm). Notably, the green turtle rookery at Poilão Island is growing (Broderick & Patricio, 2019), which can be a possible indication that, despite existing threats (P. Catry et al., 2002), RAMPAO MPAs are effectively protecting this population. We argue that lessons can be learned from the RAMPAO process, and applied globally. West African countries (and other countries around the world) are well below the previously set Aichi Target 11 of 10% of marine areas under nature protection (Failler et al., 2020). Therefore, studies of this kind provide highly relevant information to countries of ways they can expand their protected area estate to both meet the targets of the upcoming post-2020 Biodiversity Framework and contribute to international conservation efforts (Hays et al., 2019).

CHAPTER 6

GLOBAL POLITICAL RESPONSIBILITY FOR THE CONSERVATION OF ALBATROSSES AND LARGE PETRELS

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6.1 ABSTRACT

Migratory marine species cross political borders and enter the high seas, where the lack of an effective global management framework for biodiversity leaves them vulnerable to threats. Here, we combine 10,108 tracks from 5,775 individual birds at 87 sites with data on breeding population sizes to estimate the relative year-round importance of national jurisdictions and high seas areas for 39 species of albatrosses and large petrels. Populations from every country made extensive use of the high seas, indicating the stake each country has in the management of biodiversity in international waters. We quantified the links among national populations of these threatened seabirds and the regional fisheries management organizations (RFMOs) which regulate fishing in the high seas. This work makes explicit the relative responsibilities that each country and RFMO has for the management of shared biodiversity, providing invaluable information for the conservation and management of migratory species in the marine realm.

6.2 INTRODUCTION

The marine environment is characterized by high connectivity, which helps structure ecosystems and has important consequences for biodiversity conservation and human welfare (Albouy et al., 2019; D. C. Dunn et al., 2019). Distant waters are connected through the migrations of megafauna, including sea turtles, pelagic fish, marine mammals, and seabirds, as well as by ocean currents which drive the dispersal of fish larvae and other planktonic life forms (Block et al., 2011; Jönsson & Watson, 2016; Ramesh et al., 2019). In addition to connecting natural systems, these processes also connect countries, which depend on shared biodiversity elements as resources for consumption, cultural identity, and associated ecosystem services, but differ in their commitment to sustainable exploitation and conservation (Nevins et al., 2009; Ramesh et al., 2019). During their seasonal movements, migratory marine animals visit areas under different legal and management regimes, including exclusive economic zones (EEZs; up to 200 nautical miles from shore) where countries have resource rights, and areas beyond national jurisdiction (hereafter, the ‘high seas’) which are a global commons. Identifying the set of national jurisdictions and high seas areas visited by species across their seasonal cycles is vital, as strong management policy in one region may be nullified by unmitigated threats in another (Marra et al., 2011).

International cooperation and collaboration is key to the conservation of migratory species (Runge et al., 2014). On a global scale, countries can sign and actively engage in multilateral environmental agreements (MEA), such as the Convention on Biological Diversity (CBD) and the Convention on Migratory Species (CMS), and thereby contribute to international conservation by establishing common regulatory and guidance frameworks, and setting global goals (Glowka, 2000). Under CMS, there are a number of subsidiary agreements, such as the Agreement on the Conservation of Albatrosses and Petrels (ACAP), through which countries can share knowledge and promote policy measures relevant to specific elements of biodiversity (R. A. Phillips et al., 2016). However, the degree to which these MEAs apply to the high seas is debated, as the obligations of signatory countries are restricted to areas and vessels under their jurisdiction (De Santo, 2018). The primary global legal framework for maritime activities, the United Nations Convention on the Law of the Sea (UNCLOS), calls on countries to cooperate to preserve the marine environment both within national jurisdictions and in the high seas. However, explicit processes for enacting conservation and management measures for biodiversity in the high seas are lacking under UNCLOS, leaving a gap in legal responsibility (Ban et al., 2014).

The high seas have been documented as important habitat for an increasing number of migratory marine megafauna, yet, regardless, the footprint of human activities in the high seas continues to grow (Harrison et al., 2018; Merrie et al., 2014). Governance in the high seas is currently fragmented among institutional arrangements with sector-specific and/or regional mandates (Ban et al., 2014). The International Maritime Organization regulates shipping, for example, while regional fisheries management organizations (RFMOs) have mandates to regulate fishing. Fishing represents one of the largest industries operating in the high seas (Kroodsma et al., 2018), and despite the formal commitment of RFMOs to ensure sustainable harvests and minimize broader ecosystem impacts, fisheries continue to represent a profound threat to high seas biodiversity (Cullis-Suzuki & Pauly, 2010).

To address the existing governance gap in the high seas, the United Nations have agreed to develop an international legally-binding instrument under UNCLOS on the conservation and sustainable use of marine biological diversity of areas beyond national jurisdiction (aka ‘BBNJ treaty’). Core to the BBNJ treaty are provisions for protecting biodiversity through area-based management tools (e.g. marine protected areas) and the biodiversity-inclusive management of the wider ocean-space, such as through the implementation of strategic environment assessments and environmental impact assessments for planned activities (De Santo, 2018; Ma et al., 2016). However, it remains unclear how existing management organizations and bodies will interact with the future processes adopted under the BBNJ treaty (Haas et al., 2020). For countries to be able to negotiate for, and ultimately implement, effective conservation and management measures under the new treaty, and within the existing frameworks of MEAs and RFMOs, information is needed on the ways in which migratory species depend on and connect national jurisdictions and the high seas.

Tracking data from animals fitted with electronic devices have been used previously to estimate the proportion of time spent in different national jurisdictions and high seas areas, and hence their relative importance to megafauna such as seabirds, sea turtles, tuna, sharks, and marine mammals (Barkley et al., 2019; Felis et al., 2019; Harrison et al., 2018; Hays et al., 2019). Tracking data can be integrated with population sizes to better quantify the importance of areas at sea, as sample-derived patterns can be contextualized with respect to the large scale or regional distribution of each species (Frederiksen et al., 2016; Hindell et al., 2020). Population estimates are unreliable for many marine megafauna species due to their low detectability and wide distributions; yet, for seabirds, which assemble at predictable sites on land in order to breed, reasonably accurate estimations of population size can be used to weight estimates of space use at sea (Carneiro et al., 2020).

Albatrosses and large petrels have wide annual ranges spanning all major ocean basins. They are considered among the most threatened of all bird groups and are subject to several anthropogenic threats at sea, especially incidental mortality in fishing gear (termed ‘bycatch’) and competition with fisheries caused by overfishing, as well as pollution and climate-related changes to ecosystems (Dias et al., 2019; Pardo et al., 2017). Using a unique tracking dataset assembled from across the global distributions of 39 species of albatrosses and large petrels, we estimate the importance of national jurisdictions and high seas areas across the annual cycle. First, we calculate species richness for each national jurisdiction (including the dependent territories under each sovereign country) and the high seas as a whole, distinguishing between breeding and visiting species (i.e. breeding in another country). Next, we estimate the amount of time, year-round, that each breeding population spends in each of these political areas, again discriminating between time spent in breeding-origin countries and other visited areas. Then, we attribute annual time spent in the high seas to the areas of competence of RFMOs. Finally, we construct networks to reveal the geopolitical connections most important to the populations of each breeding-origin country, and to the global community of albatrosses and large petrels. These detailed quantitative estimates of interconnectivity will inform countries on which jurisdictions their biodiversity depends and how to prioritize their engagement with the BBNJ treaty and other instruments and agreements.

6.3 METHODS

6.3.1 Study taxa

For the purposes of this study, the term ‘albatrosses and large petrels’ refers to all species in the albatross Family, Diomedeidae, and the genera Macronectes, Ardenna, Calonectris, and Procellaria of the Family Procellariidae. This grouping was selected for the following reasons: 21 of these 40 species are listed as Vulnerable, Endangered, or Critically Endangered under the IUCN Red List Criteria and an additional 11 as Near Threatened (IUCN, 2020), 29 are listed by ACAP (R. A. Phillips et al., 2016), a high proportion face at-sea threats, namely incidental mortality in association with fishing, as well as direct competition with fisheries; lastly, these species are highly mobile and are relatively well-studied across their ranges, and hence the necessary tracking and population data are available for a global synthesis (Carneiro et al., 2020; Dias et al., 2019; R. A. Phillips et al., 2016).

6.3.2 Data assembly

Tracking data were obtained from the BirdLife International Seabird Tracking Database (www.seabirdtracking.org) and directly from collaborators. Data were sought from all the breeding aggregations for each species, with the goal of maximizing coverage of the global breeding population (**Table 6.1**, data S3). Each 'breeding population' was defined according to criteria adopted by the Agreement on the Conservation of Albatrosses and Petrels (ACAP) as individuals of each species found breeding at each 'Island Group'; the latter correspond with major archipelagos, and reflect current biogeographic and political separation (R. A. Phillips et al., 2016). For each breeding population with tracking data, we maximized coverage of the annual cycle (**Table 6.1**) by using data from light-level geolocation (Global Location Sensor or GLS), Platform Terminal Transmitters (PTTs), and Global Positioning System (GPS) devices. We obtained Island Group and global breeding population size estimates from the ACAP database (https://data.acap.aq/) and from the literature (data S4). We assembled requisite data for 39 of the 40 species of albatrosses and large petrels, with only Southern Royal Albatross Diomedea epomophora lacking the necessary data for analysis.

Table 6.1 Tracking data coverage of the global breeding population and annual cycle of 39 species of albatrosses and large petrels. 'Nspecies' is the estimated size (individuals) of the global breeding population. 'nsites' is the number of breeding populations tracked per species. 'nbirds' is the number of unique birds tracked. '% species pop.' is the percentage of the global breeding population made up by the sites tracked herein. '% species year known' is the percentage of the annual cycle of the global breeding population estimated by our tracking data. '% species year unknown' is the percentage of the annual cycle not estimated by our tracking data (i.e months or populations without tracking data).

Common name	Scientific name	$N_{species}$	n_{sites}	N_{birds}	% species pop.	% species year known	% species year unknown
Buller's Shearwater	*Ardenna bulleri*	700,000	1	8	100	100	0
Flesh-footed Shearwater	*Ardenna carneipes*	148,000	2	91	48	41	59
Pink-footed Shearwater	*Ardenna creatopus*	67,040	1	102	100	92	8
Great Shearwater	*Ardenna gravis*	5,000,000	1	72	100	100	0
Sooty Shearwater	*Ardenna grisea*	20,000,000	2	54	46	45	55
Wedge-tailed Shearwater	*Ardenna pacifica*	5,200,000	4	56	58	49	51
Short-tailed Shearwater	*Ardenna tenuirostris*	23,000,000	1	16	78	72	28
Cory's Shearwater	*Calonectris borealis*	423,672	4	514	98	90	10
Scopoli's Shearwater	*Calonectris diomedea*	327,250	4	228	95	80	20
Cape Verde Shearwater	*Calonectris edwardsii*	26,228	1	19	100	83	17
Streaked Shearwater	*Calonectris leucomelas*	3,000,000	2	104	59	54	46
Amsterdam Albatross	*Diomedea amsterdamensis*	90	1	74	100	100	0
Antipodean Albatross	*Diomedea antipodensis*	14,864	2	211	100	100	0
Tristan Albatross	*Diomedea dabbenena*	2,218	1	52	100	100	0

Wandering Albatross	*Diomedea exulans*	18,568	5	977	100	100	0
Northern Royal Albatross	*Diomedea sanfordi*	10,270	2	75	100	92	8
Southern Giant Petrel	*Macronectes giganteus*	95,406	5	243	25	19	81
Northern Giant Petrel	*Macronectes halli*	21,382	5	227	81	59	41
Short-tailed Albatross	*Phoebastria albatrus*	2,600	1	32	78	52	48
Laysan Albatross	*Phoebastria immutabilis*	1,333,316	1	208	100	100	0
Waved Albatross	*Phoebastria irrorata*	16,942	1	54	100	42	58
Black-footed Albatross	*Phoebastria nigripes*	140,072	1	160	96	96	4
Sooty Albatross	*Phoebetria fusca*	24,192	4	121	100	100	0
Light-mantled Albatross	*Phoebetria palpebrata*	41,046	5	73	65	58	42
White-chinned Petrel	*Procellaria aequinoctialis*	2,405,136	4	133	80	68	32
Grey Petrel	*Procellaria cinerea*	151,132	4	61	98	89	11
Spectacled Petrel	*Procellaria conspicillata*	28,800	1	8	100	50	50
Black Petrel	*Procellaria parkinsoni*	3,000	1	61	100	92	8
Westland Petrel	*Procellaria westlandica*	5,654	1	28	100	92	8
Buller's Albatross	*Thalassarche bulleri*	65,402	1	115	44	44	56
Indian Yellow-nosed Albatross	*Thalassarche carteri*	64,414	2	184	87	63	37
Shy Albatross	*Thalassarche cauta*	29,368	1	143	100	83	17
Atlantic Yellow-nosed Albatross	*Thalassarche chlororhynchos*	67,300	1	45	100	92	8
Grey-headed Albatross	*Thalassarche chrysostoma*	165,854	5	232	85	57	43
Chatham Albatross	*Thalassarche eremita*	10,592	1	50	100	92	8
Campbell Albatross	*Thalassarche impavida*	43,296	1	81	100	92	8
Black-browed Albatross	*Thalassarche melanophris*	1,374,890	5	803	88	86	14
Salvin's Albatross	*Thalassarche salvini*	82,426	1	22	3	3	97
White-capped Albatross	*Thalassarche steadi*	191,834	1	38	100	100	0
		64,302,254	87	5775	84.9	75.0	25.0

6.3.3 Filtering and standardization

Because time intervals between locations differed among device types and data sets, we used a single location per day (i.e. the lowest common interval) from each individual track, nearest to local noon, for analysis. GLS, PTT, and GPS devices provide positions in different ways, resulting in different levels of spatial accuracy. Data from GLS devices are used to estimate location based on day length and the relative timing of local noon, and have the highest spatial error, of around ±186 km (R. A. Phillips et al., 2004). We applied a series of filters to GLS data sets in addition to those employed by data contributors. We also performed a re-sampling procedure to test the sensitivity of our measures of the importance of political areas to spatial error, and concluded that the effects on estimated richness and time spent were very small and had no substantial effects on the results (See Supplementary Materials and Methods for details, and Fig. S6.3 for results). Nine species (all Diomedea. and Phoebetria spp., and Grey-headed Albatross Thalassarche chrysostoma) breed biennially, and because tracking data coverage during the non-breeding year is generally poor, we retained only data from the first 365 days following logger attachment for each individual track. Hence, all results pertain to the distribution of adult birds during a breeding year.

After filtering, there was a total of 842,527 tracking days available for analysis from 5,775 individual birds (**Fig. 6.2**A, Fig. S6.1, data S6.4). These data represent movements sampled between 1989 and 2017, across 87 breeding populations from 39 of the 40 species of albatrosses and large petrels (**Table 6.1**, data S6.3). These populations represent a total of 44 million of the estimated 64.3 million breeding albatrosses and large petrels worldwide, and a mean of 85% (range: 3-100%) of the global breeding population per species (**Table 6.1**). We identified the national jurisdictions and high seas areas visited by each breeding population for each month of the year (see section Analysis); we considered months with fewer than 10 unique tracking days to be unrepresentative and removed them from the analysis. To test the sensitivity of this threshold, we re-ran the analysis with a more conservative threshold of at least 10 tracking days across 5 different individuals. This did not alter any major patterns or conclusions but excluded valuable data for several important populations from which few birds have been tracked; therefore, we opted to use the less conservative threshold (See data S5A-B and data S6A-B). Combined tracking samples for each population spanned a mean of 300 days (SD ±56) of the annual cycle (**Table 6.1**). After filtering unrepresentative months, tracking data allowed for the calculation of the national jurisdictions and high seas areas visited during a total of 94% of the annual cycle of 44 million albatrosses and large petrels, and a mean of 76% (range: 3-100%) of the annual cycle per species (**Table 6.1**). Therefore, our results pertain to 41.3 million of a possible total of 64.3 million (65%) bird-years.

6.3.4 Analysis

Each daily location estimate was assigned to a maritime zone (herein used when simultaneously referring to the following areas: EEZs, the high seas as a whole, and the areas of legal competence of RFMOs in the high seas). First, this was done for national jurisdictions and the high seas as a whole, using a spatial union between country land borders and EEZs (VLIZ 2020, available at http://www.marineregions.org). We considered national jurisdictions to be the aggregated area of EEZs (and territorial waters) under a single country, including therein any overseas dependencies. Then, the analysis was run again, attributing points in the high seas to the areas of competence of the RFMOs, available at http://www.fao.org/geonetwork/ (Fig. S6.2). Areas with overlapping territorial claims were left named with all claimant countries listed (e.g. ‘Disputed – Russia/Japan’), unless they had breeding colonies with tracking data, which was only the case for the Falklands/Malvinas, South Georgia/Georgias del Sur, and the

Chafarinas/Zafarin Islands. For these cases, the analysis was run twice with breeding populations alternately assigned to each disputing country (See alternate results in data S6.5C-D and data S6.6C-D).

Species richness

Species richness was calculated for each national jurisdiction and the high seas as a whole based on tracking data occurrence, and reflects the number of (1) breeding species, (2) visiting species, and (3) species which both breed locally and visit from elsewhere. In order to visualize this pattern in space, maps were constructed by binning total richness on a global hexagonal grid of 452 km2, which is a grid resolution large enough to encompass the average error of GLS devices (R. A. Phillips et al., 2004). Calculations of breeding species richness for each country reflect only the breeding populations with available tracking data in order to ensure a valid comparison with the number of visiting species, therefore this will be an underestimate of true breeding richness in certain cases. Using information on all known breeding countries for each species, we calculated the degree of under-estimation in our calculations of breeding richness per country.

Time-spent estimation

To reflect the relative abundances of albatrosses and large petrels in each maritime zone, we estimated the amount of time spent by each breeding population in a year. Time spent was first calculated for each month to account for uneven sample sizes and shifting seasonal distributions, and then summed and expressed in ‘bird-years’. Each daily location within a maritime zone was considered one bird-day spent therein. The total amount of time spent (T_{spme}; in bird-months) by the breeding population p of species s in maritime zone e was calculated as:

$$T_{spme} = \frac{\sum_{\mathrm{i}=1}^{i_{max}} \left(\frac{D_{ime}}{D_{im}}\right)}{n_m} * N_p \tag{1}$$

where D_{ime} represented the number of days an individual i spent in maritime zone e in month m, and D_{im} the total number of days individual i was tracked in month m. This proportion of days spent in each maritime zone was then averaged across all tracked individuals $(i_1 \; to \; i_{max})$ by dividing the sum of proportions by the number of tracked individuals for a species and population n_m in month m. The average proportion of monthly time spent per tracked individual was then multiplied by the breeding population size N_p to extrapolate to the total amount of time (in bird-months) that breeding population p of species s spends in maritime zone e in month m.

For example, an individual (i) Cory's Shearwater Calonectris borealis (s) from the breeding population in Madeira (p) spent 10 of a total of 31 tracking days (32% of the time) in the high seas $\left(\frac{D_{ime}}{D_{im}}\right)$ during January (m). In this way, we calculated the proportion of days spent in the high seas for each of the 72 tracked individuals (n_m) of the same species and population. Next, we calculated the mean proportion of time spent across these 72 individuals, estimating that these birds spent on average 17% of January in the high seas. Multiplying this mean proportion by the breeding population size of 66,080 individuals (N_p) results in a monthly total of 11,284 bird-months spent in the high seas in January (T_{spme}).

Annual time spent

We then summarized the monthly time spent across all months to estimate the standalone importance of maritime zones e in terms of the total amount of time spent in a year $(T_e$; in bird-years) by the global community of albatrosses and large petrels

$$T_e = \sum_{p=1}^{p_{max}} \frac{\sum_{m=1}^{m_{max}} (T_{spme})}{12} \tag{2}$$

where the total time spent within each month (T_{spme}) was summed across the months for which tracking data were available (mmax) and divided by 12 to convert the unit from 'bird-months' to 'bird-years'. The number of 'bird-years' per population were then summed across all populations in maritime zone e to give an estimate of the total annual time spent there by all species.

Continuing our example of Cory's Shearwaters from Madeira, the total monthly time spent in the high seas (T_{spme}) was calculated for the 11 months of the year where tracking data existed $(m_1\ to\ m_{max})$ and then divided by the full 12 months of the year to convert the unit from 'bird-months' to 'bird-years'. To put this species and population-specific pattern in the global context, we added the resulting total amount of time spent by Cory's Shearwaters to the values of all other breeding populations visiting the high seas $(p_1\ to\ p_{max})$, giving the total amount of time spent in the high seas in a year by the global community of albatrosses and large petrels (T_e).

