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Jorge Miguel Ribeiro Pereira

CORY'S SHEARWATER AS AN INDICATOR OF HUMAN STRESSORS AND MARINE SPATIAL PLANNING IN THE NORTH ATLANTIC

Tese no âmbito do Doutoramento em Biociências, especialização em Ecologia, orientada pelo Doutor Vitor Hugo Rodrigues Paiva e co-orientada pelo Professor Doutor Jaime Albino Ramos e pelo Professor Doutor Stephen Votier e apresentada ao Departamento de Ciências da Vida da Faculdade de Ciências e Tecnologia da Universidade de Coimbra

Setembro de 2021

Departamento de Ciências da Vida
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Abstract

Seabird populations declined steeply in recent decades and their conservation status continues to deteriorate. Strategies and tools are therefore required to identify, predict, and mitigate the major sources of anthropogenic stressors affecting seabirds and the marine environment. Biologging emerged as a powerful tool to monitor biodiversity and reveal key information about the potential winners and losers of global change. By identifying important seabird habitats, tracking information can highlight areas for protection and contribute to a more sustainable exploitation of marine resources. In this context, seabirds can be used as indicators of global ocean's health and marine spatial planning, a topic that is gaining momentum. Thus, in this thesis I investigated the influence of spatio-temporal variability of environmental conditions and anthropogenic pressures on the at-sea foraging decisions of a wide-range pelagic seabird, the Cory's shearwater (*Calonectris borealis*). Combination of movement data, remote sensing and habitat modelling analysis are used to study the at-sea behaviour, foraging decisions and habitat use of Cory's shearwaters across the North Atlantic Ocean. Main results of this thesis are: (1) seabird tracking is demonstrated to be essential for ecological investigation and towards the prioritisation of conservation goals (Chapter 1); (2) individual-level memory of resource availability and predictability can be an important mechanism explaining spatial foraging segregation within seabird colonies during the breeding period (Chapter 2); (3) Cory's shearwaters from neritic and oceanic populations in the mid-North Atlantic Ocean exhibit contrasting foraging behavioural decisions in response to extreme phases of North Atlantic Oscillation (NAO) index (Chapter 3); (4) during the breeding season, Cory's shearwaters rarely forage in the same areas as industrial fishing vessels within the exclusive economic zone (EEZ) of mainland Portugal. Yet, Cory's shearwaters are more likely to overlap in the same areas as fixed gear vessels (e.g. set longlines, set gillnets, pots and traps) and purse seiners during the pre-laying than during chick-rearing, but less likely to vary among genders and individual boldness (Chapter 4); and (5) an adaptive framework is recommended to identify the important areas for seabirds that maximises conservation targets, while accounting for anthropogenic pressures in the Portuguese coast. This methodology shows that the current network of marine protected areas (MPAs) along the

Portuguese coast is effective for protecting the habitats used by breeding seabirds, but not for those used by non-breeding seabirds (Chapter 5). Overall, the results of this thesis confirm that Cory's shearwaters can exhibit great behavioural plasticity to cope with the heterogeneity of their habitats or with deteriorated climate conditions that result in decreased food availability. Moreover, it highlights the need for understanding the drivers of variation in the at-sea foraging behaviour and spatial overlap with fishing vessels within seabird populations, which can have important implications in terms of conservation and marine spatial planning.

Keywords: Biologging, Climate change, Environmental variability, Fisheries, Marine protected areas, Seabirds.