Since tracking data were unavailable for some months of the year for certain populations, T_e was underestimated in these cases because the unit conversion still divided the sum of all tracking months by 12 rather than the number of months for which tracking data were available; however, we preferred this conservative approach because calculating over the full year avoided extrapolating occurrence patterns into un-sampled periods. The sum of T_e across all maritime zones therefore equals the population size of all breeding populations with tracking data minus the un-tracked portions of the year for each population (i.e. 41.3 million bird-years estimated for 44 million birds, see section Filtering and Standardization). To visualize the time spent pattern in space, we aggregated annual time spent over hexagonal grid cells of 452 km2 using the same equation (i.e. where e signified grid cells).

6.3.4.1 Network analysis

To estimate the strength of connection between breeding-origin countries and other visited maritime zones, we developed an index based on the percentage of annual time spent per maritime zone by populations of different breeding origins. The proportion of annual time spent G_{soe} in maritime zone e by species s breeding under the jurisdiction of origin country o was calculated as:

$$G_{soe} = \frac{\sum_{p=1}^{x} \sum_{m=1}^{m_{max}} (T_{spme})}{N_s * 12} \tag{3}$$

where the total within-month time spent (T_{spme}) was summed across all months and all tracked populations x of a given species breeding in country o, and converted from ‘bird-months’ to ‘bird-years’ by dividing by 12. This annual time spent value was then divided by the global population size Ns of that species, to calculate the proportion of annual time spent in each maritime zone by all individuals of said species.

In our example of Cory’s Shearwaters from Madeira, we first added the total amount of time spent in the high seas in each month (T_{spme}) across all tracking months of the year, resulting in 115,844 bird-months. Similarly, we calculated 1,988,600 bird-months spent in the high seas across the year for Cory’s Shearwaters from the Azores and 4771 bird-months for the Berlengas population, which resulted in a total of 2,109,215 bird-months or 175,768 bird-years for all breeding populations of Cory’s Shearwater falling under the jurisdiction of Portugal. We then divided the latter value by the global population size of 423,672 individuals of that species, to estimate that the proportion of time spent (G_{soe}) in the high seas (e) attributable to Cory’s Shearwaters (s) of Portuguese breeding origin (o) was 41.5% of annual time for the species.

Then, the strength of connection between each breeding-origin country and visited maritime zones was calculated as the percentage of annual time spent in each zone summed across all the species breeding in each country:

$$G_{oe} = \sum_{s=1}^{s_{max}} G_{soe} * 100 \tag{4}$$

where G_{oe} indicated the strength of the connection between breeding-origin country o and visited maritime zone e with respect to the global breeding population for each species, and to the breeding community in each country. The connections were ranked by strength (G_{oe}) and the strongest links were then plotted in a network diagram. We represented the 'top connections' per breeding-origin country in the network as 1) the top five links in the country-to-country and the high seas analysis, and 2) the top three links in the country-to-RFMO competence area analysis (see Table S6.6 and S8 for full set of connections). All analyses were run using R statistical computing environment; maps were made using the R packages 'ddgridr', 'ggplot2', and 'sf', and networks were constructed using 'ggraph' (Barnes, 2018; Pebesma, 2018; Pedersen, 2018; R Core Team, 2020; Wickham, 2016). Analysis scripts are available at https://github.com/MartinBeal/political_connectivity.

6.4 RESULTS

6.4.1 Standalone importance of countries and the high seas

All 39 species of albatrosses and large petrels visited the high seas during their annual cycles, and except for the Shy Albatross Thalassarche cauta all species visited the areas of jurisdiction of at least one country outside their breeding origin (**Table 6.1**, **Fig. 6.1**, data S1). France had the highest total species richness (n=28) and visiting-species richness (n=26), while Argentina and Brazil had the highest number of species visiting which do not also breed in areas under their jurisdiction (n=23 and n=19, respectively; **Fig. 6.1**A). New Zealand had the highest number of breeding species (n=15) and the United Kingdom had the highest richness of species which both breed in areas under their jurisdiction and visit from elsewhere (n=10; **Fig. 6.1**B, data S1). In general, countries hosting a high diversity of breeding species also hosted a high number of visiting species, and countries with larger territories had higher richness (**Fig. 6.1**B, Fig. S6.4). Brazil, Uruguay, Namibia, and Peru were each visited by ≥10 species although have no breeding populations, and Antarctica (areas south of 60°S) was visited by 20 species (**Fig. 6.1**A, data S6.1).

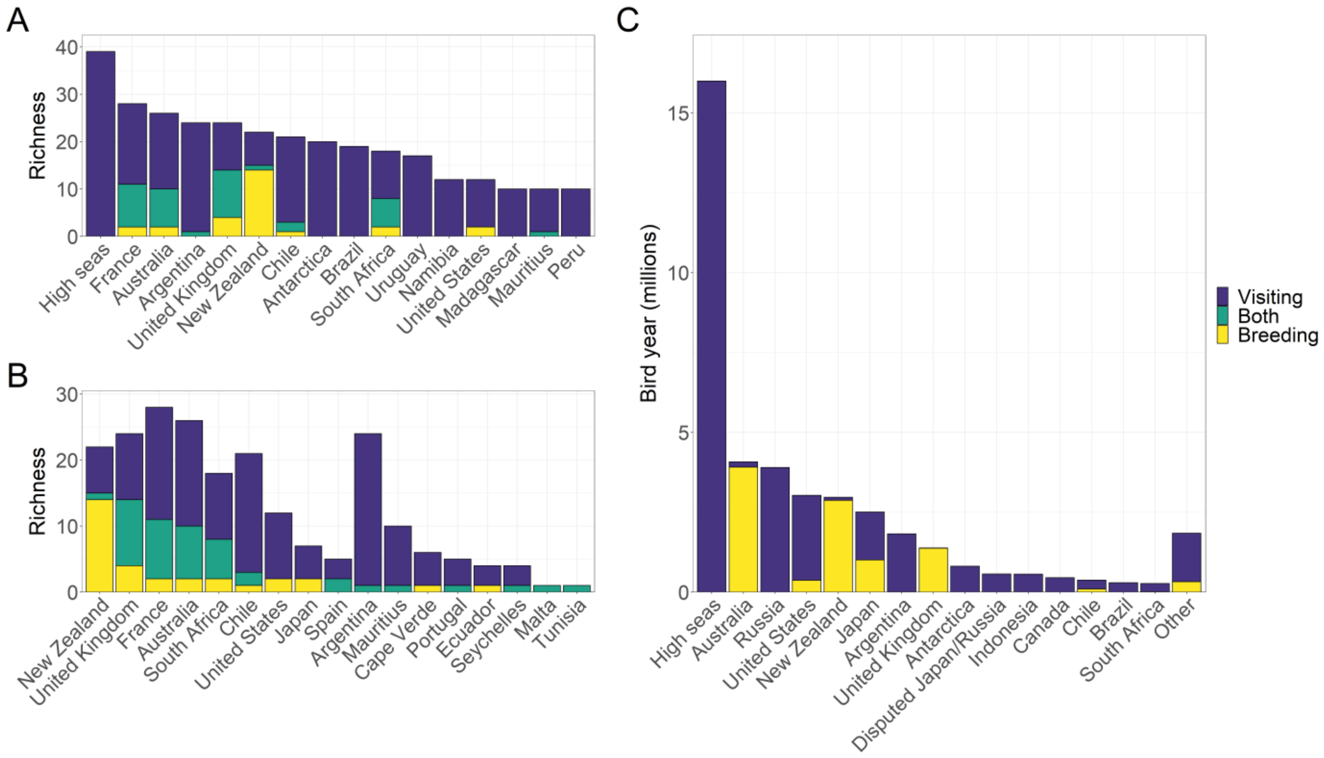

Fig. 6.1 Standalone importance of countries and the high seas for albatrosses and large petrels. (A, B) Species richness within national jurisdictions and the high seas. For each political area, richness is divided into three categories: Species which breed in the country ('Breeding'), species which visit the area but do not breed ('Visiting'), and species which both breed locally and visit from elsewhere ('Both'). (A) Top fifteen areas in terms of total species richness. (B) Species richness of countries which host breeding populations, ordered by breeding richness. (C) Most important areas in terms of annual time spent, an index of abundance, by adult albatrosses and large petrels split into visiting and breeding bird components. Areas shown host more than 0.1% of annual time spent, with all others summed into the category 'Other.' National jurisdictions refer to the aggregated exclusive economic zones (up to 200 nautical miles from shore) of each country and 'High seas' refers to all areas beyond national jurisdiction.

These species richness values were estimated directly from available tracking data; for several species, the sampled sites are not comprehensive of all breeding sites and therefore reported richness values are underestimates for certain countries. Breeding richness estimated from the tracking data was on average 1 species (mean, SD ±1.4) fewer than true breeding richness as calculated from the literature. Estimated richness was equal to true richness for 9 of the 22 countries which are known to have at least one breeding species of albatross or large petrel (data file S1). In most cases, missed breeding populations are relatively small in global terms, because our data included the majority of the global breeding population of each species (**Table 6.1**).

The high seas as a whole hosted the greatest amount of time spent by albatrosses and large petrels across the year, including 16 million of the total 41.3 (39%) million estimated bird-years (**Fig. 6.1**C). Among national jurisdictions, Australia had the highest annual time spent (i.e. by both visiting and breeding birds), with 4.0 (9.6%) million bird-years. Russia and the United States hosted the most time spent by visiting birds, representing an annual 3.9 (9.4%) and 2.7 (6.5%) million bird-years, respectively (**Fig. 6.1**C, data S1). Australia and New Zealand each hosted the highest annual time spent by their own breeding populations, with a respective 3.9 (9.4%) and 2.9 (7.0%) million bird-years (**Fig. 6.1**C, data S1). Static maps of annual species richness and time spent revealed contrasting patterns of albatross and large petrel diversity across the world (**Fig. 6.2**). The spatial pattern of time spent per month varied within a year, reflecting the dynamic seasonal distributions of albatrosses and large petrels (movie S1).

6.4.2 Geopolitical connectivity

In terms of annual time spent, the high seas as a whole represent a ‘top connection’ (i.e. one of the top five most-visited areas) for the albatross and large petrel communities of all breeding-origin countries (**Fig. 6.3**A). At the global level, the breeding communities of the United Kingdom, France, and New Zealand, have the strongest links to the high seas, indicated by the time spent there by the large breeding populations in these countries (i.e. proportions of all adult birds of each species), as well as the number of species making the connection. South Africa and Brazil were top connections for four separate breeding-origin countries (South Africa: France, Portugal, Spain, and United Kingdom; Brazil: Argentina, Cabo Verde, Portugal, and United Kingdom) and France, Peru, Mauritania, Russia, and USA, were among the top connections for populations breeding in three different countries (**Fig. 6.3**A, data S2A).

All high seas areas under the legal competence of RFMOs hosted a top connection with at least one breeding-origin country, with the exception of the smallest RFMOs (the North Atlantic Fisheries Organization – NAFO, and the Convention on the Conservation and Management of Pollock Resources in the Central Bering Sea - CCBSP; **Fig. 6.3**B). The International Commission for the Conservation of Atlantic Tunas – ICCAT, the Western and Central Pacific Fisheries Commission - WCPFC, and the South Pacific Regional Fisheries Management Organisation – SPRFMO represented the most important high seas areas, in terms of the number of top connections with breeding origin countries and the strength of connection (**Fig. 6.3**B, data S2B). The competence areas of ICCAT, WCPFC, and SPRFMO are among the largest in the world, and the size of RFMO areas was positively related to the total strength of their connections with breeding-origin countries (i.e. the sum of all connections per RFMO, **Fig. 6.3**B; R2=0.6, p<0.001, df=12, Fig. S6.4).

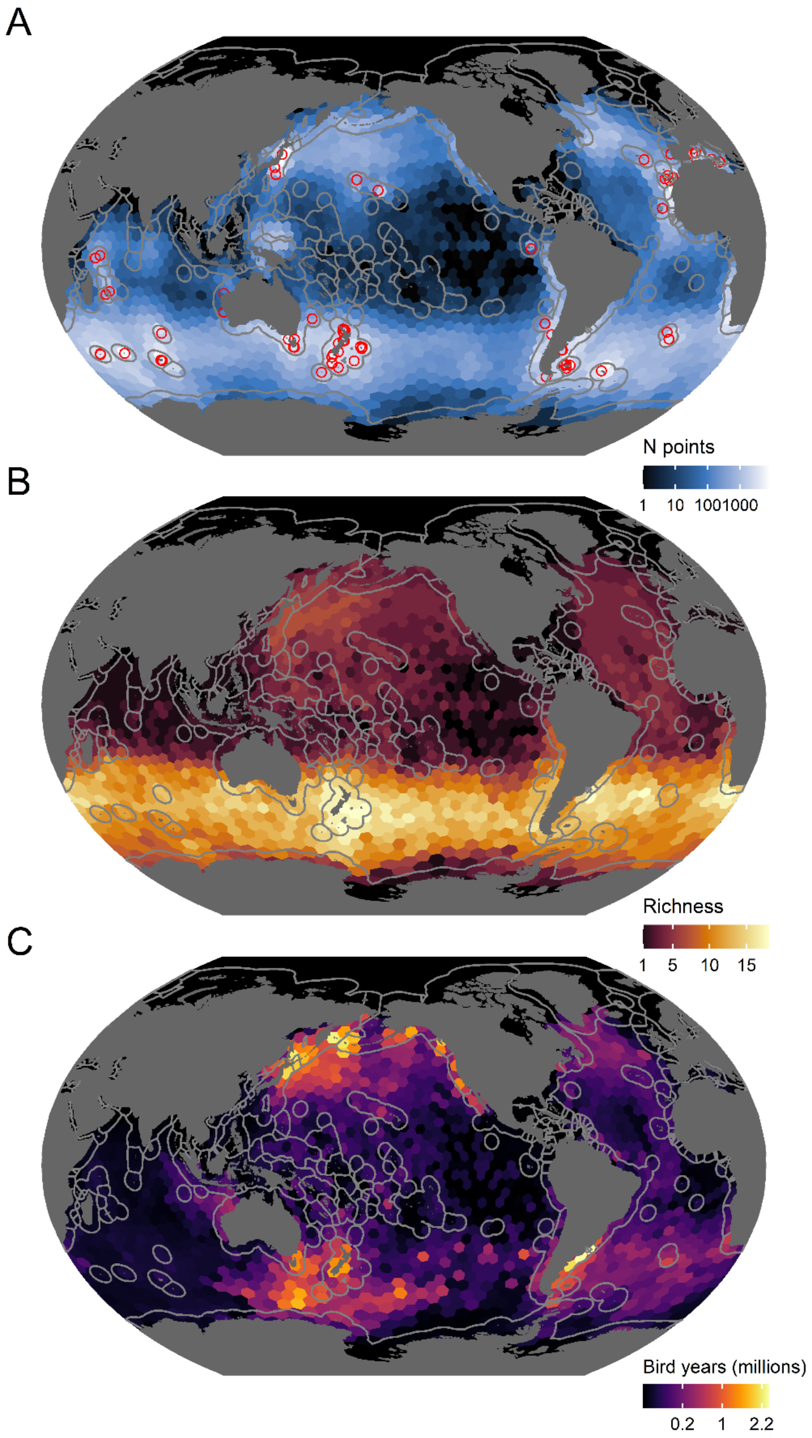

Fig. 6.2 Tracking data and year-round distributions of albatrosses and large petrels. (A) Study sites (open red circles) and the number of daily positions derived from tracked birds. (B) Species richness of adult birds in a breeding year. (C) Time spent during a breeding year. Cells indicate the total amount of time spent by the global breeding population of albatrosses and large petrels in a year. Grey lines at sea represent borders of national Exclusive Economic Zones.

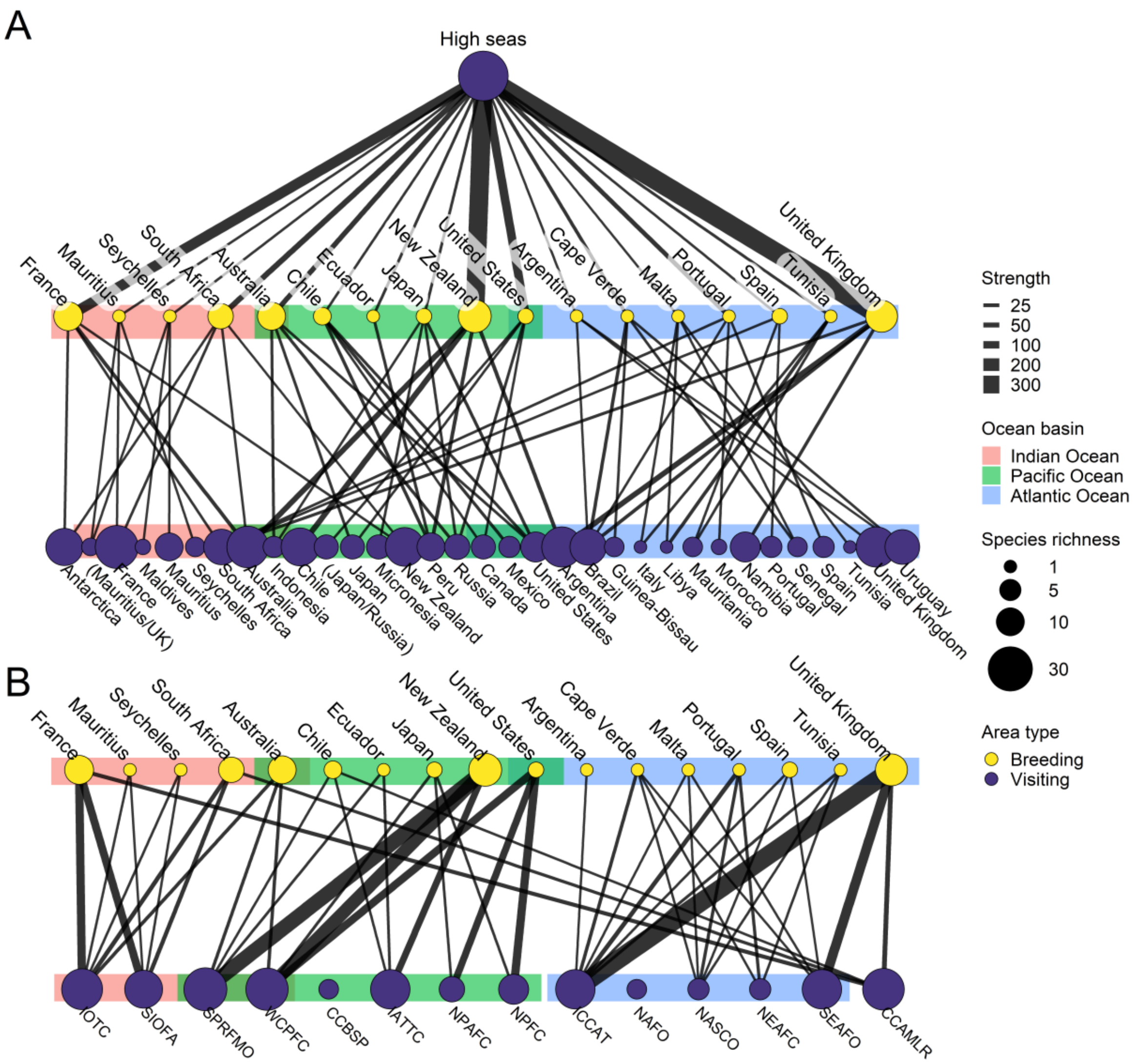

Fig. 6.3 The most important geopolitical connections for albatrosses and large petrels. Connections are between breeding-origin countries (yellow dots) and visited national jurisdictions or high seas areas (purple dots), with dot size respectively representing the breeding and visiting richness in each, and the link width signifying the strength of the connection. Connection strength is quantified as the percentage of annual time spent in the visited area, summed across the species making the connection. Annual time spent is calculated for each breeding population and weighted by the size of the population relative to global total of each species. (A) Top five connections between each breeding-origin country and the other areas visited throughout the annual cycle. (B) Top three connections between breeding-origin countries and the areas of competence of regional fisheries management organizations (RFMOs) in the high seas. Colored boxes represent the ocean basin in which most of the jurisdictional waters of each country are located. RFMO abbreviations correspond to (left to right): Indian Ocean Tuna Commission, Southern Indian Ocean Agreement, South Pacific Regional Fisheries Management Organisation, Western and Central Pacific Fisheries Commission, Convention on the Conservation and Management of Pollock

Resources in the Central Bering Sea, Inter-American Tropical Tuna Commission, North Pacific Anadromous Fish Commission, North Pacific Fisheries Commission, International Commission for the Conservation of Atlantic Tunas, Northwest Atlantic Fisheries Organization, North Atlantic Salmon Conservation Organisation, North East Atlantic Fisheries Commission, South East Atlantic Fisheries Organisation, Convention on the Conservation of Antarctic Living Marine Resources.

6.5 DISCUSSION

Migratory species cover immense distances on their seasonal movements, connecting numerous areas both within and beyond national jurisdiction and making their conservation a challenging task. By analyzing a comprehensive tracking data set and accounting for the size of each breeding population relative to the global total, our study provides the first global estimation of the relative importance of political areas to a group of highly threatened migratory megafauna, the albatrosses and large petrels. We estimated the standalone importance of national jurisdictions and the connectivity between them, providing a potential road map for international collaboration. We also quantified the connections between breeding-origin countries and areas of legal competence of RFMOs in the high seas, providing a useful scoping tool for identifying which national populations of albatrosses and large petrels may be impacted by management decisions in international fisheries. Our results showed that the high seas are important to albatrosses and large petrels from every country and in every ocean basin, indicating that effective management of international waters is of common, global interest.

By identifying the specific set of countries visited by albatrosses and large petrels originating in different countries, our findings provide support for existing bi-lateral and multi-lateral agreements and reveal additional connections of importance for these species. Our network confirms the connections, in terms of their albatross and petrel populations, among signatories of the CMS daughter agreement ACAP (which lists 29 of the 39 species studied herein) (R. A. Phillips et al., 2016), and shows that bi-lateral agreements, such as the Japan-Australia Migratory Bird Agreement or the New Zealand-Chile arrangement for protecting seabirds affected by fisheries, have measurable importance. However, our results also reveal important gaps; for example, many birds from both Australia and Japan use Russian waters, yet there are no treaties or agreements between these countries which reflect this relationship. South Africa and Brazil host large numbers of birds from breeding populations across the Atlantic Ocean, and despite the engagement of these countries in CMS instruments, the most numerous species (i.e. Calonectris and Ardenna shearwaters) which contribute to these connections are not listed in CMS appendices and are therefore at risk of being omitted from international policy developments concerning migratory marine animals. In order to minimize gaps in protection, we suggest that any international conservation efforts for albatrosses and large petrels would benefit by considering the relative importance of countries for these species as identified herein.

Our maps of species richness and annual time spent reveal contrasting patterns in these two measures of biodiversity, and identify hotspots both within and beyond national jurisdictions. Areas of high species richness were concentrated in the Southern Ocean, whereas areas of high annual time spent were generally distributed in the productive waters of continental shelf or upwelling regions, like the Patagonian Shelf in the South Atlantic Ocean and the Kuril Trench in the North Pacific Ocean. Notably, some areas of high annual time spent occurred in specific regions in the high seas, such as the Southern Ocean south of Tasmania, the northwest Pacific Ocean, and north-central Atlantic Ocean. The identified hotspots largely reflect the distributions of several species that are highly abundant trans-equatorial migrants, which number in the millions in the Atlantic (Great Shearwater Ardenna gravis) and Pacific Oceans (Sooty A. grisea and Short-tailed shearwaters A. tenuirostris). Our synthesis provides global snapshots of albatross and large petrel diversity, which have markedly seasonal distributions (see Supplementary animation). The extensive and dynamic ranges of migratory marine megafauna, such as albatrosses and large petrels, indicate that static, area-based conservation measures alone, like marine protected areas, are not sufficient to address threats (S. M. Maxwell et al., 2020; Oppel et al., 2018). Very large MPAs or those with dynamic management, with boundaries that shift across space and time, can be effective during the breeding season for certain species (29). However, during the non-breeding season, when the movements of seabirds are less restricted, process-oriented, and ecosystem-based management across the wider seascape is required (Oppel et al., 2018). Regardless of the spatio-temporal scale of the approach, for any at-sea area-based protection to have positive outcomes for albatross and large petrel conservation, the implementation of effective fisheries measures is vital.

The high seas constitute the most important at-sea area for albatrosses and large petrels globally. Our estimates provide countries with tangible, quantitative indicators of the relative importance of the high seas for their respective communities of breeding seabirds, which is highly pertinent for countries involved in the ongoing discussions on the BBNJ treaty. The treaty objective is the conservation and sustainable use of high seas biodiversity; however, based on the precondition of “not undermining” pre-existing management organizations and bodies, fisheries have been excluded from treaty discussions (Haas et al., 2020). As the major, immediate at-sea threats to albatrosses and large petrels relate largely to fisheries (Dias et al., 2019), this may represent a missed opportunity to improve fisheries governance; nevertheless, there are still a number of ways in which the BBNJ treaty could influence RFMOs to the benefit of albatrosses and large petrels (Haas et al., 2020). These include, by formalizing a global process for establishing area-based management tools with appropriate regulations regarding bycatch and overfishing, by improving transparency and information sharing (particularly related to bycatch) via the establishment of an independent scientific committee, and by setting specific thresholds of impact that trigger the need for fisheries (or any other industry) to implement environmental impact assessments (Haas et al., 2020; Marciniak, 2017).

Our results also provide information to breeding-origin countries about the RFMO management areas in the high seas which are most important to each of their seabird populations. Despite being important due to their ocean-basin scale, the tuna RFMOs (ICCAT, WCPFC, Indian Ocean Tuna Commission - IOTC, and Inter-American Tropical Tuna Commission - IATTC) are particularly relevant to albatross and large petrel conservation as industry practices have frequently been linked with overfishing and high bycatch rates (Clarke et al., 2014; Cullis-Suzuki & Pauly, 2010). Fishing fleets operating in the high seas are under the jurisdiction of their flag states (White et al., 2019); therefore, despite not hosting albatrosses and large petrels within their national jurisdictions, some countries still impact them through poor fishing practices (Clay et al., 2019). The effectiveness of regulatory measures ultimately depends on the attitude of each country in terms of implementation and monitoring of compliance; however, as RFMOs operate on a consensus basis, it is the countries with a will to protect non-target biodiversity that must push for effective regulation. Our results confirm that national measures for albatrosses and large petrels must be coupled with coordinated, international efforts if they are to successfully mitigate threats occurring across the ranges of these species. For example, while many species of conservation concern breeding on South African, French, UK, and Australian islands benefit from national action plans for reducing bycatch within national waters and fleets (Good et al., 2020), birds are still at risk from longline effort in the high seas of the Indian Ocean, where they spend a considerable part of the year (**Fig. 6.3**B). Despite this, these countries have not advocated for the improvement of bycatch mitigation measures at the Indian Ocean Tuna Commission since 2012.

The tracking data set used herein spanned the global ranges and annual cycles for most of our focal group, the albatrosses and large petrels, providing a uniquely representative picture of their global distribution (85% and 75% on average, respectively; **Table 6.1**). Nevertheless, gaps remain in terms of untracked populations and un-sampled months of the year. Using knowledge of known breeding sites and population sizes, we quantified these sampling limitations (**Table 6.1**) and thereby identified gaps at the species level where future work may be focused (Campbell et al., 2015; Dias et al., 2014). Tracking and population data were only analyzed for breeding adults and therefore our results pertain to the global breeding populations of each species in a given year. A substantial proportion of the global population is made up of juveniles, immatures, and deferring breeders (particularly for biennial species), which may have different annual distributions and hence geopolitical connectivity (Campioni et al., 2019; Sergio et al., 2014). These are important gaps to fill in terms of tracking and monitoring effort; however, as these data accumulate, syntheses across ranges, taxonomic groups, and life stages can become standard practice (Carneiro et al., 2020).

Here we stress that, when possible, population delineations and size estimates should be incorporated when identifying areas that are important for migratory species (Hindell et al., 2020; Schuster et al., 2019), or subject to particular threats (J. M. Handley et al., 2020; S. M. Maxwell et al., 2013). Our results show how such analyses can quantify political responsibility and reveal unexpected linkages, providing opportunities for improving the conservation of migratory species. The high seas are a global commons, where there is a lack of effective legal processes for ensuring the conservation and sustainable use of biodiversity. We show that migratory seabirds across the world connect numerous countries and the high seas, thereby contributing to the connectivity of the global ocean. As human endeavor in the marine environment expands, it becomes more important than ever that our systems of management and protection reflect this interconnected reality.

CHAPTER 7

GENERAL DISCUSSION

Animal tracking has advanced the field of marine biology and contributed in crucial ways to conservation efforts (Hays et al., 2019). This thesis helped further the application of tracking data to the field of marine conservation by: (Chapter 3) introducing a tool for identifying important sites for biodiversity from tracking data, and providing novel insights into the conservation of marine wildlife based on analyses of existing data. Specifically, the results presented in this thesis provide: (Chapter 4) estimates of the relevance of multi-annual tracking of seabird populations to identify important sites, (Chapter 5) assessments of the spatial coverage of a marine protected area network for a globally important population of sea turtles and (Chapter 6) a global scale quantification of the importance of connections among national jurisdictions and high seas areas for conserving a highly threatened group of seabirds, the albatrosses and large petrels.

7.1 AREA-BASED CONSERVATION: A PIECE OF THE PUZZLE

A major focus of this thesis was to inform area-based conservation efforts (S. L. Maxwell et al., 2020). Important sites provide spatial layers of biodiversity value, which can be used in marine spatial planning exercises, such as protected area establishment and other zoning deliberations (Wright et al., 2019). By introducing the R package ‘track2KBA’ this thesis contributes directly to the identification of important sites for marine biodiversity, namely Key Biodiversity Areas. Chapter 3 illustrates how this user-friendly data analysis tool can be used to identify important sites for a wide variety of taxa in different seasons. The availability of accessible analysis tools helps facilitate the conversion of tracking data into conservation-relevant information (Hays et al., 2019), and by being flexible in implementation, ‘track2KBA’ can contribute to ensuring that networks of important sites, and ultimately protected areas, reflect the varying needs and vulnerabilities of different taxa.

Identifying sites of ecological importance and establishing protected areas are vital to conserving marine biodiversity in both coastal and offshore areas (Brander et al., 2020). However, it is important to recognize that area-based measures alone are not a conservation panacea (Kaiser, 2005). Process-oriented regulation will also be crucial to effectively managing the impacts of human activities on wildlife (Kaiser, 2005; Oppel et al., 2018). For example, where implemented (and enforced), fishing regulations meant to decrease the incidence of seabird bycatch have had great effect, such as the recent 98.4% reduction in albatross bycatch in Namibian hake fisheries (Da Rocha et al., 2021). Chapter 6 showed that albatrosses and large petrels spend nearly 40% of their time in high seas areas managed by regional fisheries management organizations (RFMOs). This indicates that even if countries have strong conservation and management regulations within national waters, successful cooperation at international fora, such as RFMOs, are necessary to ensuring that albatrosses and large petrels are protected throughout their seasonal ranges. Although some positive changes to fisheries practices have been made, a number of cost-effective solutions remain un-adopted and a current lack of transparency undermines confidence in the progress of RFMOs to reduce impacts on non-target species (Gilman et al., 2014). Nevertheless, to attain functioning ecosystem-based management of the ocean environment, it is essential to combine both area-based strategies with appropriate regulation of human activities (e.g., extractive and transport), both within protected areas and across the wider seascape (Dias et al., 2018; Juan-Jordá et al., 2018).

7.2 BEYOND THE INDIVIDUAL

Tracking devices record the movements of individual animals, however, the real power for informing conservation comes when patterns can be interpreted at the population or species level (Gutowsky et al., 2015). To accurately do so, it is important to quantify how much information a sample contains when extrapolating results to higher levels of biological organization (Canessa et al., 2015; Shimada et al., 2020). For this reason, a key step in identifying important sites for biodiversity using the R package ‘track2KBA’, introduced in Chapter 3, is to assess the representativeness of the tracked sample for the wider population. The different examples given in Chapter 3 showed how quantifying the representativeness of tracking samples helps ensure robust inference of the number of individuals in the wider population using delineated sites.

The number of years a population is tracked may influence how robust an important site derived from such data will be. The results of Chapter 4 showed that given a large enough sample of individuals, a single year of tracking data can be sufficient for important site identification. However, in cases where the environment is highly variable or shifting under climate change, it will be important to re-evaluate the long-term relevance of sites derived from one or few years of tracking data (Fromant et al., 2021; Osborne et al., 2020). These results are highly relevant for the continued development of guidelines for implementing important site identification criteria, such as the KBA Standard, which recommend a set minimum number of years of data be used when identifying sites (KBA Standards and Appeals Committee, 2020).

When making inference at the species level, it is additionally important to consider the size of the tracked population to the global total. In Chapter 6, the relative contribution of the tracked study populations to the global numbers for each species was considered, allowing for species-level calculations of total time spent in national jurisdictions and high seas areas throughout the year. This is particularly important for widespread species, or where the behavior and habitat use of tracked populations may differ from those in other parts of the species' range (Torres et al., 2015).

7.3 MIGRATION CORRIDORS

For many migratory species, a major gap in protection occurs during the migratory period, when a series of sites and habitats are used which are often separated by large distances and may be located in different countries (Runge et al., 2014). The methods used in the R package 'track2KBA' identify locations where high numbers of individuals spend relatively long periods of time (B. G. Lascelles et al., 2016). Chapter 3 showed how, for a migrating White Storks, these methods can identify stopover and staging sites, which support resting and refueling and are thereby vital to the viability of migratory routes (Arizaga et al., 2018).

During migration, landscape topography (e.g., coastlines and mountains) and environmental conditions (e.g., wind or ocean currents) influence the routes migrants take, which can lead to spatial constrictions of passable travel conditions and cause animals to aggregate (Buechley et al., 2018; Cardenas-Ortiz et al., 2020). Such "corridors" (or "bottlenecks, in the extreme case), represent constrained areas through which relatively high numbers of individuals transit, not stopping to rest or re-fuel (Torres et al., 2017). Chapter 5 identified corridors where female Green Turtles concentrate while migrating to remote foraging grounds, including a notable bottleneck around the Cap Vert peninsula of Senegal. Future work could further test the methods used in Chapter 5 to identifying migration corridors, with the goal of integrating the approach into important site identification analysis protocols, such as under the KBA Standard. This would allow for the identification of important transit sites, complementing the "track2KBA" approach, which mainly identifies important foraging and resting sites.

Further, by using tracking datasets from multiple species or combining with conventional survey data, the importance of bottleneck 'hotspots' could be quantified. For example, while our results indicate the importance of the Cap Vert peninsula to migrating turtles, seabirds are also known to concentrate there, however little work has been done to quantify the apparent importance of this site for both aerial and sub-surface migrants (Dubois et al., 2009). Existing initiatives, such as the Migratory Connectivity in the Ocean Project (https://mico.eco/) provide hopeful beginnings to such work, by identifying migratory corridors using standard analysis protocols and converting tracking data into policy-relevant outputs (D. C. Dunn et al., 2019).

7.4 ARE THE KIDS ALRIGHT?

Historically, tracking data has been biased towards the reproductive portions of populations, either due to welfare or practical concerns (Bernard et al., 2021; Wikelski et al., 2007). This bias extends to the results of this thesis, where the tracking data used in each chapter came from adult animals only. However, this does not undermine the relevance of this work, as reproductive adults are indeed the most important population cohort, from a conservation standpoint. Nevertheless, the spatial distributions of immature age groups represent a major gap in our knowledge of many marine species (Hazen et al. 2012). As indication of this, the years between which sea turtles hatch and return to the same beach to nest are known as the “lost years” (Putman & Naro-Maciel, 2013).

As a result of this sub-adult information gap, our ability to integrate the needs of these age classes into conservation and management planning is limited, putting population viability at risk (Frankish et al., 2021). This is beginning to change, thanks in part to the continuing miniaturization and general improvement of tracking technologies. As tracking data from sub-adult age classes begins to accumulate, similar studies could be performed as those presented in this thesis. For example, the political connectivity of immature albatrosses and large petrels could be interesting to quantify, as available information suggests that, compared to adults, younger age classes are more exploratory in their movements and may be more at risk to be caught in fisheries (Afán et al., 2019; Frankish et al., 2021; Orben et al., 2018). Such future studies could shine light on to what conservation and management considerations are lacking to successfully protect animal populations from the cradle to the grave.

7.5 ANIMAL TRACKING: ONE TOOL TO RULE THEM ALL?

The use of animal tracking continues to grow, and the wealth of information this affords is supporting efforts across the world to conserve marine species (Hays et al. 2019). However, it is important to recognize that, rather than being mutually exclusive, other techniques for studying marine life remain important and can complement and validate results derived from tracking data. In a recent example, estimates from ship-based surveys of the importance of an area for a seabird community in the North Atlantic were similar to those derived from tracking data (Davies et al., 2021; Wakefield et al., 2021). These independent results lent support to successful efforts to establish a high seas marine protected area to conserve this seabird ‘hotspot’ (Davies et al., 2021). As important as the role animal tracking will be in the future of marine ecology and conservation, it is but one of many tools necessary to understand and protect the marine environment.

7.6 CONCLUDING REMARKS

"*In the end we will conserve only what we love; we will love only what we understand; and we will understand only what we are taught."* (Baba Dioum, 1968.)

This thesis endeavored to show how animal tracking has and continues to help us understand the marine world by affording a view into intimate aspects of the lives of wild animals. This insider view helps answer basic questions of where animals go and when, setting a foundation from which to pose new questions and on which to build conservation efforts. This thesis illustrated ways in which tracking data can inform local spatial protection as well as broader international efforts to cooperate for marine conservation. However, perhaps one of the most important contributions of tracking data is to help make visible the lives, in all their diversity and complexity, of marine animals and thereby grow social awareness of and appreciation for this ‘blue’ part of our planet, for its own sake and for ours.

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ANNEX: SUPPLEMENTARY MATERIALS AND METHODS

CHAPTER 3

TRACK2KBA: AN R PACKAGE FOR IDENTIFYING IMPORTANT SITES FOR BIODIVERSITY FROM TRACKING DATA

1: Supplementary methods

Importance of the ‘dataGroup’

The movement patterns and spatial distributions of highly mobile species often change across seasons. Therefore ‘track2KBA’ is designed to identify important sites for a source population year-round or during a specific seasonal life-cycle stage. It is important that input tracking data represent movements sampled from periods in which the animals in the source population are moving in a similar manner to one another. In the initial analytical functions in the ‘track2KBA’ workflow, the input argument for tracking data is ‘dataGroup’, and is intended to represent tracks of animal movements sampled from the same source population and seasonal life-cycle stage. The package is available for download from CRAN, and a simple example of the package workflow analyzing available data from a ‘dataGroup’ of Masked Boobies (*Sula dactylatra*) tracked from St. Helena island during the chick-rearing period may be found at https://github.com/BirdLifeInternational/track2kba (Oppel et al., 2015).

Utilization distributions

In ‘track2KBA’, utilization distributions for each track (i.e., animal or independent trip) are estimated using the estSpaceUse function, which is a wrapper of the kernelUD function in the tracking analysis package ‘adehabitatHR’ (Calenge, 2006). KDE derives a probability surface (i.e., utilization distribution [UD]) by overlaying Gaussian kernels on point data. For an accurate representation of core areas using kernel density estimation (KDE), tracking data should be projected to an equal-area coordinate reference system and approximate an even temporal sampling regime (i.e., points spaced evenly in time), which may be achieved by interpolating or down-sampling tracking data to the lowest common interval. The ‘track2KBA’ function projectTracks can be used for spatial projection, and the packages ‘adehabitatLT’, ‘crawl’, and ‘ctmm’ provide interpolation methods (Calabrese et al., 2016; Calenge, 2006; Johnson & London, 2018).

Setting the ‘*h*’ or smoothing parameter is an all-important step, as the results of KDE are highly sensitive to this value; a small parameter value could result in disjointed kernels surrounding each tracking location (‘under-smoothing’, e.g., Fig. S6.1A), whereas a large value may result in over-estimated space use areas for each animal (‘over-smoothing’, e.g., Fig. S6.1C).

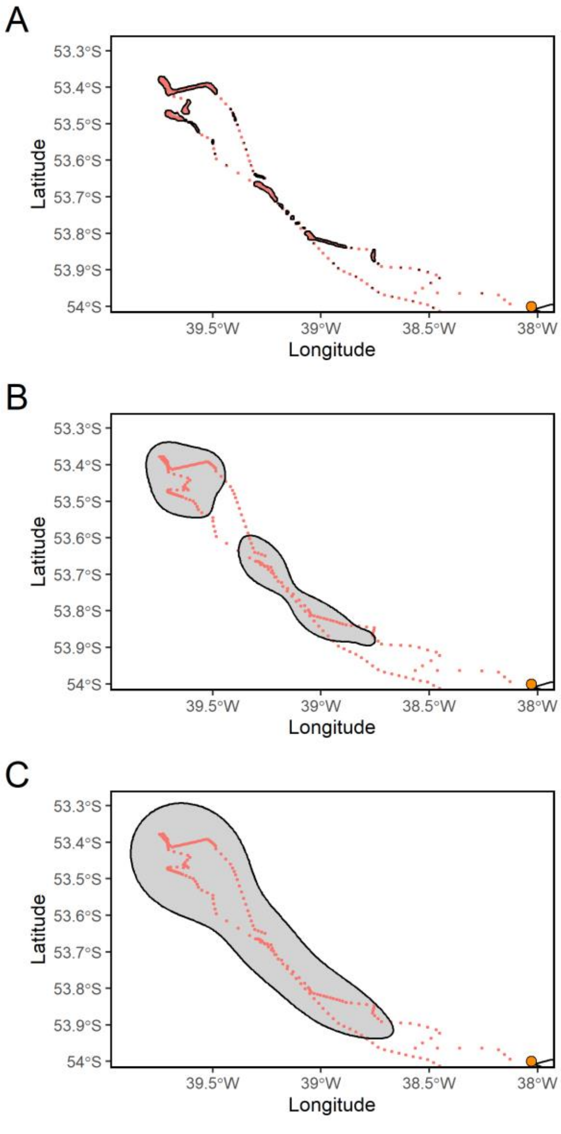


Fig. S3.1. Effect of different *h* (smoothing) parameter values on the resulting 50% UD (core area) estimated (grey area) for a foraging trip of an adult Antarctic fur seal. (A) An *h* parameter of 0.5 km results in an ‘under-smoothed’ estimate of the core areas used by the seal, with the space use estimate closely hugging the data. (B) An *h* parameter of 4.65 km, calculated as the log of the foraging range among all 118 tracked seals (findScale option ‘mag’), results in an ecologically sensible estimate in this case, with areas where the animal spent roughly 50% of its time being delineated by the core area border. (C) An *h* value of 11 km, calculated as the average reference value across the tracked seals (findScale option 'href'), gives an 'over-smoothed' estimate of the core area used during the foraging trip, including a very large area and >80% of all trip locations.