Resumo

As populações de aves marinhas diminuíram drasticamente nas últimas décadas e o seu estatuto de conservação continua a deteriorar-se. Como tal, é necessário criar estratégias e ferramentas para identificar, prever e mitigar os impactes das pressões antropogénicas que afetam as aves marinhas e o ambiente marinho. Os dispositivos de seguimento emergiram como uma poderosa ferramenta para monitorizar a biodiversidade e revelar informação sobre os efeitos positivos e negativos das alterações climáticas. Estes dispositivos podem identificar os habitats importantes para as aves marinhas e, assim, definir áreas protegidas e contribuir para uma exploração mais sustentável dos recursos marinhos. Neste contexto, as aves marinhas são frequentemente utilizadas como indicadores do estado de saúde dos oceanos e do planeamento marinho. Nesta tese eu investiguei a influência da variabilidade espácio-temporal das condições ambientais e pressões antropogénicas nas estratégias de procura de alimento de uma ave marinha pelágica, a cagarra (*Calonectris borealis*). Para isso foram monitorizadas a distribuição no mar e o uso do habitat desta ave, a qual se reproduz em diferentes arquipélagos ao longo do Oceano Atlântico Norte. As principais conclusões desta tese são: (1) a informação sobre a distribuição das aves marinhas é essencial para o estudo de mecanismos ecológicos bem como a priorização de esforços de conservação (Capítulo 1); (2) o conhecimento individual ou memória dos locais onde os recursos são mais abundantes e previsíveis pode ser um mecanismo importante para explicar a variabilidade intra-populacional na ecologia espacial das aves marinhas, durante o período reprodutor (Capítulo 2); (3) cagarras que nidificam em populações costeiras e oceânicas ao longo do Atlântico Norte exibem diferentes estratégias de procura de alimento em resposta a fases extremas de índices climáticos, nomeadamente da Oscilação do Atlântico Norte (Capítulo 3); (4) durante a época de reprodução as cagarras raramente procuram alimento nas mesmas áreas das embarcações de pesca industrial, que operam dentro da zona económica exclusiva (ZEE) de Portugal Continental. No entanto, comparativamente ao período de alimentação às crias, as cagarras podem intensificar a procura de alimento nas mesmas áreas que as embarcações de aparelho (por exemplo, palangreiros, redes de emalhar e armadilhas) e arte de cerco, durante o período anterior à colocação do ovo. Pelo contrário, a sobreposição espacial entre cagarras e embarcações de pesca é menos provável de variar de acordo com o sexo e a personalidade dos indivíduos (Capítulo 4); e, por fim, (5) foi proposta uma metodologia adaptativa para identificar áreas importantes para as aves marinhas, de modo a maximizar os esforços de conservação, considerando as pressões antropogénicas na costa Oeste de Portugal Continental. Esta metodologia mostra que a rede actual de áreas marinhas protegidas (AMPs) ao longo da costa Oeste de Portugal Continental é eficiente para proteger os habitats usados por espécies de aves marinhas que se reproduzem no território continental, mas não para as espécies migradoras (Capítulo 5). Em suma, os resultados desta tese confirmam que as cagarras podem exibir uma grande plasticidade comportamental nas estratégias de procura de alimento para se adaptarem à heterogeneidade dos habitats em redor das colónias ou às condições climáticas, as quais resultam na redução da disponibilidade de alimento. Destaca-se ainda a importância e necessidade de compreender os mecanismos responsáveis pelas variações nas estratégias de procura de alimento e nas interações com embarcações de pesca dentro das populações de aves marinhas, e as suas implicações em termos de conservação e planeamento marinho.

Palavras-Chave: Alterações climáticas, Áreas marinhas protegidas, Aves marinhas, Dispositivos de seguimento, Pescas, Variabilidade ambiental.

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Scientific Outputs

The scientific outputs produced during the period of this doctoral thesis (2017-2021) are listed below:

Peer-reviewed publications

First author publications

Chapter 1: **Pereira JM**, Paiva VH, Krüger L and Votier SC (2022) Tracking seabirds for conservation and marine spatial planning. In: *Seabird biodiversity and human activities.* Ramos JA and Pereira L (eds) CRC Press, Boca Raton, Florida, USA.

Chapter 2: **Pereira JM**, Ramos JA, Almeida N, Araújo PM, Ceia FR, Geraldes P, Marques AM, Matos DM, Rodrigues I, dos Santos I and Paiva VH (2nd review) The role of colony size and foraging cost in explaining within-colony spatial segregation in two shearwater species. *Oecologia*.

Chapter 3: **Pereira JM**, Paiva VH, Ceia FR and Ramos JA (2020) Facing extremes: Cory's shearwaters adjust their foraging behaviour differently in response to contrasting phases of North Atlantic Oscillation. *Regional Environmental Change* 20:77.

Chapter 4: **Pereira JM**, Ramos JA, Marques AM, Ceia FR, Krüger L, Votier SC and Paiva VH (2021) Low spatial overlap between foraging shearwaters during the breeding season and industrial fisheries off the West coast of Portugal. *Marine Ecology Progress Series* 657: 207-219.