To guide the choice, it is useful to understand the scale at which animals are moving and the expected size of the areas of importance, based on the ecology of the focal species. If the study species is a central-place forager (e.g., when breeding or roosting), the functions tripSplit and tripSummary may be used to split the data into individual trips, and derive characteristics such as the maximum distance travelled from the central place (i.e., foraging range). findScale uses these trip characteristics, as well as the average step length (i.e., distance between sequential locations) to facilitate comparison with candidate *h* values.

findScale calculates candidate *h* values in three ways: First, for central-place foragers, the log of the median foraging range is taken to provide a value scaled to the spatial extent of movement bouts (findScale output 'mag'). Second, the median reference bandwidth (i.e., the average based on the number and spatial variance of tracking locations per individual) is calculated (findScale output 'href'; Calenge, 2006). Third, the log-variance in first-passage time (i.e., time spent within a circle of radius *r*) can be compared across a range of scales (i.e., radii) to identify peaks, indicating the scale at which the animal is interacting with the environment (Fauchald and Tveraa, 2003). By taking the median of these peak radii across the tracked individuals we derive an average value of interaction, which can be used as the smoothing parameter, *h*, for KDE (findScale output 'scaleARS').

Once an *h* value is selected, it is important to consider the resolution of the spatial grid over which the KDE will be calculated using estSpaceUse. The grid cell size (i.e., grid resolution) should be less than the selected *h* value*,* otherwise the entire space use area of the animal may be encompassed in few cells. Conversely, selecting a very small grid cell size exponentially increases computation time, and may lead to spurious precision (e.g., if the grid resolution is 100 m and the tracking device provides daily locations with animals moving tens of kilometers each day). Finally, the user must choose a quantile of probability that reflects the core areas of the distribution ('UDLev'); 50% is a standard choice, but in some cases other values may be more appropriate (Boitani & Powell, 2012; Dias et al., 2018).

Assess sample representativeness

The function repAssess allows users to estimate how representative their tracked sample is for the wider population. To do so, repAssess iteratively selects sub-samples of individual tracks, averages them into a pooled UD and outlines a desired quantile (e.g., 50%), and then calculates the proportion of out-of-sample tracking locations within the resulting area (i.e., the ‘inclusion rate’). After estimating this inclusion rate over a user-defined number of iterations and across a range of sample sizes, a non-linear generalized least squares regression is fitted to the relationship between sample size and inclusion rate:

$$y = \frac{an}{1 + bn} \tag{1}$$

where y is inclusion rate and n is sample size. By fitting the model, the sample size at which the group-level space-use pattern is unlikely to change upon further tracking (i.e., the asymptote) is estimated. Based on the modelled relationship between sample size and inclusion rate, repAssess then estimates the representativeness of the tracked sample as:

$$R = \frac{y_n}{A} * 100 \tag{2}$$

where R is the percentage of the asymptote A in the model achieved by the inclusion rate y estimated at sample size n. This proportion (inclusion rate) approximates the specified UD quantile when the tracked sample is fully representative (e.g., approximately 50% of locations for the entire source population would be expected to fall within the 50% UD of the sample). The repAssess function returns the percent representativeness, the estimated asymptote, and derives the minimum sample sizes needed to achieve 70% and 95% representativeness at the population level. Although the appropriate number of iterations to run will be dataset-specific, a minimum of 100 iterations is recommended; if variation in estimated inclusion rates is large (e.g., Fig. S4), then users can compare results across an increasing number of iterations until the percent representativeness stabilizes. To reduce bias caused by over-sampling across iterations, inclusion rate is calculated up to n – 3 for sample sizes of less than 50 tracks, to n – 2 for samples between 50 and 100 tracks, and n – 1 for samples above 100 tracks (Gutowsky et al., 2015). Therefore, repAssess requires a minimum of four independent tracks, but we caution users that estimation of the asymptote estimation is unreliable for small sample sizes (e.g., $n <$ 10 independent tracks).

Site delineation

The final step in the ‘track2KBA’ workflow is to identify and delineate important sites for the source population (i.e. areas used by a substantial portion of the population), and produce quantitative information about the site. To delineate a candidate site, the function findSite first calculates the proportion of individual core areas (i.e., % UD areas) overlapping per grid cell. This proportion of overlapping tracks is then multiplied by the proportional representativeness of the tracked sample to adjust the sample-derived pattern by the degree of representativeness. The result is a scaled estimate of the proportion of the source population that predictably uses each grid cell in the study region during the season of interest (Fig. S3.2). Important sites for the source population are delineated by grouping together grid cells used by a threshold percentage of the study population (Fig. S3.2; findSite output ‘potentialSite’).

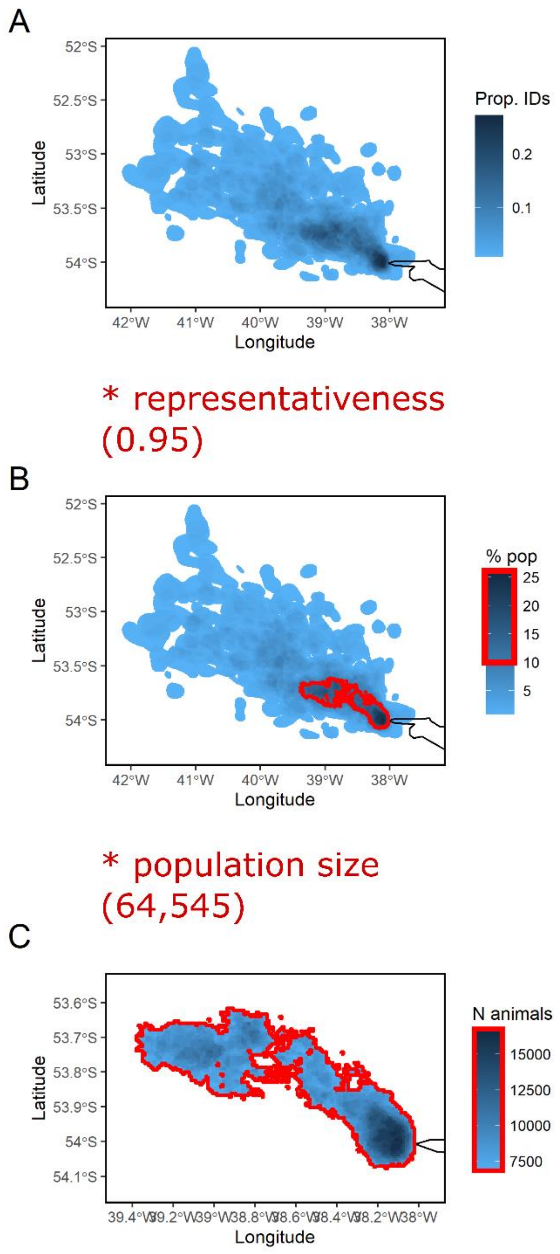


Fig. S3.2. Delineation steps taken within the function findSite, using the example of the Antarctic Fur Seals tracked from Bird Island. First, (A) the proportion of individual fur seal core areas (50% UDs) overlapping in space is calculated for each grid cell. Next, (B) the proportion of overlapping core areas is multiplied by the estimated representativeness (in this case 95%) to estimate the percentage of the broader source population which use each grid cell. At this step, grid cells used by at least 10% of the population are outlined in red, signifying an area of importance for the source population. Finally, (C) the proportion of the source population using each grid cell is multiplied by the estimated population size (64,545 adult female seals), providing the number of animals in the population which predictably use areas within the delineated site. Note that panel C shows only the delineated site and is therefore at a different scale from panels (A) and (B).

By default, findSite sets the threshold of site importance for the source population based on the degree of tracking sample representativeness following Lascelles et al. (2016): i.e., samples that are ≥90%, 80-89%, 70-79%, and <70% representative set the threshold for delineating a site as important for the local source population at 10%, 12.5%, 25%, and 50%, respectively (Fig. S3.3). Although population scaling using findSite is possible with samples of low representativeness, 70% is a recommended minimum level for assessing sites against global or regional criteria (Lascelles et al., 2016). When representativeness is <70%, the degree of certainty regarding population-level use of a particular site is likely too low, but could be appropriate in specific cases, (e.g., when the source population represents much or all of the global species population). Threshold values can be set by users using the 'thresh' argument to ensure they reflect levels of importance that contribute to population or species persistence.

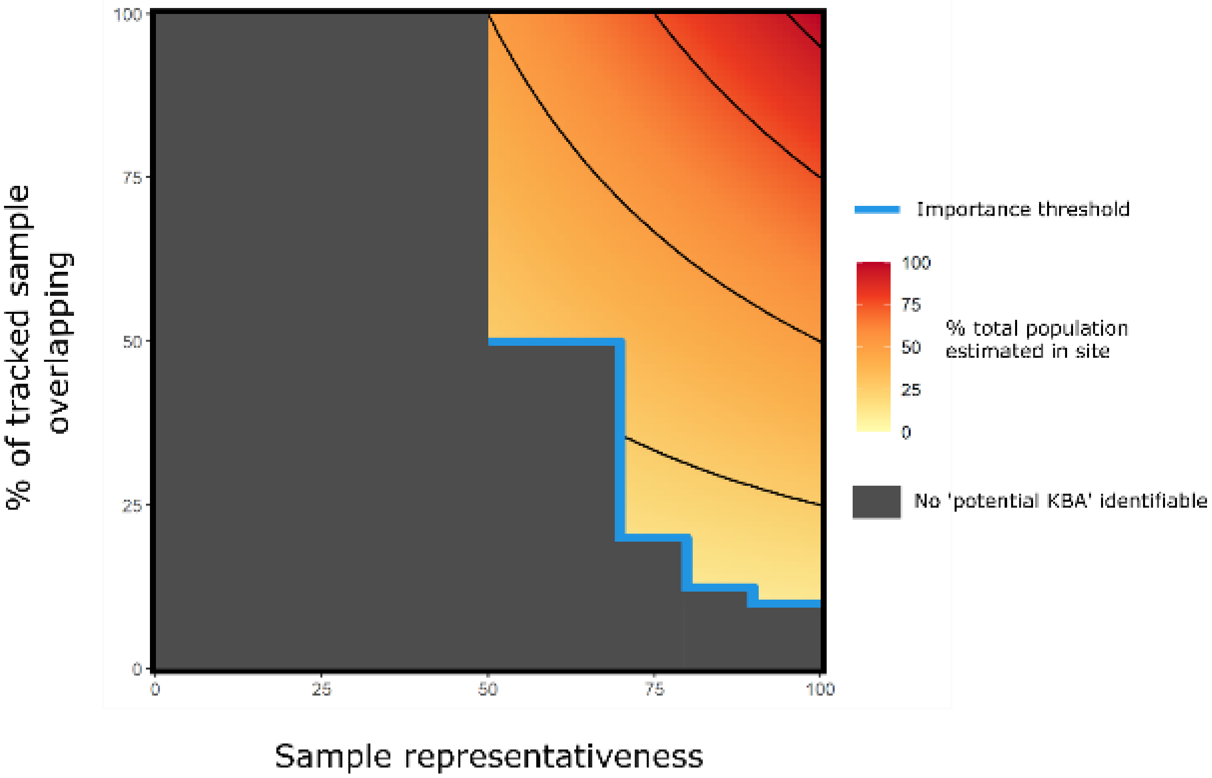


Fig. S3.3. Illustration of how potential sites of importance for a population are delineated from a sample of tracked animals, using the default importance thresholds of Lascelles et al. 2016. The X-axis signifies the percent representativeness of the tracked sample for the space use of the source population. The Y-axis indicates the percentage of tracked individual core areas (based on kernel density estimates) which overlap in any given grid cell in the study area. The color gradient signifies what proportion of animals in the source population are assumed to use a site for a given observed percentage of overlap among tracked individuals and a correction factor linearly related to the representativeness. The blue line then indicates the percent threshold of the population needed in a grid cell for it to be considered as part of a site of importance for the source population (i.e. a ‘potentialSite’). For example, if a sample of 25 tracked animals was estimated to be 90% representative of the wider source population, a vertical line up the figure at this level of representativeness represents the range of abundance values (in % of tracked population size) possible to estimate as using a site for this sample. Any grid cells used by >= 10% of the population would therein be considered ‘important’ for that local source population. Gray zones indicate situations in which grid cells would not be considered part of an important site, e.g., when sample representativeness is less than 50%.

When the size of the source population is known or estimated, this value can be used to provide an estimate of abundance across space. What defines the source population, and the resulting size estimate used, should be determined by study design and an understanding of the ecology of the focal species. For example, if space-use patterns are known a priori to vary from one part of the distribution to another (or across seasonal life-cycle stages), the population size estimate used should reflect only the portion of animals which the tracked animals actually represent (see White Stork application for an example). The function findSite multiplies the user-specified population size estimate by the estimated proportion of the source population using each grid cell. The resulting scaled estimate of abundance represents the number of animals predictably using the site, which is useful for assessing delineated sites against global standardized criteria, such as the KBA Standard (IUCN, 2016).

Table S3.1. List of each function in the package ‘track2KBA’, and a description of purpose, inputs and outputs.

Key functions	
findScale	Calculate a set of candidate *h* parameter values for Kernel Density Estimation. Input is SpatialPointsDataframe object in equal-area projection. Output is ‘data.frame’ object of candidate *h* parameter values.
estSpaceUse	Calculate track-level (e.g. individual) utilization distributions using Kernel Density Estimation. Input is SpatialPointsDataframe in equal-area projection. Output is either an ‘estUDm’ object or a list including an ‘sf’ object with the core areas per track.
repAssess	Estimate the degree of representativeness of a tracked sample to the source population. Input is projected ‘SpatialPointsDataFrame’ object of tracking data, and utilization

	distributions for each track. Output is a ‘data.frame’ with the estimated representativeness of the sample.
findSite	Calculate among-track spatial overlap, and scale up the sample pattern to the population based on the degree of representativeness. Input is ‘estUDm’ or ‘SpatialPixelsDataFrame’ of utilization distributions, and the sample representativeness. Output is object of class ‘sf’ or ‘SpatialPixelsDataFrame’ with information on overlap among tracks and potential important sites.
Optional functions	
formatFields	Format the key data fields to the standard used in ‘track2KBA’. Input and output are 'data.frame’ objects.
move2KBA	Import and format a data set stored in MoveBank. Input is MoveBank study ID and user information. Output is a list with tracking data and study site information.
projectTracks	Project tracking data to equal-area projection. Input is ‘data.frame’ or ‘SpatialPointsDataFrame’ of tracking data. Output is ‘SpatialPointsDataFrame’.
indEffectTest	Compare the degree of within-group to between-group spatial overlap. Input is projected ‘SpatialPointsDataFrame’ of tracking data and the column names corresponding to each group. Output is a list with overlap information and results of a Kolmogorov-Smirnov test.
tripSplit	Split tracking dataset into discrete trips, based on distance and/or time away from a given location. Input is a ‘data.frame’ of tracking data and the central-place location. Output is a ‘SpatialPointsDataFrame’.
tripSummary	Summarize the spatiotemporal characteristics of trips. Input is ‘SpatialPointsDataFrame’ from tripSplit. Output is ‘data.frame’ summary of trip characteristics.
mapTrips	Plot the output of tripSplit to visualize trips for each track.
mapKDE	Plot the output of estSpaceUse to visualize utilization distributions for each track.
mapSite	Plot the output of findSite to visualize spatial overlap and borders of important sites.

2: Walk-through of fur seal analysis

117 adult female fur seals were tagged at Bird Island (54°00’S, 38°03’W) during 1996-1999 using Platform Terminal Transmitters (Staniland et al., 2020). To standardize the data before analysis with ‘track2KBA’, we excluded erroneous positions based on a speed filter and re-sampled (linear interpolation) positions to achieve a regular 30-minute sampling interval using

the adehabitatLT package (Calenge, 2006). In this example, the ‘dataGroup’ analyzed represents adult female fur seals from the Bird Island population during the breeding.

During the breeding season, fur seals forage at sea and regularly return to their breeding colony on land, so we split tracking data into discrete foraging trips to characterize the scale of movement. Using the function tripSplit, we defined trips as periods of ≥ 12 hours spent away from the colony at a distance of ≥ 5 km (Fig. 3.2A).

```
seal.trips <- tripSplit(dataGroup=seal.data, innerBuff=5, duration=12, rmNonTrip=T)
```

Because our interest was in estimating aggregations away from the colony and not nearby loitering sites, we removed all except the first and last locations of each trip that fell within a 5 km radius of the colony from the analysis (argument ‘rmNonTrip’). 5 km was selected as an appropriate ‘innerBuff’ distance by inspecting individual tracks to ensure that loitering behavior near the colony was excluded.

We then calculated trip characteristics using the function tripSummary,

```
seal.summary <- tripSummary(dataGroup=seal.trips, colony=seal.colony)
```

which showed that seals travelled a mean maximum distance of 114 km (max 296 km) and spent a median of 5.6 days (max 19.8 days) at sea per foraging trip.

Next, we projected the movement tracks to a custom-centered, azimuthal equal-area projection with the function projectTracks, and then estimated individual core areas as the 50% UDs using the function estSpaceUse with an *h* parameter value of 4.65 km (Fig. 3.2B). The *h* value was calculated using the function findScale and represents the log of the median foraging range (in km); this value was selected as it captured areas that represent ecologically realistic estimates of the space in which individuals spent most of their time while at sea (fig. S3.1B).

```
seal.trips.proj <- projectTracks(seal.trips, type=’azim’, custom=TRUE)

seal.scale <- findScale(seal.trips.proj, sumTrips=seal.summary)

seal.UDs <- estSpaceUse(seal.trips.proj, scale=seal.scale$mag, levelUD=50)
```

We used the function repAssess to estimate the representativeness of this tracked sample for the core area distribution of the wider Bird Island population.

```
seal.rep <- repAssess(seal.trips.proj, KDE=seal.UDs, iteration=200, levelUD=50)
```

We bootstrapped the analysis over 200 iterations at each sample size from *n*=1 to *n*=116 (i.e., one less than the total *n* of 117 seals), resulting in an estimated representativeness of 96%

for the full sample (Fig. 3.2C). Next, we provided the individual core areas, the representativeness estimate, and the population size estimate as input to the function findSite and delineated sites used by at least 10% of the Bird Island population (i.e., the default importance threshold for the source population for a sample with > 90% representativeness; Fig. 3.2D, fig. S3.2, fig. S3.3):

```
seal.site <- findSite(KDE=seal.UDs, represent=seal.rep$out, popSize=64545)
```

We identified an area of 1,576 km^2 to the north-west used by up to 23.6% (16,787 seals) of the Bird Island female population (Fig. 3.3D, Fig. 3.4A), which translates to an estimated 1.7-2% of the 700,000-1,000,000 fur seals in the global population that predictably use the site during breeding, and could thereby meet the criteria for a global KBA under 'Demographic aggregations' criterion D1 (IUCN, 2016).

3. Supplementary applications information

Green Sea Turtles

In 2018 and 2019, a total of 23 female turtles were tagged with tracking devices (15 with PTT and 8 with both PTT and Fastloc Global Positioning System [FGPS]) on the nesting beaches of Poilão Island (10° 51′ N, 15° 43′ W). We omitted low-quality PTT positions of class A, B, and Z, and used a data-driven speed and interior angle filter provided by the package 'SDLfilter' to remove erroneous FGPS points (Shimada et al., 2012). After filtering the data, we retained only post-laying and post-migratory foraging periods for analysis with 'track2KBA', and distinguished these on a track-by-track basis as extended sedentary periods away from the nesting island. The median sampling rate was 2.3 h (IQR 10 h) (Fig. S3.4).