Chapter 5: **Pereira JM**, Krüger L, Oliveira N, Meirinho A, Silva A, Ramos JA and Paiva VH (2018) Using a multi-model ensemble forecasting approach to identify key marine protected areas for seabirds in the Portuguese coast. *Ocean & Coastal Management* 153:98–107.

Others

[10] Bastos R, Martins B, Ramos JA, Paiva VH, **Pereira JM**, Ceia FR, Gouveia C, Rodrigues I, Santos M and Cabral J (2nd review) Nocturnal foraging as a driving mechanism of the shearwaters' nest attendance patterns throughout the lunar cycle: Are oceanographic conditions decisive for the timing and light intensity of nest arrival? *Journal of Experimental Marine Biology and Ecology*.

[9] Almeida N, Ramos JA, Rodrigues I, dos Santos I, **Pereira JM**, Matos DM, Araújo PM, Geraldes P, Melo T and Paiva VH (2021) Year-round at-sea distribution and trophic resources partitioning between two sympatric Sulids in the tropical Atlantic. *PLOS ONE* 16:e0253095.

[8] Laranjeiro MI, Alves LMF, da Silva JM, **Pereira JM**, Norte AC, Paiva VH, Lemos MFL, Ramos JA, Novais SC and Ceia FR (2021) Year-round element quantification of a wide-ranging seabird and their relationships with oxidative stress, trophic ecology, and foraging patterns. *Environmental Pollution* 284:117502.

[7] Lopes CS, Paiva VH, Vaz PT, Pais de Faria J, Calado JG, **Pereira JM** and Ramos JA (2021) Ingestion of anthropogenic materials by yellow-legged gulls (*Larus michahellis)* in natural, urban, and landfill sites along Portugal in relation to diet composition. *Environmental Science and Pollution Research* 28:19046–19063.

[6] Calado JG, Veríssimo S, Paiva VH, Ramos R, Vaz P, Matos DM, **Pereira JM**, Lopes CS, Oliveira N, Quaresma A, Ceia FR, Velando A and Ramos JA (2021) Influence of fisheries on the spatio-temporal feeding ecology of gulls along the western Iberian coast. *Marine Ecology Progress Series* 661:187–201.

[5] Semedo G, Paiva VH, Militão T, Rodrigues I, Dinis HA, **Pereira JM**, Matos DM, Ceia FR, Almeida N, Geraldes P, Saldanha S, Barbosa N, Hernandéz-Montero M, Fernandes C, González-Solís J and Ramos JA (2021) Distribution, abundance, and on-land threats to Cabo Verde seabirds. *Bird Conservation International* 31:53–76.

[4] Cerveira LR, Ramos JA, Rodrigues I, Almeida N, Araújo PM, dos Santos I, Vieira C, **Pereira JM**, Ceia FR, Geraldes P, Melo T and Paiva VH (2020) Inter-annual changes in oceanic conditions drives spatial and trophic consistency of a tropical marine predator. *Marine Environmental Research* 162:105165.

[3] Krüger L, **Pereira JM**, Paiva VH and Ramos JA (2019) Personality influences foraging of a seabird under contrasting environmental conditions. *Journal of Experimental Marine Biology and Ecology* 516:123–131.

[2] Abreu J, Staniland I, Rodrigues C, Queirós JP, **Pereira JM** and Xavier JC (2019) Squid in the diet of Antarctic fur seals: potential links to oceanographic conditions and Antarctic krill abundance. *Marine Ecology Progress Series* 628:211–221.

[1] Krüger L, **Pereira JM**, Ramírez I, Ramos JA and Paiva VH (2018) How the future climate may modulate the non-breeding distribution of a Vulnerable gadfly petrel. *Marine Ecology Progress Series* 599:253–266.

Conference papers

Oral Communications

[1] Paiva VH, Ceia FR, Krüger L, **Pereira JM**, Geraldes P and Ramos JA (2019) Driven by the climate: Cory's shearwater (*Calonetris borealis*) as a sentinel species for the effects of climate on the marine environment. In *X Portuguese Ornithology Conference*. Peniche (Portugal).

Posters

[5] Cerveira LR, Rodrigues I, Araújo PM, dos Santos I, Vieira C, **Pereira JM**, Geraldes P, Melo T, Ramos JA and Paiva VH (2019) Implications of seasonal and annual changes in oceanic productivity on the at-sea spatial e temporal consistency of Cape Verde shearwaters (*Calonectris edwardsii*). In *X Portuguese Ornithology Conference*. Peniche (Portugal).

[4] Marques AM, Ramos JA, **Pereira JM**, Krüger L and Paiva VH (2019) I am different from my neighbours: how personality influences the spatial ecology of Cory's shearwaters (*Calonectris borealis*) from two close sub-colonies. In *X Portuguese Ornithology Conference*. Peniche (Portugal).

[3] Laranjeiro MI, da Silva JM, Alves LMF, Norte AC, Paiva VH, **Pereira JM**, Ramos JA, Lemos MFL and Ceia FR (2019) The demanding phase of the breeding season: how do stress levels vary in Cory's shearwater (*Calonectris borealis*) during pre-laying and chick-rearing periods? In *X Portuguese Ornithology Conference*. Peniche (Portugal).

[2] Ramos JA, Rodrigues I, Melo T, Geraldes P, Araújo PM, Vieira C, **Pereira JM** and Paiva VH (2018) Variation in ocean conditions and chick growth measures in Cory's and Cape Verde shearwater. In *27th International Ornithological Congress*. Vancouver (Canada).

[1] Abreu J, Staniland I, Queirós JP, **Pereira JM** and Xavier JC (2018) Squid prey of Antarctic fur seals as an environmental change indicator. In *POLAR 2018 Conference*. Davos (Switzerland).

Table of Contents

Chapter 1

Introductory Review

This chapter is submitted for publication as part of a book chapter:

Pereira JM, Paiva VH, Krüger L and Votier SC (2022) Tracking seabirds for conservation and marine spatial planning In: *Seabird biodiversity and human activities*. Ramos JA and Pereira L (eds) CRC Press, Boca Raton, Florida, USA.

1.1. Seabirds as indicators of global change

The global oceans are in crisis. The rapidity of environmental change requires novel approaches to conservation and management (Palumbi et al. 2009, Steffen et al. 2015, Lenton et al. 2019). Marine megafauna has been severely impacted during the Anthropocene but are also important ecosystem sentinels (Hazen et al. 2019).

Seabirds have been the focus of scientific research for several decades and therefore particularly well-studied in comparison with other marine animals. Seabirds travel widely and feed across many trophic levels but are also relatively prominent and accessible when they return to land to breed, making them effective sentinels (Parsons et al. 2008). Seabird monitoring enables information gathering across a range of spatio-temporal scales. For instance, diet and demographic monitoring have been used as indicators of ecosystem health and to prioritise conservation goals (Furness 1997, Piatt & Sydeman 2007). Moreover, they may act as important umbrella species facilitating protection of habitats and less charismatic taxa (Lescroël et al. 2016). In this way, seabird tracking has emerged as a powerful compliment with the ability to monitor biodiversity and reveal key information about the potential winners and losers of global change (Brisson-Curadeau et al. 2017, Hays et al. 2019).

1.2. Advances in tracking devices to study seabird distribution

For much of the 20th Century, seabird research focussed on demography, behaviour and physiology at their breeding colonies (Piatt & Sydeman 2007), as well as opportunistic research from boats (Hudson & Furness 1989). In the early 1970’s however, the first seabirds were fitted with radio transmitters to study colony attendance patterns and short-term foraging movements (Southern 1970). These devices provided novel insights and were relatively inexpensive, but were also limited in terms of detection range (approximately 15-20 km) and precision (Burguer & Shaffer 2008, Ponchon et al. 2013, López-López 2016).

One of the most significant advances in seabird ecology was the development and deployment of platform terminal transmitters (PTTs) in the early 1990's. This led to detailed reconstructions of albatross and penguin at-sea behaviour in the Southern Ocean (Jouventin & Weimerskirch 1990, Ancel et al. 1992, Weimerskirch et al. 1993). PTTs (Fig. 1.1) transmit radio signals to the Argos Satellite System and variations in doppler shift created by the moving satellite allows location (to within approximately 500 m) to be estimated in near real time without the need to recover devices (BirdLife International 2009). It was also possible to incorporate solar-panels to increase battery capacity for long-term tracking (Wilson et al. 2002), and to study hitherto cryptic behaviours such as dispersal and immature movement (Weimerskirch et al. 2006, Votier et al. 2011, Péron & Grémillet 2013).