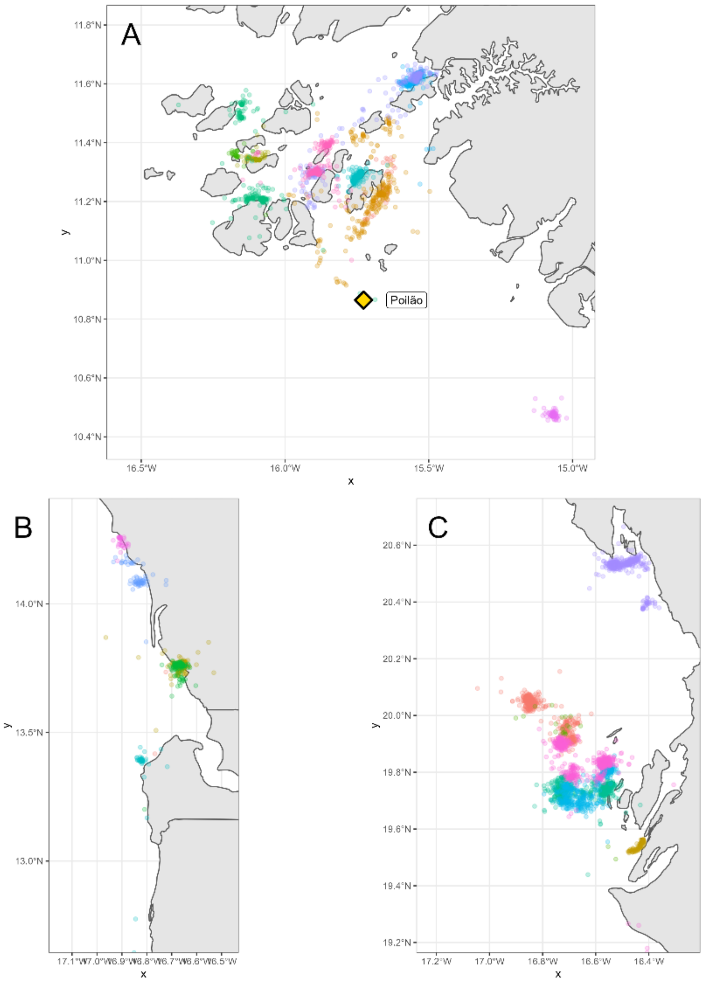


Fig. S3.4. Tracking locations collected from 23 adult female green turtles (*Chelonia mydas*) during the post-nesting foraging period in (A) the Bijágos Archipelago of Guinea-Bissau, (B) Senegal and The Gambia, (C) and the Banc D'Arguin region of Mauritania. The yellow diamond in panel A indicates the nesting island of Poilão, where all individuals were tagged during egg-laying. Each color indicates the locations of a different individual turtle.

The estimated size of the laying population at Poilão of 18,573 adult females was calculated as follows: In 2017 there was an estimated 29,537 nests, in 2018 there were 14,941 nests, and in 2019 there were 11,240 nests, giving a total of 55,718 nests across this period. Assuming each female returns once in three years and lays three nests: 55,718 nests / 3 nests per individual = 18,573 adult females laying at Poilão.

For each individual turtle, we estimated core areas (50% UD) using an *h* parameter of 2.18 km, which was the median of the reference bandwidth across individuals (Fig. S3.5A). We chose this parameter value as the resultant core area estimates reflect ecologically realistic space use known for the species during the foraging period (Pilcher et al., 2014). We then estimated the sample representativeness by calculating the inclusion rate from sample sizes of *n*=1 to *n*=20, iterating the process 800 times to ensure a robust calculation of the mean inclusion rate (Fig. S3.5B). Due to the broad area over which turtles disperse in the post-laying period, coupled with the restricted scale of their movement when foraging, the sample achieved only 32% representativeness, and is therefore not considered representative of the population-level distribution.

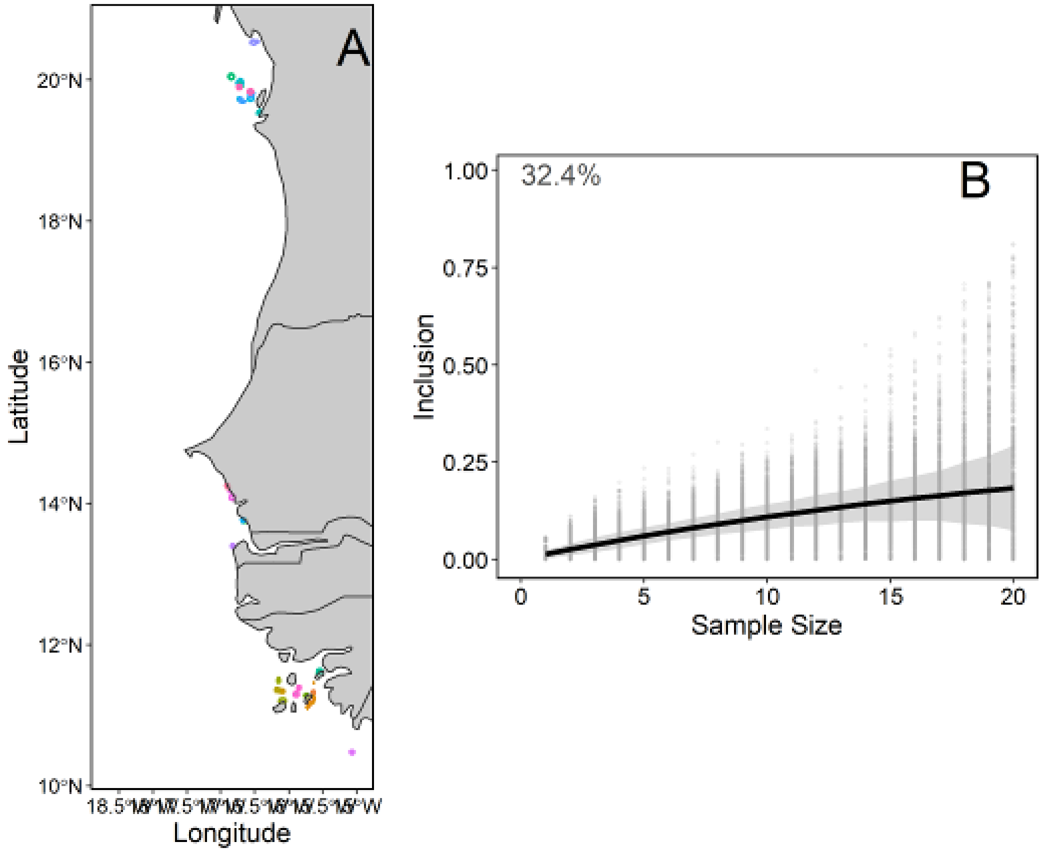


Fig. S3.5. (A) Individual core use (50% utilization distributions with *h* parameter of 2.18 km) estimated for 23 Green Sea Turtles during the post-egg laying period. All individuals were tagged during egg-laying on Poilão Island of the Bijagós Archipelago in Guinea-Bissau. (B) Estimation of the representativeness of the sample for the wider Poilão laying population, bootstrapped across 800 iterations. Sample achieved an average of 32% of the asymptotic relationship fitted between inclusion rate and sample size, indicating there is substantial space use not represented in this sample.

White storks

The dataset analyzed here of 76 storks tagged with GPS-GSM loggers during 2016-2019 was assumed to be an appropriate sample of the migratory patterns of the Portuguese population as storks were tagged at a total of 23 unique sites, including nesting colonies, solitary nests, and garbage dumps located throughout southern Portugal (between 37.04 N and 38.93 N); 60 individuals were juveniles, 2 immatures (1-3 years of age), and 14 adults. An estimated 75% of the adult population remain resident in Portugal each year, and migratory adults, immatures, and juveniles do not differ in their choice of migratory routes nor stopovers, so all tracks were analyzed together (I. Catry et al., 2017). Migratory periods (north and southbound) were distinguished from breeding and over-wintering based on close inspection of each individual track. The grand mean (mean of individual medians) sampling rate was 20 min (SD 4 min) (Fig. S3.6).

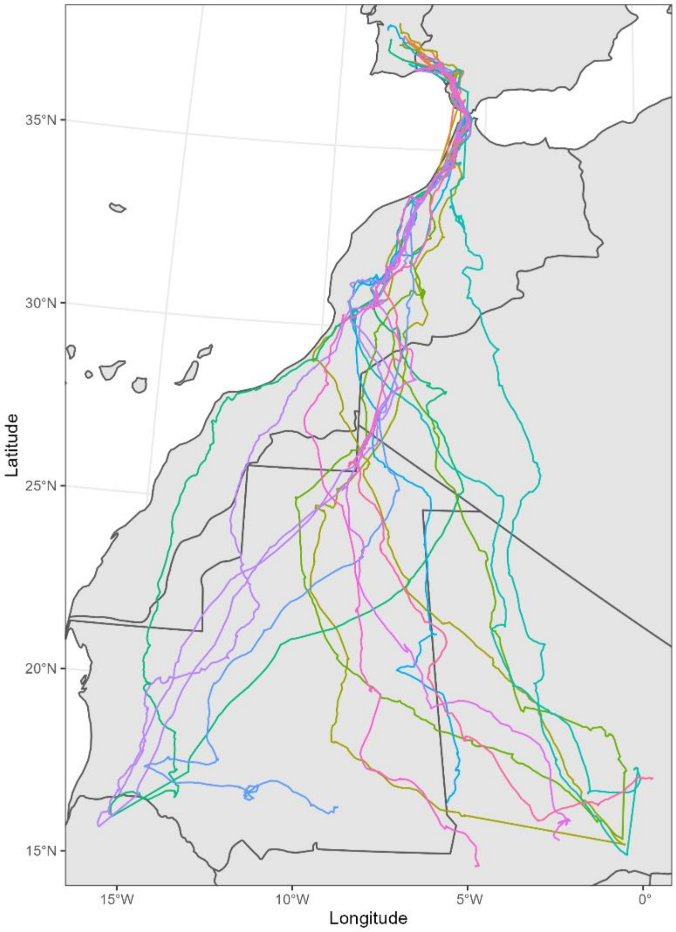


Fig. S3.6. Example subset of the movement tracks of 15 White Storks (*Ciconia ciconia*) tracked between their breeding grounds in southern Portugal and the over-wintering areas in northern and sub-saharan Africa. Each color represents a different individual.

The annual population size estimate for Portugal of 46,027 White Storks was calculated as follows: based on the known number of breeding pairs (23,382 adult individuals * 25% migrate = 5846 migratory adults) the number of birds fledged into the population was estimated (14,997 juveniles, 100% of which migrate), and the number of immatures was estimated based on a juvenile and immature survival rates of 30% and 70% respectively and an immature migration rate of 70% (5,354 migratory immatures). Summing the results of these calculations, we estimated that 26,196 of the total population of White Storks in Portugal migrate each year.

We estimated core areas (50% UD) for each individual using an *h* parameter of 7.5 km, which was determined as the median peak in the variance of the log of First-Passage Time across individuals (Fig. S3.7A). We chose this method as it identifies the spatial scale at which the storks are spending the most time (Fauchald & Tveraa, 2003), which on migration should represent stopover sites. The representativeness of the sample was then estimated by calculating the inclusion rate from sample sizes of *n*=2 to *n*=74, across 200 iterations. The sample was estimated to be 96% representative of the source population distribution (Fig. S3.7B).

We delineated nine stopover sites, covering areas of between 19 km^2 and 1,150 km^2, in Spain and Morocco used by at least 10% of the Portuguese population of migrating white storks. Of these sites, four are predictably used by up to 8,600 (2 sites), 9,600, and 11,580 storks, respectively representing 18.7%, 20.9%, and 25.2% of the total Portuguese population (i.e., migratory and resident birds) of white storks. Assuming that 22% of the migratory population are adults, we estimated that these sites were used by at least 0.27-0.37% of the global adult population of 700,000 storks, and 0.43-0.57% of the estimated population in Europe of 447,000 adult storks (BirdLife International, 2016). These values likely underestimate the regional and global importance of these sites, as a number of other white stork populations in Europe are known to pass through this region during migration (Flack et al., 2016).

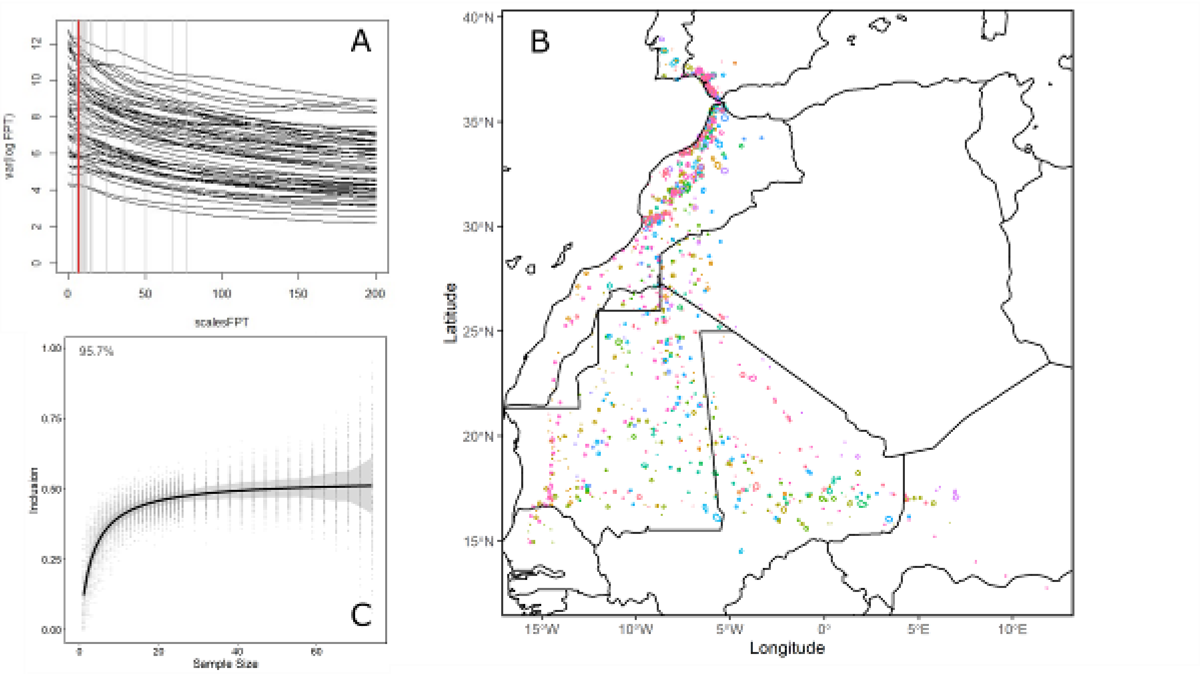


Fig. S3.7. (A) Calculation of the smoothing (*h*) parameter for kernel density analysis. X-axis are the radii within which the variance in log first passage time was calculated and the peak identified for each individual stork. The median across individuals was calculated as 7.5 km and represents the average spatial scale of interaction, i.e., the scale at which storks tend to spend the most time. (B) Individual core use areas (50% utilization distributions) during the migratory phase from the breeding grounds in Portugal to sub-Saharan Africa. (C) Estimated representativeness of the tracked sample of 76 individuals for the wider population of Portuguese storks during the migratory period, bootstrapped across 200 iterations. The tracked sample was estimated to achieve 95.7% of the asymptote, suggesting the sample is highly representative of the distribution of the source population.

CHAPTER 4

QUANTIFYING ANNUAL SPATIAL CONSISTENCY IN BREEDING SEABIRDS: IS ONE YEAR OF TRACKING DATA SUFFICIENT FOR IDENTIFYING IMPORTANT SITES FOR CONSERVATION?

Supplementary methods

Population habitat classification

Based on visual inspection of foraging trips over bathymetric data, we classified the predominant foraging habitat of each population as either ‘shelf’, ‘oceanic’ or ‘mixed’. We classified a species as a ‘Shelf’ forager when ~90% of foraging trips were in shallow waters (< 200 m) of a continental shelf or over fixed seafloor features (e.g., seamounts, shelf-breaks), and as ‘oceanic’ foragers when ~90% of trips were over deep waters off the shelf (> 200 m). When large portions of a population used both shallow and deep waters for foraging, we classified the species as a ‘mixed’ forager. See Table S4.1 for results of the classification.

Figures

Note: Figures S4.5-25 are available from M. Beal at request.

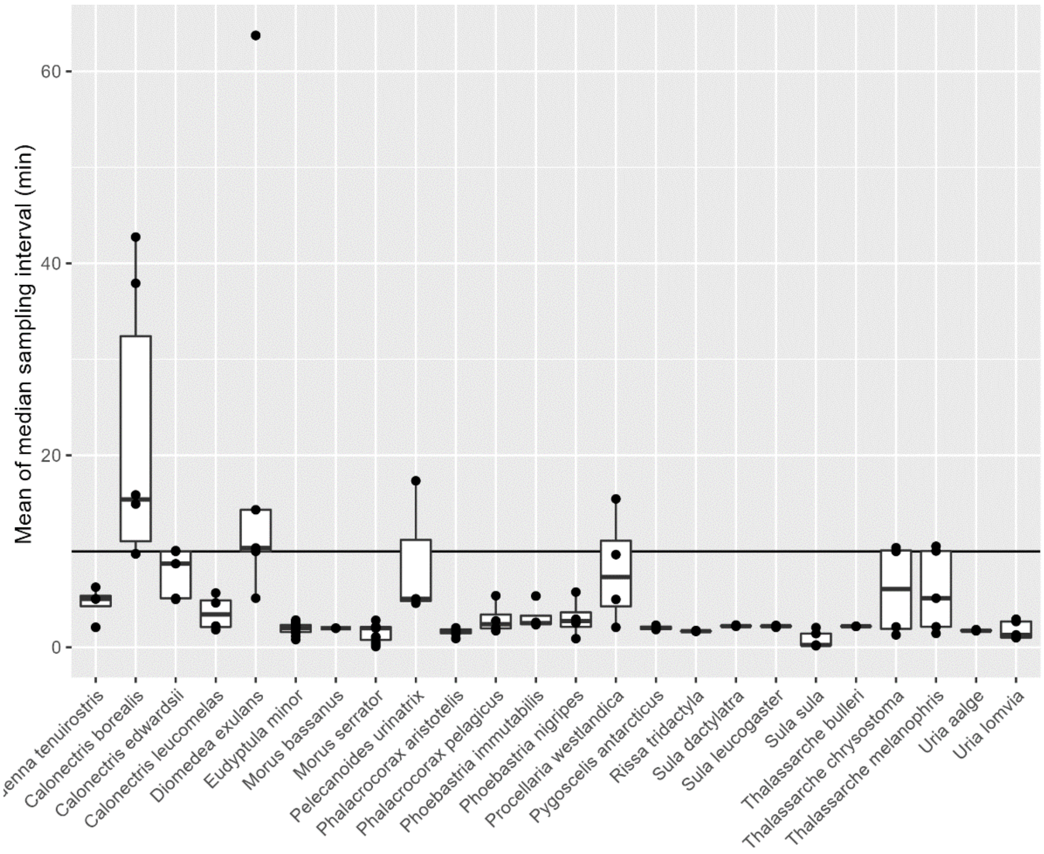


Fig. S4.1 Mean of median sampling interval of un-interpolated, speed filtered data from 23 species of seabirds. Points represent the mean of median calculated for each yearly dataset for each species. The black horizontal line represents the interpolation interval of 10 min, used to standardize all datasets to the same sampling interval.