Figure 1.1: *An adult Wandering albatross (Diomedea exulans) from Bird Island in South Georgia equipped with a platform terminal transmitter (PTT) on its back. Photo credit: José C. Xavier.*

Following the success of PTTs, archival global positioning system (GPS) tags were another significant milestone in the study of seabird movement ecology (Fig. 1.2A). These devices record precision locations (10 m maximum error) (Bridge et al. 2011), potentially at high frequencies (10 Hz and above) (Gibb et al. 2017). In the past 20 years or so, not only did these devices decrease in size but they also became significantly cheaper, driven by mass-produced components and demand for recreational use (e.g. for hiking and pet tracking). In addition to these inexpensive tags repurposed by researchers, several companies manufactured devices specifically designed for tracking birds, including smaller and lighter tags weighing as little as 1 g (Fig. 1.2B). This led to the mass deployment of GPS tags across a wide range of locations and approximately 216 seabird species from 17 families over the last four decades (Bernard et al. 2021). However, there is very little information on the at-sea distribution of smaller species such as gadfly-petrels, storm-petrels, diving-petrels and prions.

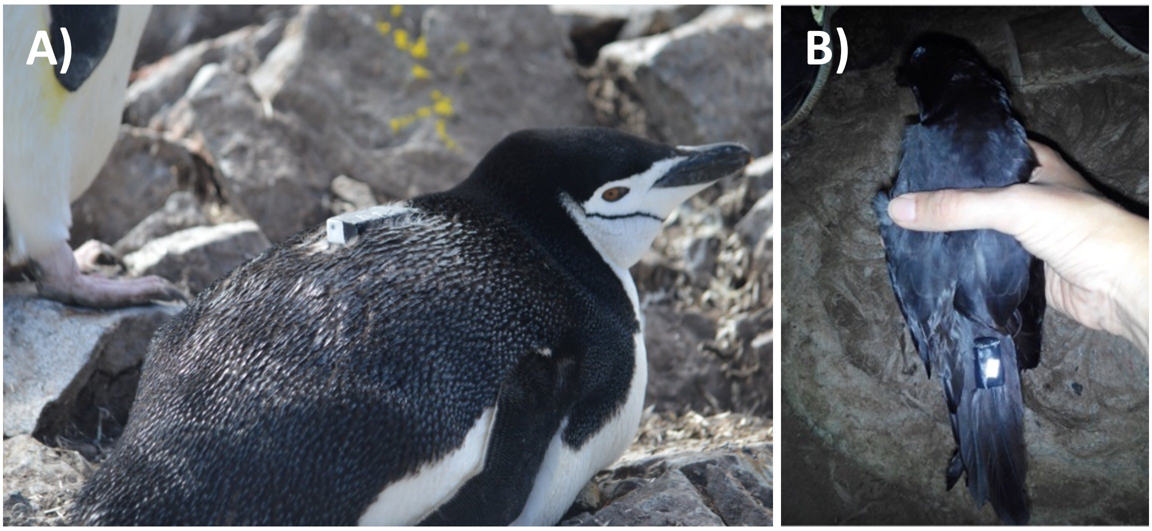

Figure 1.2: *(A) An adult Chinstrap penguin (Pygoscelis antarcticus) from Harmony Point, Nelson Island, in the Maritime Antarctic Peninsula, equipped with an archival global positioning system (GPS) tag on its back. Photo credit: Lucas Krüger; (B) An adult Bulwer's petrel (Bulweria bulwerii) from Raso Islet in the Cabo Verde archipelago, equipped with a 2 g archival GPS tag. Photo credit: Biosfera I. Archival GPS tags are smaller, lighter and more affordable when compared to PTTs, enabling to track a greater number of seabirds, including many poorly-studied smaller species. Nevertheless, due to battery constraints these tags are mainly used to track short-term movements of individual seabirds during the breeding season.*

While most GPS tags are archival with a primary-cell battery, some also transmit and have photovoltaic cells greatly increasing their utility. GPS-PTTs relay positions via satellite, while others upload information via the global system for mobile communications (GPS-GSM) or relay information vary a base-station (Bouten et al. 2013). Solar-powered GPS-GSM tags (Fig. 1.3) have the potential to remain active during long periods of time, providing fine-scale longitudinal movement information throughout the annual cycle in near-real time (Navarro et al. 2016). However, GPS-GSM tags tend to be expensive (e.g. > 500€), by an order of magnitude more than archival GPS loggers (e.g. < 50€). Overall, archival GPS loggers are more suited for use in short-term studies during the breeding season, when seabirds return repeatedly to the nest site while central-place foraging (Sansom et al. 2018). As a consequence, fine-scale information on at-sea distribution of non-breeding seabirds is generally poorly represented or virtually absent, especially during immaturity (Péron & Grémillet 2013).

Figure 1.3: *An adult Southern giant petrel (Macronectes giganteus) from Harmony Point, Nelson Island, in the Maritime Antarctic Peninsula, equipped with a solar-powered GPS transmitter on its back. Photo credit: Denyelle Corá. Despite the high costs of acquisition, solar-powered GPS transmitters have the potential to provide fine-scale longitudinal movement information of individual birds throughout the annual cycle in near-real time.*

Geolocation has been instrumental in the study of long-range seabird movements, revealing, for example, remarkable ocean-wandering migration feats (Croxall 2005, Shaffer et al. 2006, Egevang et al. 2010). Geolocators (Fig. 1.4) record ambient light intensity multiple times daily which can be used, together with an internal clock, to calculate day length and midday/midnight and in turn, latitude and longitude (Wilson et al. 1992, Phillips et al. 2005). This generates twice daily location estimates with average error of 185 ± 115 km, although the method works only poorly near to the poles and during the equinoxes (Phillips et al. 2004). In addition, most models are archival necessitating device recovery.

Despite these limitations, geolocators have a number of advantages. Because they can store up to 60 months of data means it is possible to investigate the degree of inter-annual migratory site fidelity (Phillips et al. 2005, Grecian et al. 2019). Moreover, devices with temperature/saltwater sensors provide the opportunity not only to improve location precision by integrating remotely sensed environmental data (Merkel et al. 2016), but also to link distribution with activity behaviour (Mackley et al. 2010). In comparison to satellite transmitters, geolocators also tend to be smaller, lighter (the smallest are 0.3 g) and more affordable (e.g. > 250€), although the cost and size of tags is changing rapidly.

Figure 1.4: *An adult Macaronesian shearwater (Puffinus baroli) from Selvagem Grande, Madeiran archipelago, in the subtropical North Atlantic Ocean, equipped with a geolocator (GLS) on its leg. Photo credit: Luís Ferreira. GLS tags are smaller, lighter and more affordable than the majority of tags and are capable of storing multiple years of data. As a consequence, these tags have been instrumental in the study of long-range movements of individual seabirds, revealing remarkable ocean-wandering migrations.*

Overall, device choice is a major consideration in study design involving trade-offs between required spatio-temporal accuracy, deployment duration, size of the study species, likelihood of tag recovery, potential device effects and cost of acquisition. Tracking devices are now very popular in seabird ecological studies, and hundreds of papers reporting data collecting with the different devices were published annually (Bernard et al.

2021). The technical details and applications of tracking devices are reviewed in detail by Burguer and Shaffer (2008), Bouten et al. (2013) and López-López (2016). Miniaturisation has also allowed the deployment of multiple devices to record detailed information on physiology (e.g. heart-rate sensors, stomach-temperature probes, piezoelectric-film probes), local environment (e.g. immersion loggers, compass-temperature loggers) or behaviour other than movement (e.g. accelerometers, magnetometers, time-depth recorders, beak sensors, video cameras) (Ropert-Coudert & Wilson 2005, Yoda 2019). When combined with positional loggers these can generate valuable new biological insight, as well as opening the potential that seabirds can act as live environmental monitors (Yonehara et al. 2016). However, at present, such multi-logger deployments are only appropriate for larger seabird species.