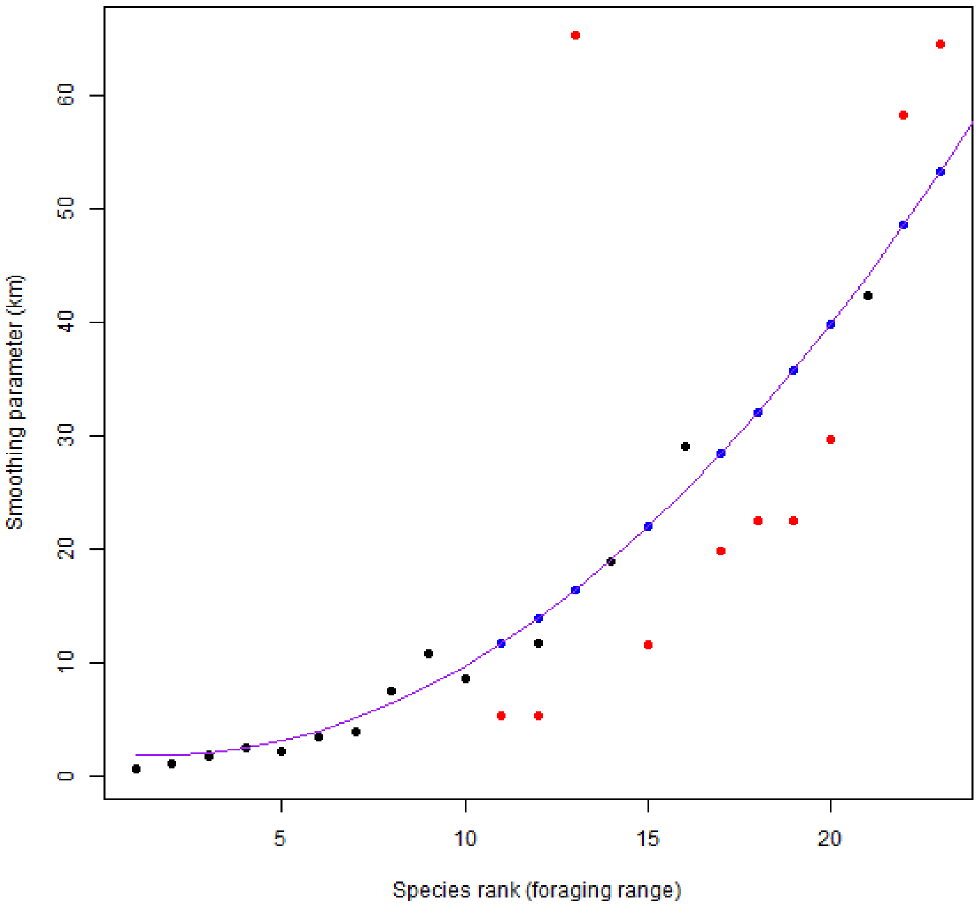


Fig. S4.2 Smoothing parameter calculations. Purple line represents the fit of a second-order polynomial model to the species ranks, ordered by median maximum foraging range (km). Black points represent the reference parameter values calculated directly from tracking data, while the red values represent outlier values deviating by greater than 5 km from the model fit. Blue points show the model predicted values for outlier species. Blue and black points are then the final smoothing parameter values used for each species.

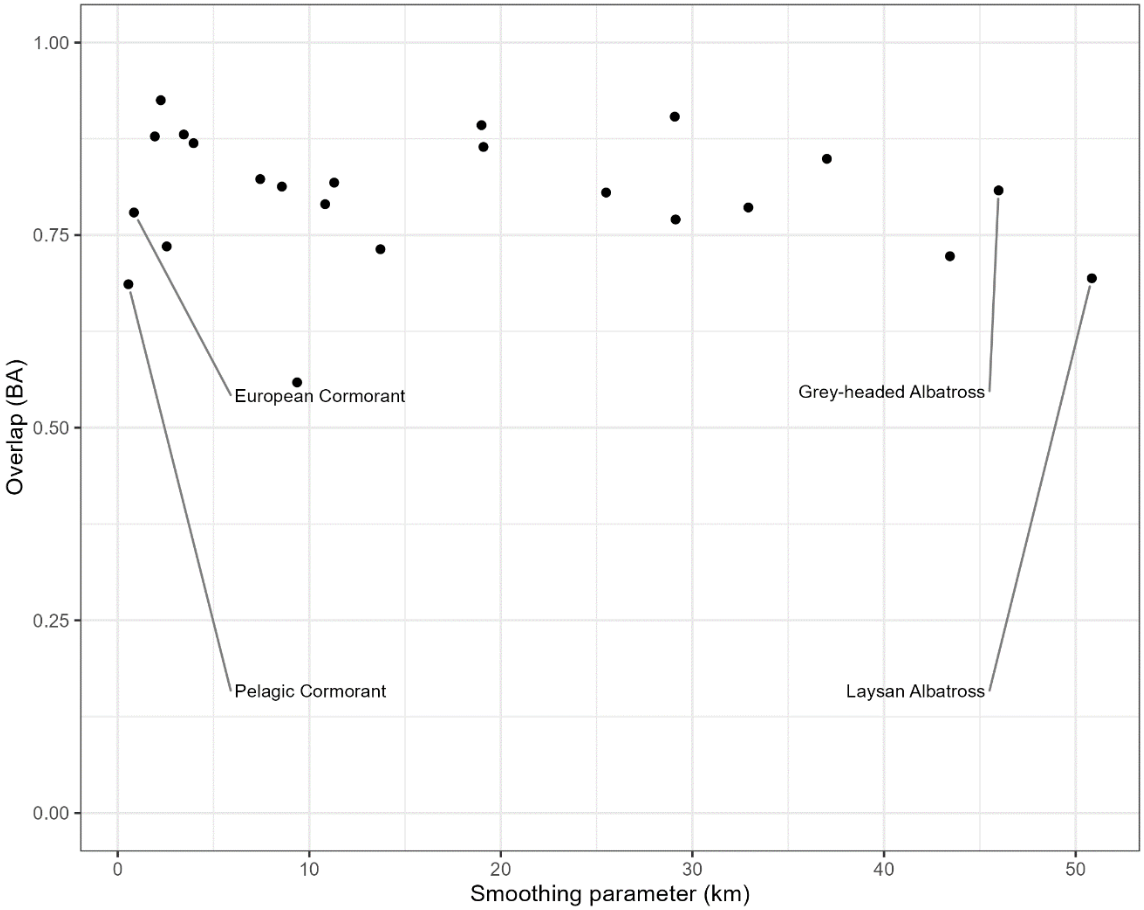


Fig. S4.3 The smoothing parameter used in kernel density estimation to derive single-year distributions against the consistency estimate for each species. The smoothing parameter was calculated based on the number of tracking locations and their spatial variability (‘href’ method), which accounts for difference in spatial scale of movements between species. Overlap represents the mean annual spatial consistency for each species, measured as the Bhatacharyya’s Affinity overlap among all single-year distributions.

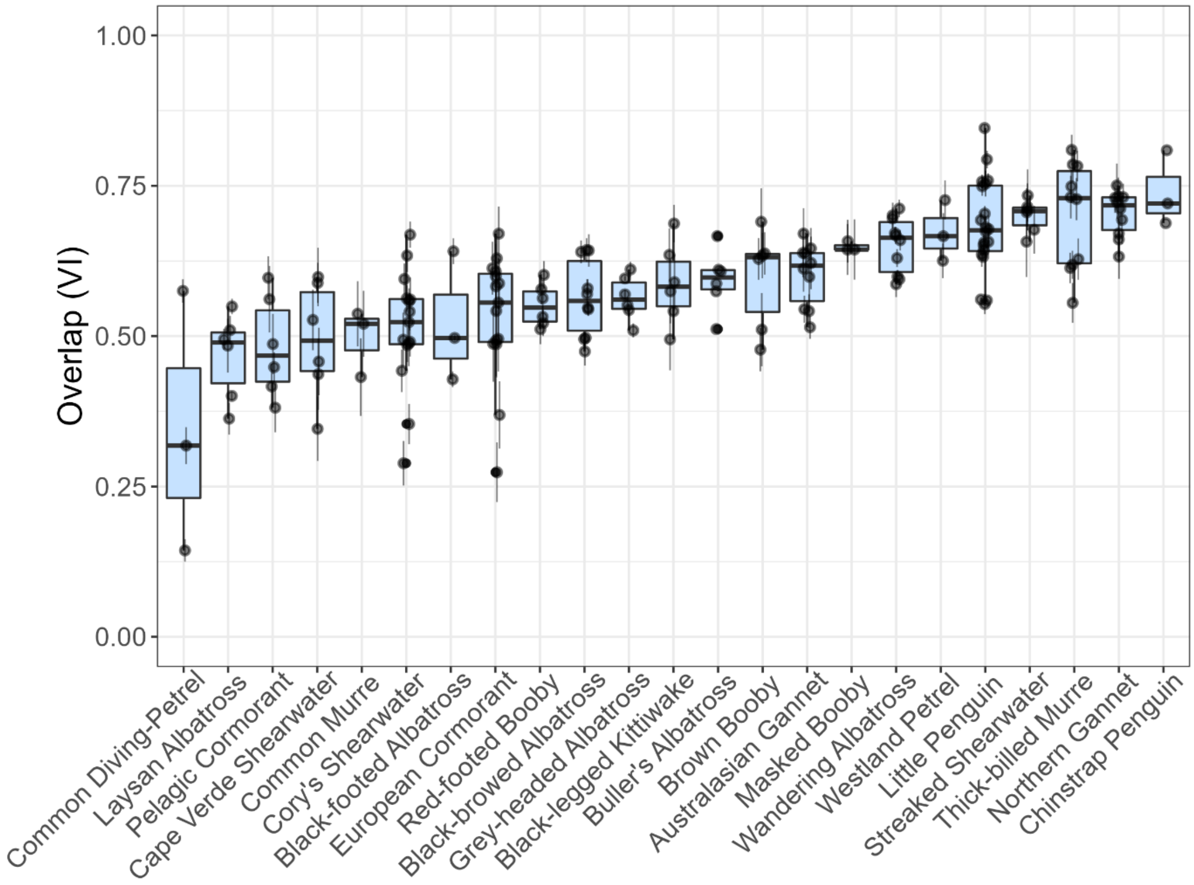


Fig. S4.4 Annual spatial consistency of 23 species of seabirds during the chick-rearing period. Consistency was estimated as the degree of spatial overlap between pairwise combinations of yearly distributions using the Volume of Intersection index (VI), a probabilistic measure of distribution similarity. This index was calculated to compare with the primary index used, Bhattacharyya's Affinity index (BA) (see Fig. 1 in main text). Species were ranked (from right to left) in terms of their mean level of annual consistency. Boxes represent the distribution of overlaps calculated across all pairwise combinations of years. Dots represent the mean overlap (and lines the standard deviation) calculated across 20 iterations of re-sampling, in each of which a single foraging trip was selected per individual to contribute to the yearly distribution of the population.

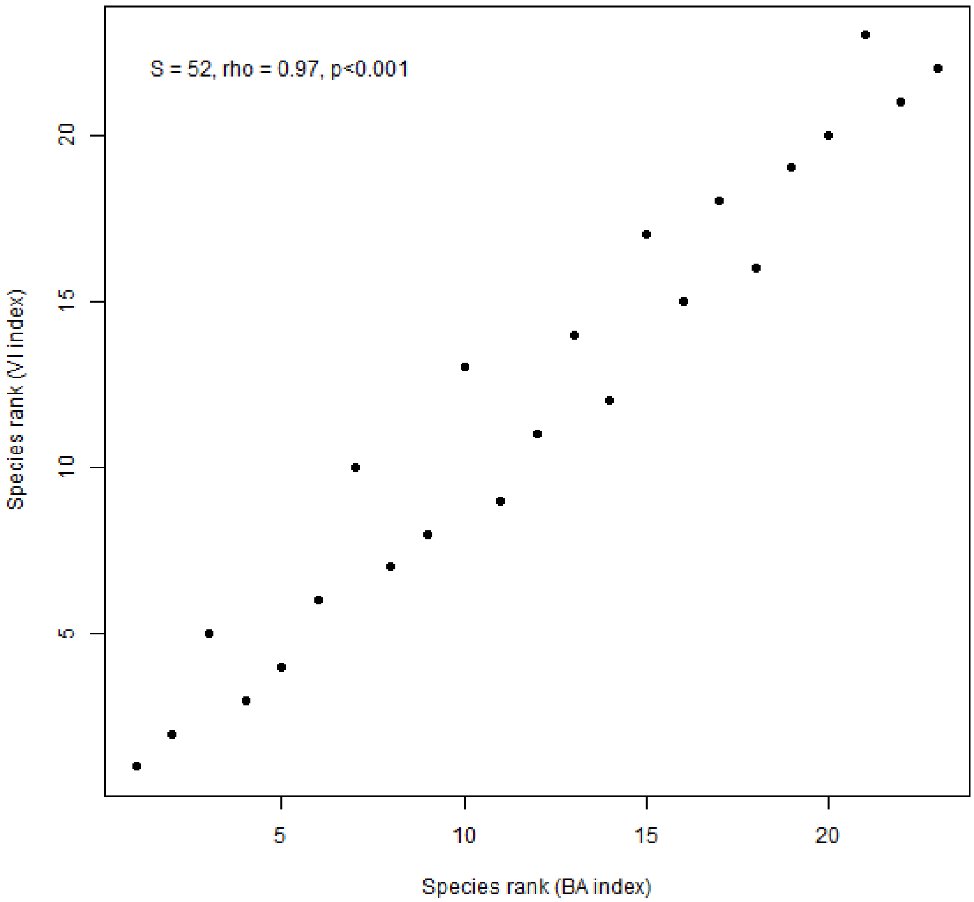


Fig. S4.5 Correlation between species ranked by annual consistency, as measured by two different spatial overlap indices. BA is the Bhattacharyya's Affinity index, and the VI is the volume of intersection index; both are probabilistic measures of utilization distribution similarity.

Tables

Table S4.1. Summary of the parameters used to filter and analyze tracking data from each of 23 species of seabird. Forward travel speeds (in km/h) above the travel speed threshold were omitted. Tracking positions outside the inner colony buffer (km) were considered foraging trip movements, and trips that made it to within the return buffer distance to the colony were considered complete trips. Trips were retained for analysis if they were at least as long as the duration threshold (h). After filtering the data, the foraging range was calculated per species as the median maximum travel distance from the colony (km), and the smoothing parameter for kernel density analysis (h value) was calculated using the reference parameter method (href). The main foraging habitat for each species was classified into three categories, based on the degree to which foraging trips from our study populations visited deep oceanic waters, or shallower waters of the continental shelf, shelf break or seamounts, or utilized both (i.e., 'mixed')

Species	Travel speed threshold	Inner colony buffer	Trip return buffer	Trip duration threshold	Foraging range	h value	Habitat
Common Murre	70	5	20	2	18.3	2.6	shelf
Thick-billed Murre	70	5	20	2	26.7	3.5	shelf
Black-legged Kittiwake	70	5	50	2	52.0	8.6	shelf
Wandering Albatross	70	10	500	6	317.4	37.0	mixed
Laysan Albatross	70	10	550	6	706.6	50.8	oceanic
Black-footed Albatross	70	10	250	6	481.0	43.4	oceanic
Buller's Albatross	70	10	200	6	198.4	25.5	mixed
Grey-headed Albatross	70	10	200	6	694.1	46.0	oceanic
Black-browed Albatross	70	10	200	6	218.3	32.9	mixed
Common Diving-Petrel	70	6	40	1	59.6	9.4	shelf
Cory's Shearwater	70	9	500	5	160.3	29.1	mixed
Cape Verde Shearwater	70	10	150	6	92.4	13.7	mixed

Streaked Shearwater	70	10	100	6	93.9	19.0	mixed
Westland Petrel	70	10	80	6	147.7	19.1	shelf
Little Penguin	30	1	5	1	16.9	1.9	shelf
Chinstrap Penguin	30	1	15	3	20.4	2.3	shelf
European Shag	70	1	5	0.5	1.7	0.9	shelf
Pelagic Cormorant	70	1.1	5	0.5	5.3	0.6	shelf
Northern Gannet	70	10	50	6	202.1	29.1	shelf
Australasian Gannet	70	10	65	6	81.2	11.3	shelf
Masked Booby	70	5	50	2	24.4	4.0	oceanic
Brown Booby	70	5	50	2	43.4	7.4	oceanic
Red-footed Booby	70	5	50	2	50.0	10.8	oceanic

Table S4.2. Summary of tracking samples sizes and timing for each species and site. "stage_start" and "stage_end" indicate stage at beginning (min_date) and end (max_date) of tracking. BG = brood-guard, PG = post-guard, ECR = early chick-rearing (during first half of chick-rearing period), LCR = late chick-rearing (during second half of chick-rearing), CR = chick-rearing (not possible to distinguish further).

Species	**Breeding region**	**season_year**	**n_birds**	**min_date**	**max_date**	**median_date**	**stage_start**	**stage_end**
Cory's Shearwater	Madeira	2009	12	Aug-05	Aug-21	Aug-08	ECR	ECR
Cory's Shearwater	Madeira	2010	21	Aug-15	Aug-20	Aug-17	ECR	ECR
Cory's Shearwater	Madeira	2011	34	Aug-07	Aug-16	Aug-11	ECR	ECR
Cory's Shearwater	Madeira	2013	13	Aug-01	Aug-06	Aug-02	ECR	ECR
Cory's Shearwater	Madeira	2016	41	Aug-04	Aug-17	Aug-09	ECR	ECR
Cory's Shearwater	Madeira	2018	28	Jul-19	Aug-07	Aug-01	ECR	ECR
Cape Verde Shearwater	Raso Islet	2015	12	Sep-18	Oct-02	Sep-22	LCR	LCR
Cape Verde Shearwater	Raso Islet	2017	27	Aug-23	Sep-12	Aug-31	ECR	LCR
Cape Verde Shearwater	Raso Islet	2018	34	Aug-18	Sep-10	Aug-27	ECR	ECR
Cape Verde Shearwater	Raso Islet	2019	29	Sep-03	Sep-22	Sep-07	ECR	LCR
Streaked Shearwater	Awashima Island	2013	41	Aug-16	Oct-08	Sep-11	ECR	LCR
Streaked Shearwater	Awashima Island	2014	39	Aug-18	Oct-14	Sep-12	ECR	LCR
Streaked Shearwater	Awashima Island	2015	42	Aug-16	Oct-09	Sep-12	ECR	LCR
Streaked Shearwater	Awashima Island	2016	27	Aug-20	Oct-09	Aug-27	ECR	LCR
Wandering Albatross	Bird Island	2003	15	Mar-18	Apr-05	Mar-29	BG	BG
Wandering Albatross	Bird Island	2004	16	Mar-10	Apr-03	Mar-23	BG	BG
Wandering Albatross	Bird Island	2015	36	Mar-13	Apr-02	Mar-21	BG	BG
Wandering Albatross	Bird Island	2019	30	Mar-09	Mar-24	Mar-17	BG	BG
Wandering Albatross	Bird Island	2020	25	Mar-13	Mar-28	Mar-21	BG	BG
Little Penguin	Gabo Island	2011	20	Nov-03	Nov-06	Nov-04	BG	BG

Little Penguin	Gabo Island	2012	30	Sep-02	Sep-19	Sep-17	BG	BG
Little Penguin	Gabo Island	2013	52	Sep-12	Dec-18	Oct-07	BG	PG
Little Penguin	Gabo Island	2014	20	Oct-06	Nov-28	Oct-07	BG	PG
Little Penguin	Gabo Island	2016	28	Oct-17	Nov-27	Oct-22	BG	BG
Little Penguin	London Bridge	2011	19	Sep-26	Oct-04	Oct-02	BG	PG
Little Penguin	London Bridge	2012	35	Aug-19	Dec-14	Oct-30	BG	PG
Little Penguin	London Bridge	2013	27	Oct-14	Oct-19	Oct-16	BG	BG
Little Penguin	London Bridge	2014	43	Aug-16	Dec-26	Nov-05	BG	PG
Little Penguin	London Bridge	2015	10	Oct-19	Oct-21	Oct-19	BG	BG
Northern Gannet	East Lothian	2015	31	Jun-19	Aug-05	Jul-13	ECR	ECR
Northern Gannet	East Lothian	2016	16	Jun-29	Aug-03	Jul-09	ECR	ECR
Northern Gannet	East Lothian	2017	13	Jun-26	Aug-05	Jul-09	ECR	ECR
Northern Gannet	East Lothian	2018	27	Jul-06	Aug-01	Jul-16	ECR	ECR
Northern Gannet	East Lothian	2019	21	Jun-22	Jul-29	Jul-08	ECR	ECR
Australasian Gannet	Point Danger	2012	17	Nov-28	Dec-04	Dec-01	ECR	ECR
Australasian Gannet	Point Danger	2014	29	Dec-21	Jan-08	Dec-27	ECR	LCR
Australasian Gannet	Point Danger	2015	21	Jan-03	Jan-19	Jan-10	ECR	ECR
Australasian Gannet	Point Danger	2016	13	Dec-09	Dec-11	Dec-09	ECR	ECR
Australasian Gannet	Point Danger	2018	10	Jan-07	Jan-09	Jan-08	ECR	ECR
Australasian Gannet	Pope's Eye	2011	14	Nov-07	Nov-23	Nov-18	ECR	ECR
Australasian Gannet	Pope's Eye	2012	18	Dec-11	Jan-29	Dec-21	LCR	LCR
Australasian Gannet	Pope's Eye	2014	38	Dec-04	Dec-26	Dec-09	ECR	ECR
Australasian Gannet	Pope's Eye	2015	20	Nov-30	Dec-14	Dec-07	ECR	ECR
Common Diving-Petrel	Kanowna Island	2017	38	Oct-12	Nov-01	Oct-21	CR	CR
Common Diving-Petrel	Kanowna Island	2018	11	Nov-18	Dec-08	Dec-01	CR	CR
Common Diving-Petrel	Kanowna Island	2020	15	Oct-21	Oct-24	Oct-22	CR	CR
European Shag	Isle of May	2003	10	Jun-01	Jun-11	Jun-06	ECR	ECR