Seabird tracking studies are based on the assumption that birds are not influenced by device attachment to such a degree that this fundamentally alters their behaviour. Earlier studies focussed on tag weight as a proportion of body mass such as the 3% body mass guidance (Phillips et al. 2003). However, more recently most studies report no effects of the devices on seabird behaviour, but exact data is often not detailed. Previous meta-analysis have documented the impacts of device deployments on breeding success, physiology, foraging behaviour, survival and fitness in a variety of bird species (Barron et al. 2010, Bodey et al. 2018, Geen et al. 2019), even when the devices were below 3% of birds' body mass (Sun et al. 2020). Hence, careful consideration in the study design is vital to evaluate the impacts of device deployments on seabirds (Chivers et al. 2016), including not only the effects on breeding performance by directly comparing groups of untagged and tagged birds (Ludynia et al. 2012a), but also evaluate whether devices may lead to short- and long-term behavioural changes (Gillies et al. 2020).

1.3. Tracking seabirds for conservation and marine spatial planning

Seabird populations have declined steeply in recent decades and their status continues to deteriorate (Paleczny et al. 2015, Grémillet et al. 2018). The three most grave threats to seabirds are alien species, bycatch and climate change, although there are also pressures from overfishing, pollution and energy production (Dias et al. 2019a). Strategies and tools are therefore required to identify, predict, and mitigate the conflicts that arise between anthropogenic activities and seabirds. Seabird tracking has emerged as a powerful tool to aid conservation and inform marine spatial planning (Lennox et al. 2019, Hays et al. 2019). By identifying important seabird habitats (e.g. migratory routes, foraging grounds and breeding areas) tracking can highlight areas for protection and contribute to a more sustainable exploitation of marine resources (Lascelles et al. 2012, Ronconi et al. 2012). In this context, the use of seabirds as indicators of marine spatial planning is gathering momentum to put this group of animals as central users of the global oceans and indicators of ocean health. It is now time to look forward to the key research directions that these new efforts are taking. Below, we consider some of the main applications of tracking to understand how or where seabirds may be exposed to anthropogenic threats and towards the prioritisation of conservation goals.

1.3.1. Environmental and climate change

To elucidate the ecological consequences of climate change, a detailed understanding of where seabirds go and the drivers of movement is required to predict future consequences. Monitoring the distribution and activity patterns of seabirds chimes with calls for marine spatial planning to become more fluid to reflect the dynamic nature of marine environments (Maxwell et al. 2015). Yet, practical examples where tracking led to clearly identifiable real-world changes in conservation or marine spatial planning efforts are scarce (Hays et al. 2019). One of the most frequent strategies used to understand seabirds' response to global change is to combine tracking with environmental monitoring such as from satellite imagery. Such approach has the potential to study seabird-environmental interactions remotely and assess inter-annual migratory/foraging fidelity (Wakefield et al. 2015, Grecian et al. 2019) or shifts in distribution ranges due to detrimental environmental conditions induced by climate change (Poloczanska et al. 2016). Therefore, understanding shifts in seabird habitat use through long-term series with changing environmental and oceanographic conditions is key for implementing dynamic ecosystem-level management (McGowan et al. 2013).

The physical dynamics of the marine environment, influenced by wind patterns and currents, determine the occurrence of fronts where mobile pelagic prey concentrate and are the target of seabirds (Wakefield et al. 2009, Scales et al. 2014). Changes in the strength and persistence of fronts may be linked with a reduced foraging and breeding success, because the prey disperse into a wider area (Ropert-Coudert et al. 2009). It is unclear how climate change will alter ocean fronts, but seabird tracking is likely to prove important for understand any consequences of change.

Other environmental changes affecting some seabird communities is the increased frequency, severity and duration of extreme climatic events such as marine heatwaves, increased storminess and effects of changing wind. For example, GPS tracking breeding Black-legged kittiwakes (*Rissa tridactyla*) at Middleton Island, Alaska, revealed increased foraging effort during and immediately after a heatwave event, with possible population-level consequence (Osborne et al. 2020). Moreover, GPS tracking of Great frigatebirds (*Fregata minor*) and Red-footed boobies (*Sula sula*) breeding at Europa Island, located in the Mozambique Channel, revealed that both species adjusted their behaviour to avoid the centre of tropical cyclones (Weimerskirch & Prudor 2019). Although extreme climatic events are poorly studied, long-term tracking data may reveal the mechanisms underpinning the effects of those events, particularly when combined with data on breeding parameters (Jenouvrier et al. 2015, Ropert-Coudert et al. 2018, Pereira et al. 2020). Indeed, there is a greater need to integrate monitoring of demography with at-sea behaviour from biologging (Carneiro et al. 2020).