European Shag	Isle of May	2009	28	Jun-03	Jun-20	Jun-06	ECR	ECR
European Shag	Isle of May	2010	33	Jun-08	Jun-24	Jun-11	ECR	ECR
European Shag	Isle of May	2012	16	May-29	Jun-05	May-31	ECR	ECR
European Shag	Isle of May	2013	16	Jun-25	Jul-01	Jun-28	ECR	ECR
European Shag	Isle of May	2014	28	Jun-02	Jun-10	Jun-06	ECR	ECR
Pelagic Cormorant	Middleton Island	2006	14	Jun-20	Aug-01	Jul-19	BG	PG-ECR
Pelagic Cormorant	Middleton Island	2007	17	Jun-25	Aug-06	Jul-07	BG	PG-ECR
Pelagic Cormorant	Middleton Island	2008	22	Jun-20	Jul-22	Jul-06	BG	PG-ECR
Pelagic Cormorant	Middleton Island	2018	22	Jul-11	Jul-31	Jul-20	PG-ECR	PG-ECR
Laysan Albatross	Midway Island	2013	11	Jan-03	Feb-02	Jan-28	BG	BG
Laysan Albatross	Midway Island	2014	10	Jan-28	Feb-05	Feb-02	BG	BG
Laysan Albatross	Midway Island	2015	11	Jan-24	Jan-31	Jan-29	BG	BG
Laysan Albatross	Midway Island	2018	25	Jan-31	Feb-10	Feb-04	BG	BG
Black-footed Albatross	Midway Island	2013	13	Dec-26	Jan-31	Jan-26	BG	BG
Black-footed Albatross	Midway Island	2015	12	Jan-22	Jan-31	Jan-27	BG	BG
Black-footed Albatross	Midway Island	2018	23	Jan-31	Feb-10	Feb-04	BG	BG
Westland Petrel	Punakaiki	2012	12	Aug-30	Sep-10	Sep-02	PG-ECR	PG-LCR
Westland Petrel	Punakaiki	2016	16	Aug-11	Aug-18	Aug-14	PG-ECR	PG-ECR
Westland Petrel	Punakaiki	2017	14	Aug-11	Aug-18	Aug-14	PG-ECR	PG-ECR
Chinstrap Penguin	South Shetland Islands	2006	18	Dec-26	Jan-19	Jan-07	BG	BG
Chinstrap Penguin	South Shetland Islands	2009	11	Dec-30	Jan-23	Jan-16	BG	BG
Chinstrap Penguin	South Shetland Islands	2014	19	Dec-29	Jan-18	Jan-09	BG	BG
Black-legged Kittiwake	Bempton Cliffs	2010	13	Jun-12	Jul-04	Jul-01	ECR	ECR
Black-legged Kittiwake	Bempton Cliffs	2013	14	Jun-29	Jul-03	Jul-01	ECR	ECR

Black-legged Kittiwake	Bempton Cliffs	2014	16	Jun-24	Jun-28	Jun-25	ECR	ECR
Black-legged Kittiwake	Bempton Cliffs	2015	13	Jun-22	Jun-28	Jun-24	ECR	ECR
Masked Booby	Dog Island	2014_8	68	Aug-20	Aug-31	Aug-23	BG	BG
Masked Booby	Dog Island	2015_7	22	Jul-13	Jul-22	Jul-17	BG	BG
Masked Booby	Dog Island	2016_6	19	Jun-02	Jun-10	Jun-08	BG	BG
Brown Booby	Dog Island	2012_3	19	Mar-28	Apr-03	Mar-30	BG	BG
Brown Booby	Dog Island	2013_11	41	Nov-23	Nov-28	Nov-25	BG	BG
Brown Booby	Dog Island	2014_10	32	Oct-01	Oct-08	Oct-03	BG	BG
Brown Booby	Dog Island	2015_9	26	Sep-16	Sep-22	Sep-19	BG	BG
Red-footed Booby	Europa Island	2003	11	Sep-14	Sep-28	Sep-24	BG	BG
Red-footed Booby	Europa Island	2011	21	Sep-18	Oct-17	Oct-04	BG	BG
Red-footed Booby	Europa Island	2012	25	Oct-21	Oct-31	Oct-24	BG	BG
Red-footed Booby	Europa Island	2013	39	Sep-23	Jan-31	Oct-26	BG	BG
Buller's Albatross	The Snares	2008	11	Apr-04	Apr-06	Apr-06	BG	BG
Buller's Albatross	The Snares	2009	22	Apr-06	Apr-09	Apr-07	BG	BG
Buller's Albatross	The Snares	2010	23	Apr-08	Apr-12	Apr-10	BG	BG
Buller's Albatross	The Snares	2011	18	Apr-08	Apr-12	Apr-09	BG	BG
Grey-headed Albatross	Bird Island	2009	26	Dec-31	Jan-13	Jan-03	BG	BG
Grey-headed Albatross	Bird Island	2011	30	Jan-02	Jan-12	Jan-05	BG	BG
Grey-headed Albatross	Bird Island	2019	24	Dec-23	Jan-11	Jan-05	BG	BG
Grey-headed Albatross	Bird Island	2020	30	Dec-25	Jan-05	Jan-01	BG	BG
Black-browed Albatross	Bird Island	2009	30	Jan-02	Jan-12	Jan-08	BG	BG
Black-browed Albatross	Bird Island	2014	27	Jan-04	Jan-19	Jan-09	BG	BG
Black-browed Albatross	Bird Island	2018	26	Jan-07	Jan-22	Jan-11	BG	BG
Black-browed Albatross	Bird Island	2019	27	Jan-04	Jan-23	Jan-13	BG	BG
Black-browed Albatross	Bird Island	2020	24	Jan-04	Jan-25	Jan-09	BG	BG
Common Murre	Colonsay	2011	16	Jun-21	Jul-13	Jul-02	ECR	ECR

Common Murre	Colonsay	2012	10	Jun-25	Jul-11	Jul-07	ECR	ECR
Common Murre	Colonsay	2014	12	Jun-26	Jul-13	Jul-06	ECR	ECR
Thick-billed Murre	Coats Island	2010	18	Jul-23	Aug-11	Jul-31	BG-ECR	BG-ECR
Thick-billed Murre	Coats Island	2013	57	Jul-24	Aug-05	Aug-01	BG-ECR	BG-ECR
Thick-billed Murre	Coats Island	2017	54	Jul-20	Aug-01	Jul-27	BG-ECR	BG-ECR
Thick-billed Murre	Coats Island	2018	55	Jul-30	Aug-04	Aug-01	BG-ECR	BG-ECR
Thick-billed Murre	Coats Island	2019	55	Jul-23	Aug-07	Jul-29	BG-ECR	BG-ECR

CHAPTER 5

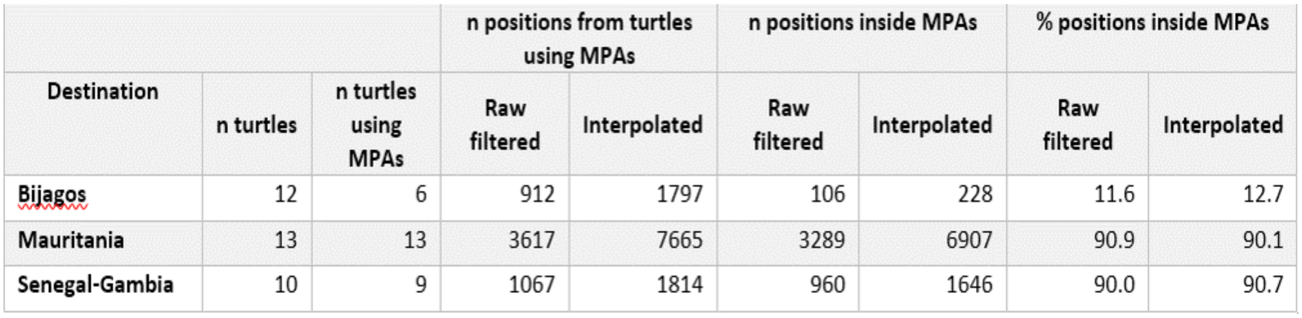
GREEN TURTLES HIGHLIGHT CONNECTIVITY ACROSS A REGIONAL MARINE PROTECTED AREA NETWORK

Supplemental methods – attachment of satellite tags on green turtles

We deployed the satellite transmitters on two occasions: when turtles were laying and when turtles were resting in intertidal pools. In the first case, we waited for the turtles to start laying their eggs, and then executed the attachment procedure within 20 minutes, while the turtle continued to lay. First, we sanded the second vertebral scute, where the tag was to be attached (Fig. S5.1), and cleaned it with acetone. Then we applied a base of fibreglass and a two-part fast-dry epoxy (®Devcon-5min Epoxy) and allowed it to dry for five minutes. We prepared a ‘cushion’ for the tag with a two-part steel resin (®Loctite Magic Metal), placed it on the tag base and pressed the tag gently on top of the fibreglass base (on the scute), and allowed ten minutes for the resin to dry. For the last step, we applied again fibreglass with the epoxy (®Devcon-5min Epoxy) around the tag, to secure it, and allowed another five minutes for the second fibreglass and epoxy application to dry. All turtles continued with their nesting activity throughout the tag application and successfully laid their eggs, and covered and camouflaged the nest; therefore, we are confident that the procedure did not disturb them.

In the second scenario, we approached turtles that were resting inside intertidal pools, waiting for the high tide to cross the intertidal rocks; we started sanding their second vertebral scute and observed their reaction. In most cases, the turtles would carry on resting with their heads under water, only surfacing from time to time to take a breath, as if unaware of our presence. Thus, we proceeded as above to deploy the tags. In the case of the few turtles that started walking, we left them undisturbed. We observed all tagged turtles normally returning to the sea with the coming of the high tide.

Table S5.1. Comparison of the percentage of points that fall within marine protected areas during the post-nesting foraging period calculated using raw filtered tracking positions and positions interpolated to regular, 3 h intervals.



			n positions from turtles using MPAs		n positions inside MPAs		% positions inside MPAs	
Destination	**n turtles**	**n turtles using MPAs**	**Raw filtered**	**Interpolated**	**Raw filtered**	**Interpolated**	**Raw filtered**	**Interpolated**
Bijagos	12	6	912	1797	106	228	11.6	12.7
Mauritania	13	13	3617	7665	3289	6907	90.9	90.1
Senegal-Gambia	10	9	1067	1814	960	1646	90.0	90.7

Table S5.2. Comparison of marine protected area coverage of turtle tracking positions calculated separately using Doppler-effect derived ARGOS data against FastLoc GPS data collected from the same individuals. ARGOS data were filtered by retaining locations of quality classes 1, 2, and 3, while GPS data were retained when 6 satellites were used to fix a position and after passing a speed-angle filter to ensure biological realism. There is little difference between the estimates, suggesting that the data-quality filtering procedure ameliorated the potential effects of spatial error on estimating MPA coverage of tracking positions. Calculations were made separately for the internesting, and post-nesting foraging periods.

Period	Device type	n turtles	n positions	n positions inside MPAs	% positions inside MPAs
foraging	Argos doppler shift	20	1548	1107	71.5
foraging	GPS	20	846	567	67
internesting	Argos doppler shift	21	1489	1420	95.4
internesting	GPS	18	1141	1096	96.1

Supplemental figures and tables

Table S5.3. Metadata of adult female green turtles equipped with satellite tags for the present study, at Meio and Poilão islands, in the Bijagós Archipelago, Guinea-Bissau. CCL: curved carapace length. FG: foraging ground. IN: internesting. M: Migration.

PTT ID	PTT model	Type of position data	Year	CCL (cm)	Start date	End date	Duration (days)	F location	Date leaving IN	Date starting F	Time foraging	Number of positions				Periods with data		
												Argos (raw)	GPS (raw)	Argos (filter)	GPS (filter)	IN	M	F
60863	Spot375B	Argos	2018	97.0	02/11/2018	21/02/2019	111	Bolama-Bijagós, Guinea-Bissau	03/11/2018	03/11/2018	110	1585	0	204	0	no	no	yes
60865	Spot375B	Argos	2018	113.5	29/10/2018	01/09/2019	307	Banc d'Arguin, Mauritania	23/11/2018	17/12/2018	258	2483	0	695	0	yes	yes	yes
60866	Spot375B	Argos	2018	104.0	05/11/2018	23/11/2018	18	?	05/11/2018	na	na	43	0	0	0	no	no	no
60867	Spot375B	Argos	2018	88.0	02/11/2018	15/02/2019	105	Bolama-Bijagós, Guinea-Bissau	05/11/2018	07/11/2018	100	1220	0	289	0	yes	no	yes
60868	Spot375B	Argos	2018	91.0	08/11/2018	30/12/2018	52	?	29/11/2018	04/12/2018	26	263	0	45	0	yes	no	no
60886	Spot375B	Argos	2018	104.0	20/08/2018	29/10/2018	70	Banc d'Arguin, Mauritania	04/09/2018	22/09/2018	37	755	0	300	0	yes	yes	yes
60887	Spot375B	Argos	2018	105.0	15/09/2018	10/01/2019	117	Banc d'Arguin, Mauritania	06/12/2018	31/12/2018	10	1291	0	576	0	yes	yes	yes
60888	Spot375B	Argos	2018	109.0	28/10/2018	26/11/2018	29	?	09/10/2018	na	na	294	0	54	0	yes	no	no
60889	Spot375B	Argos	2018	104.0	30/10/2018	11/09/2019	316	Banc d'Arguin, Mauritania	13/11/2018	11/12/2018	274	2458	0	971	0	yes	yes	yes
60890	Spot375B	Argos	2018	98.5	07/11/2018	17/01/2019	71	Saloum Delta, Senegal	12/11/2018	19/11/2018	59	791	0	235	0	yes	no	yes
60891	Spot375B	Argos	2018	92.5	31/10/2018	19/06/2019	231	Banc d'Arguin, Mauritania	11/11/2018	09/12/2018	192	1993	0	857	0	yes	yes	yes
60892	Spot375B	Argos	2018	106.0	29/10/2018	23/04/2019	176	Banc d'Arguin, Mauritania	09/11/2018	07/12/2018	137	1930	0	737	0	yes	yes	yes
60893	Spot375B	Argos	2018	90.2	23/08/2018	12/11/2018	81	Tanji Bijol Islands, Gambia	25/09/2018	02/10/2018	41	688	0	209	0	yes	no	yes
60894	Spot375B	Argos	2018	87.0	23/08/2018	18/11/2018	87	South of Poilão, Guinea-Conakry	06/10/2018	09/10/2018	40	835	0	157	0	yes	no	yes
60896	Spot375B	Argos	2018	91.0	05/10/2018	22/11/2018	48	Joal Fadiouth, Senegal	06/10/2018	17/10/2018	36	588	0	208	0	no	yes	yes
60897	Spot375B	Argos	2018	78.0	01/09/2018	04/12/2018	94	Bolama-Bijagós, Guinea-Bissau	26/09/2018	26/09/2018	69	1255	0	352	0	yes	no	yes
60898	Spot375B	Argos	2018	95.0	01/09/2018	30/07/2019	332	Banc d'Arguin, Mauritania	13/09/2018	15/10/2018	288	2505	0	1033	0	yes	yes	yes
60899	Spot375B	Argos	2018	103.0	19/10/2018	16/12/2018	58	Joal Fadiouth, Senegal	30/10/2018	07/11/2018	39	557	0	187	0	yes	yes	yes
60900	Spot375B	Argos	2018	102.0	20/08/2018	14/10/2018	55	?	na	na	na	567	0	164	0	yes	no	no
182450	F6G 376A	Argos/FGPS	2019	104.3	14/08/2019	05/11/2019	83	Saloum Delta, Senegal	14/10/2019	25/10/2019	11	708	593	253	428	yes	no	yes
182451	F6G 376A	Argos/FGPS	2019	96.0	15/08/2019	25/11/2019	102	Bolama-Bijagós, Guinea-Bissau	14/10/2019	21/10/2019	35	802	429	166	99	yes	no	yes
182452	F6G 376A	Argos/FGPS	2019	98.5	13/08/2019	02/01/2020	142	Bolama-Bijagós, Guinea-Bissau	22/10/2019	03/11/2019	60	1161	340	276	196	yes	no	yes
182453	F6G 376A	Argos/FGPS	2019	91.8	23/08/2019	27/10/2019	65	Bolama-Bijagós, Guinea-Bissau	05/09/2019	12/09/2019	45	266	112	35	68	yes	no	yes
182454	F6G 376A	Argos/FGPS	2019	90.3	19/08/2019	27/10/2019	69	Bolama-Bijagós, Guinea-Bissau	27/09/2019	30/09/2019	27	448	134	98	96	yes	no	yes
182455	F6G 376A	Argos/FGPS	2019	105.5	13/08/2019	29/10/2019	77	?	na	na	na	607	161	146	130	yes	no	no
182456	F6G 376A	Argos/FGPS	2019	102.0	14/08/2019	26/10/2019	73	?	na	na	na	588	255	88	178	yes	no	no
182457	F6G 376A	Argos/FGPS	2019	99.5	14/08/2019	01/12/2019	109	Bolama-Bijagós, Guinea-Bissau	01/10/2019	01/10/2019	61	1151	345	232	198	yes	no	yes
182458	F6G 376A	Argos/FGPS	2019	84.0	15/08/2019	21/11/2019	98	Bolama-Bijagós, Guinea-Bissau	27/09/2019	29/09/2019	53	1251	337	327	193	yes	no	yes

Table S5.4. List of marine protected areas within the limits of the spatial distribution of the female green turtles nesting at Poilão and Meio islands, with in the João Vieira – Poilão Marine National Park.

Country	WDPA Reference	Name	Designation	Surface (ha)	Status year
Mauritania	20388	Banc d'Arguin	World Heritage Site	1208012.74	1989
Senegal	866	Delta du Saloum	National Park	88566.14	1976
Senegal	869	Langue de Barbarie	National Park	2097.7	1976
Senegal	870	Iles de la Madeleine	National Park	49.78	1976
Senegal	3217	Kalissaye	Bird Reserve	428.35	1978
Senegal	352612	Foret de Leybar	Forest Reserve	273	not reported
Senegal	352692	Foret de Djibelor	Forest Reserve	176	not reported
Senegal	352704	Saint Louis	Marine Protected Area	48110.71	2004
Senegal	352705	Kayar	Marine Protected Area	16809.21	2004
Senegal	352706	Joal-Fadiouth	Marine Protected Area	14245.32	2004
Senegal	352707	Abéné	MPA	11809.94	2004
Senegal	555651496	Bamboung	Marine Protected Area	6102.02	2004
Senegal	555651498	Palmarin	Community Nature Reserve	11071.65	2001
Senegal	555651501	Somone	Marine Protected Area	734.49	2020
Senegal	555651502	Sangomar	Marine Protected Area	70143.89	2014
Gambia	2289	Kiang West	National Park	12032.47	1987
Gambia	2290	Niumi	National Park	4938.85	1986
Gambia	31330	Baobolon	Wetland Reserve	20581.4	1996
Gambia	555703735	Jokadu Wetland Park Amd Extension	Wetland Park	19294	2014
Guinea Bissau	33047	Orango	National Park	157828.26	2000
Guinea-Bissau	317051	Rio Grande de Buba	Reserved fishing area	110846	2015
Guinea Bissau	317052	Joao Vieira Poilao	Marine National Park	49601.97	2000
Guinea Bissau	342655	Ilhas Formosa, Nago & Tchedia (Urok)	Marine Community Protected Area	62657.63	2005
Guinea Bissau	555626105	Tarrafes do Rio Cacheu	Ramsar Site	89744	2000
Guinea	67983	Alcatraz	Ramsar Site	453.1	1992
Guinea	67984	Tristao	Ramsar Site	101316.16	1992
Guinea	67985	Rio Kapatchez	Ramsar Site	30477.61	1992
Gambia	555547524	Tambi	National Park	6759.05	2003

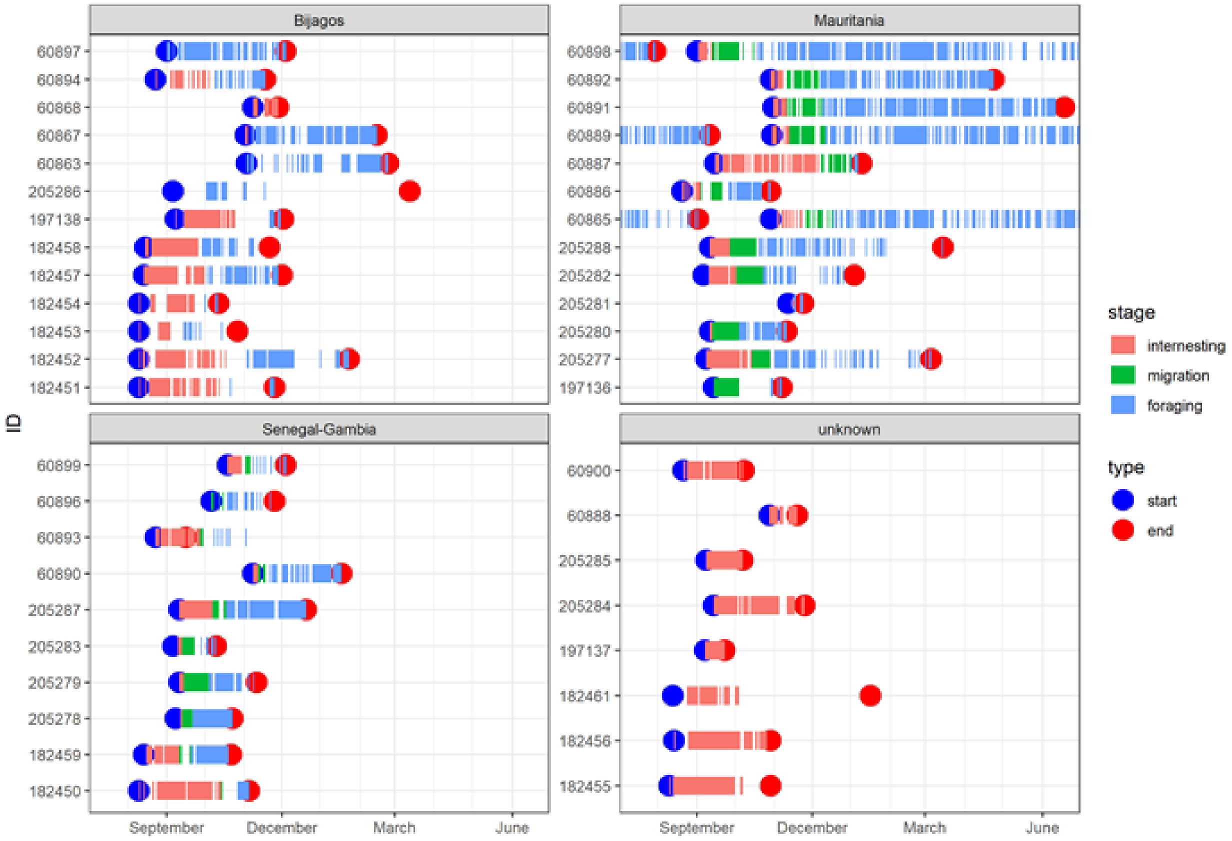


Fig. S5.1. Temporal coverage of tracking data of three major annual-cycle periods for 44 female turtles. Colored bars show stretches of data without gaps of >=24 h for each period (breaks in bars represent gaps), while colored circles indicate the start and end of the tracking period for each individual (ID). These data represent the high-quality subset of data from the raw tracks of each individual, which have been filtered using data quality threshold like speed and the number of satellites used for triangulation and ARGOS location codes. Each panel shows the data according to the post-nesting foraging destination of each individual, where the ‘unknown’ category represents individuals which were not successfully tracked to a definitive foraging location.

CHAPTER 6

GLOBAL POLITICAL RESPONSIBILITY FOR THE CONSERVATION OF ALBATROSSES AND LARGE PETRELS

GLS filtering and sensitivity analysis

We did not standardize the processing of the raw light-level geolocation (GLS) underlying the data sets analyzed herein. However, the majority of data sets have already been published in species-specific accounts whereby authors used accepted methods ranging from state-space models and incorporation of sea-surface temperature for refinement of latitudes (Shaffer et al., 2005) to speed-distance-angle thresholds for filtering (Delord et al., 2010), or expert judgement of light-level interference (Dias et al., 2011).

In order to set a common standard of reliability across GLS data sets, a series of filters were used to remove obviously erroneous fixes. For all data sets, fixes above 65°N and below -75°S latitude were removed, as albatrosses and large petrels do not frequent these latitudes. An additional equatorial filter was applied to three data sets from Black-footed Albatross, Laysan Albatross, and Grey Petrels. These were applied so as to remove false positives of species occurrence in countries in the wrong hemispheres (Southern: Black-footed and Laysan; Northern: Grey Petrel). These fixes were deemed erroneous, rather than true vagrancy movements, by close inspection of individual trajectories. All fixes falling within landlocked countries were removed, to reduce the detection of false positive species occurrence in these jurisdictions. Species-specific filters were used to remove fixes during breeding which were located further than the known maximum foraging range of *C. diomedea* plus the average error of GLS devices (i.e. max. forage range + 186 km) from the breeding colony (Dias et al., 2011; Oppel et al., 2018; R. A. Phillips et al., 2004). These filters removed a mean of 0.45% (+/- 1.52) of all fixes for each breeding site-species combination.

Since latitudinal estimates from GLS data are unreliable around the equinoxes, an asymmetrical filter was also used to remove fixes during these periods (March equinox: -21, +7 days; September equinox: -7, +21 days) (Hill & Braun, 2001). As GLS data sets from 4 species (*Ardenna bulleri*, *A. carneipes*, *A. grisea*, *Procellaria parkinsoni*) used sea-surface temperature (SST) to estimate latitudes, fixes during the equinox periods were retained in these cases.

To test the potential effect of the spatial error of GLS devices on the quantification of species richness and time spent, we performed in iterated re-sampling procedure. For each iteration, we re-sampled all GLS points by combining a random direction drawn from a uniform distribution (0-360) with a distance drawn from a normal distribution (mean=0, SD=186 km) and then calculated the species richness and time spent by albatrosses and large petrels. The results of this analysis are presented in Fig. S6.3.

Supplementary Figures

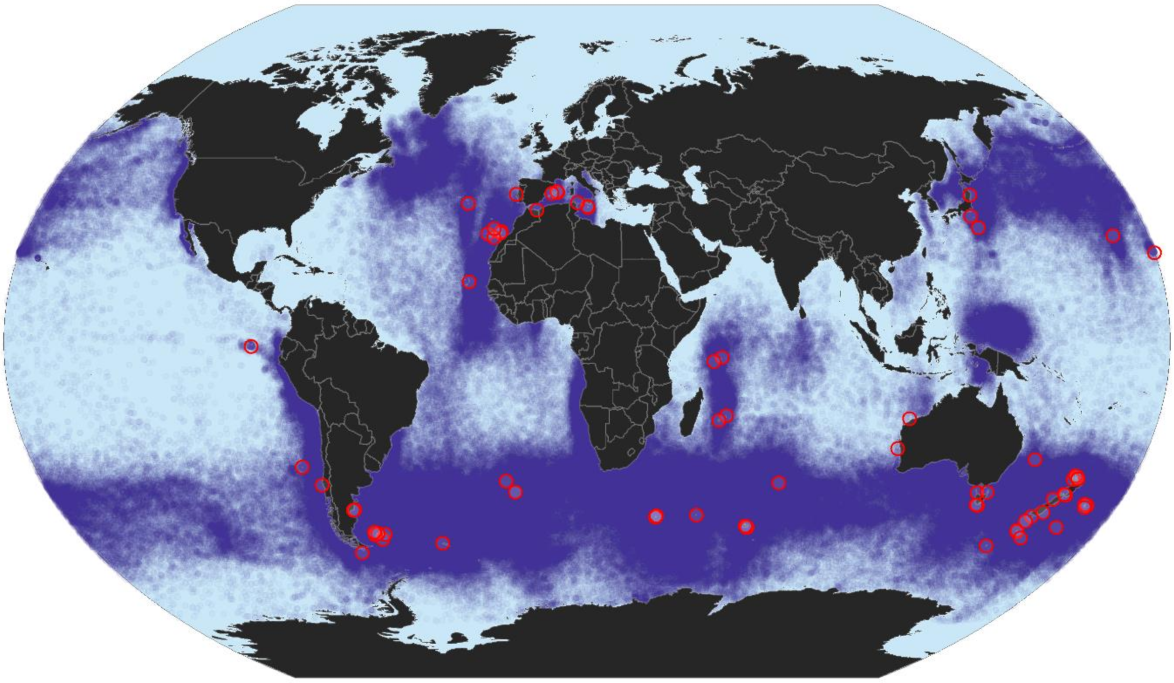


Fig. S6.1. Global map of tracking data set. Red circles are 87 different tagging locations, and purple dots signify the resultant tracking data, post-filtering, used to analyze annual distributions of albatrosses and large petrels with respect to political borders.

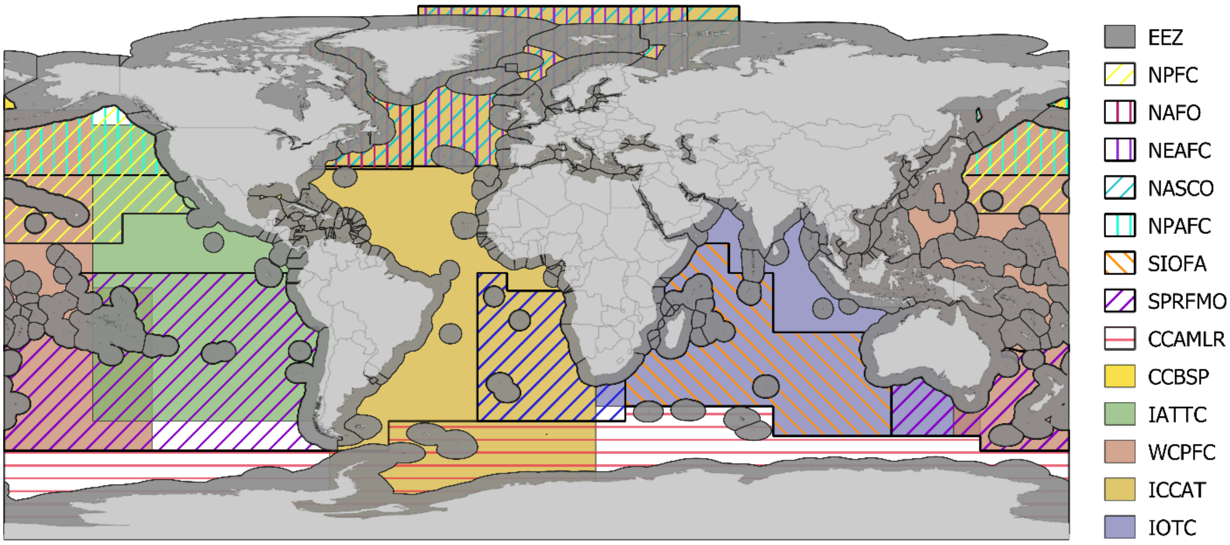


Fig. S6.2. Areas of competence of Regional Fisheries Management Organizations. Dark gray polygons outlined in black represent Exclusive Economic Zones of countries. Outside this, areas variably colored and patterned represent Areas of Competence for RFMOs. *NPFC=North Pacific Fisheries Commission, NAFO=Northwest Atlantic Fisheries Organization, NEAFC=North East Atlantic Fisheries Commission, NASCO=North Atlantic Salmon Conservation Organisation, SEAFO=South East Atlantic Fisheries Organisation, NPAFC = North Pacific Anadromous Fish Commission, SIOFA=Southern Indian Ocean Agreement, SPRFMO=South Pacific Fisheries Management Organisation, CCAMLR=Convention on the Conservation of Antarctic Living Marine Resources, CCBSP=Convention on the Conservation and Management of Pollock Resources in the Central Bering Sea, IATTC=Inter-American Tropical Tuna Commission, WCPFC=West Central Pacific Fisheries Commission, ICCAT=International Commission for the Conservation of Atlantic Tunas, IOTC=Indian Ocean Tuna Commission*

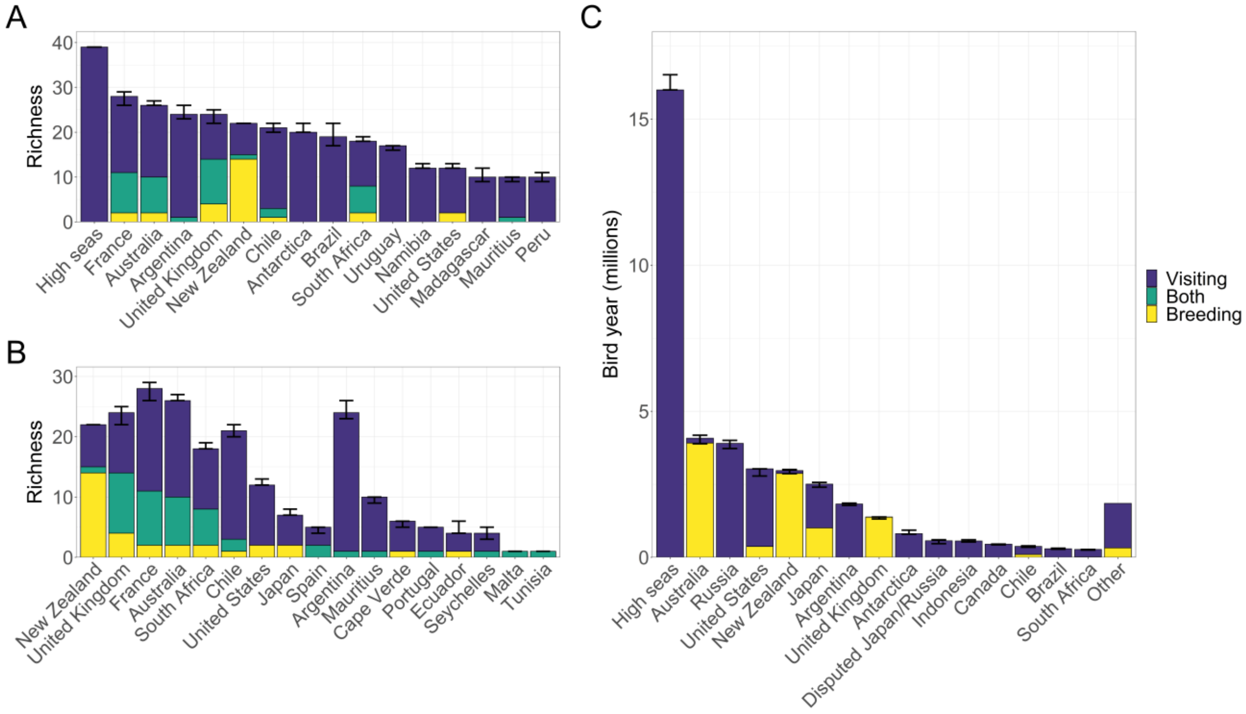


Fig. S6.3 Sensitivity of importance measures to GLS spatial error. Importance of political areas to albatrosses and large petrels, measured in terms of species richness (A-B) and total annual time spent (C). Error bars show the range in the total estimated richness and time spent (ignoring visiting or breeding categories) for each political area calculated across 100 iterations, wherein GLS points were re-sampled to simulate the effect of GLS spatial error, which has an average effect of +/- SD 186 km displacement from the estimated location.

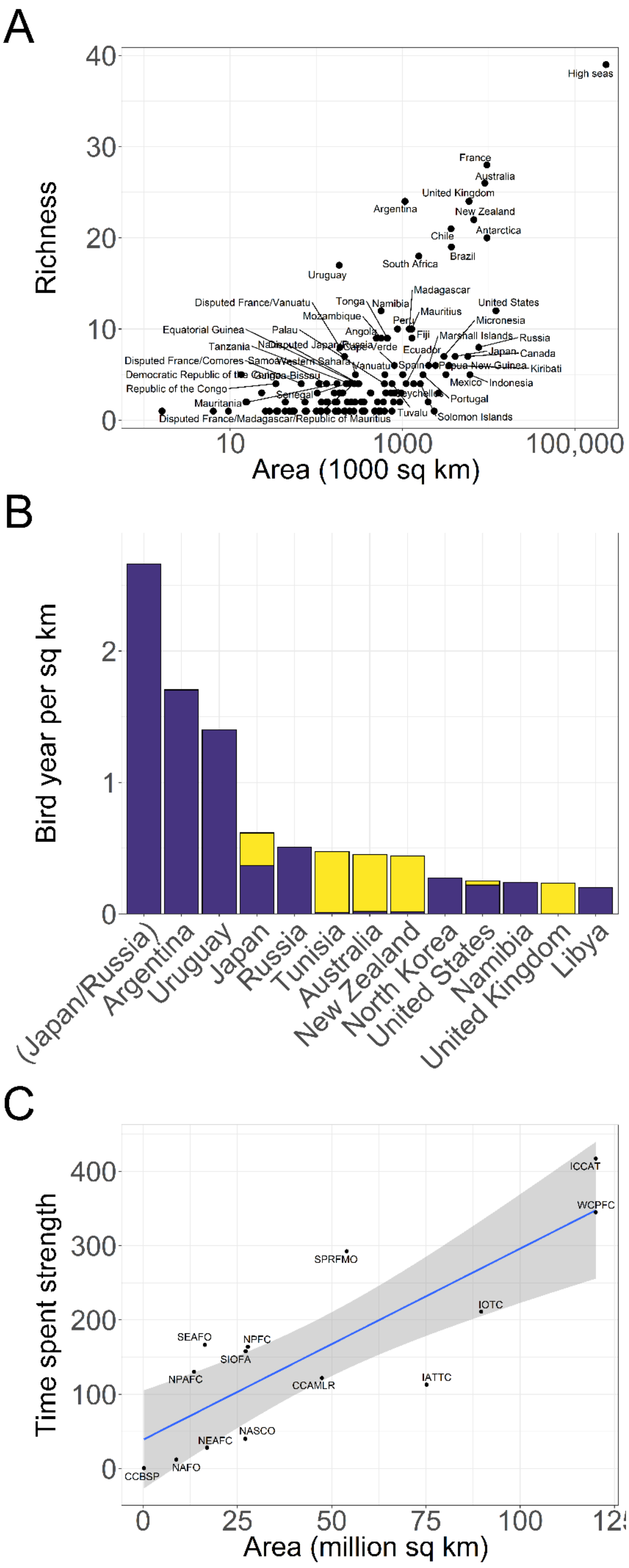


Fig. S6.4 Importance estimates and jurisdiction area

(A) Species richness estimated from tracking data and area of national jurisdictions and the high seas (log scale). (B) Estimated annual time spent in national jurisdictions per square kilometer of area. Sovereignty of jurisdictions in parentheses are disputed by the listed countries. (C) Time spent strength per area of legal competence for each RFMO against the size of the area. 'Time spent strength' is an index of importance calculated as the percentage of the species' annual time spent in an area, summed across all species visiting the area.

Other Supplementary Material
(Files available for download at: https://www.science.org/doi/10.1126/sciadv.abd7225)

data file S6.1. (Excel) Estimated species richness of albatrosses and large petrels and annual time spent per country. (A) Breeding origin countries. (B) Countries visited that do not host breeding. "Total" is the total estimated richness, "Breeding" is the total richness of breeding species, "Visiting" is the total richness of species which visit from other countries. "Breed only" is the number of species which only occur via breeding populations located there. "Visit only" is the component of the total richness made up of species which occur in the country but do not have any breeding populations there. "Both" signifies the number of species whose occurrence in the country is made up of both birds that breed in the country and those that breed elsewhere. "Total breeders" is the number of total estimated individual breeding albatrosses and large petrels under each jurisdiction. "Total (Time Spent)" is the estimated total amount of annual time spent in the country by the global population of albatrosses and large petrels. "Breeders" is the annual time spent in the country by breeding populations originating in that country, and "Visitors" is the time spent by birds which breed in another jurisdiction. "True breeding richness" is the number of breeding species counted from all known breeding sites in the literature. "Diff" is the difference between the true and estimated richness based on available tracking data (column "Breeding").

data file S6.2. (Excel) All connections between breeding origin countries and other political areas. This is the full data set underlying Fig. 3. (A) All connections between breeding origins and other countries and the high seas. (B) All connections between breeding countries and high seas RFMO competence areas. N_{breed} is the number of albatross and large petrel species breeding in the country. Visited jurisdictions are in descending order of the relative strength of connection between the jurisdictional areas. Strength reflects the amount of annual time spent by the populations of large petrels breeding under the countries' jurisdiction, as well as the relative contribution of said populations to the global breeding population of each species. N_{visit} is the number of species which constitute this connection between political areas.

data file S6.3. (Excel) Population estimates. Island group and global population estimates for the populations and species of albatrosses and large petrels studied herein.

data file S6.4. (Excel) Summary of tracking data sets from each breeding population of albatrosses and large petrels after filtering steps. N_{tracks} is the number of tracks of a certain device-type (‘Device’), collected from a total of N_{birds} in the population. D_{total} is the number of total tracking days, where Min and Max represent the range of track durations. $Y_{covered}$ and Y_{missed} are then, respectively, the resulting number of days of the year with and without tracking data for the population.

data file S6.5. (Excel) Estimated species richness and annual time spent with high data filtering threshold (A) and alternate sovereignty assignment (B).

data file S6.6. (Excel) All connections between breeding origin countries and other political areas with high data filtering threshold (A) and alternate sovereignty assignment (B).

movie S6.1. Animated global monthly distribution of time spent. Distribution of adult albatrosses and large petrels is calculated on a monthly basis, in terms of time spent in 452 sq. km grid cells across the world.