1.3.2. Interaction with fisheries and marine traffic

Tracking has provided crucial information on how fisheries influence seabirds (Le Bot et al. 2018). For instance, by comparing the distribution of tracked Procellariiformes with spatio-temporal patterns of fishing effort in the Southern Ocean provided important evidence for the catastrophic impact of bycatch in seabird populations (Phillips et al. 2006). Moreover, precision tracking of individual seabirds and vessels revealed the extent to which birds are attracted to vessels to feed on discards (Votier et al. 2010, 2013, Patrick et al. 2015), or not in some cases (Granadeiro et al. 2011, Cianchetti-Benedetti et al. 2018, Clark et al. 2020). This has also enabled us to quantify the ecological footprint of individual boats (Bodey et al. 2014), as well as the impact of fishing activity on broad-scale search patterns (Bartumeus et al. 2010). Tracking is also important for assessing how competition with fisheries impacts seabird movements. For example, experimental fisheries closures close to African penguin (*Spheniscus demersus*) colonies created fluctuations in foraging fish availability, and revealed increased foraging effort of tracked adults as well as decreased offspring condition as forage fish abundance declined (Pichegru et al. 2010, 2012, Campbell et al. 2019). However, long-term tracking studies together with population dynamic studies are necessary to evaluate population consequences of seabird fisheries competition (Clay et al. 2019b).

Vessel location data can be obtained either through the use of vessel monitoring system (VMS) or automatic identification system (AIS) programs, although this approach is limited by data resolution and accessibility due to poor coverage in the high seas and because of illegal unreported and unregulated (IUU) fishing (Corbeau et al. 2019). However, global initiatives such as Global Fishing Watch (Kroodsma et al. 2018) have improved transparency of fishing activity data by making it publicly accessible, enabling a more complete understanding of seabird-fishery interactions (Pereira et al. 2021, Fischer et al. 2021, Orben et al. 2021). Tags designed to detect the presence of vessels through radio emissions produced by marine radar offer information on vessels not using VMS or AIS, and hence have the potential to detect IUU fishing (Weimerskirch et al. 2018, 2020a, Grémillet et al. 2019). Simultaneously, accelerometers, geolocators and bird-borne cameras not only provide information on vessel interactions, but also details on the behaviour, nature of such associations such as prey capture and interactions with fishing gear (Votier et al. 2013, Cianchetti-Benedetti et al. 2018, Dupuis et al. 2021). Moreover, seabird tracking combined with diet sampling and stable isotopes also provide insight into the use of fishery discards (Votier et al. 2010, Matos et al. 2018, Giménez et al. 2021).

Marine traffic may also impact some seabirds via disturbance, and tracking could prove important understanding on this poorly studied stressor (Schwemmer et al. 2011). Yet, few studies have attempted to quantify the collision risk with marine traffic which may be illuminated at night (Merkel & Johansen 2011). Of the few studies in this area, precision tracking of individual seabirds and marine traffic provide fine-scale information on the bird-ships encounters and quantify the disturbance of marine traffic on seabirds (Burger et al. 2019, Lieske et al. 2020).

1.3.3. Offshore energy production

Seabird tracking data is important for quantifying potential impacts of offshore energy developments by estimating the collision risk (Soanes et al. 2013b) and costs of displacement (Dierschke et al. 2016). Research evaluating collision risk with marine renewable energy installations (MREIs), particularly offshore windfarms (Vanermen et al. 2020), estimate spatial overlap with tracked birds (Thaxter et al. 2015, Garthe et al. 2017, Peschko et al. 2020). This approach has benefits from Eulerian approaches (i.e. observations of birds from a fixed position) because it provides information about connectivity, age/sex and because it is not constrained by weather or time of day. Tagging can also provide information on flight heights, which is important for accurate collision risk modelling (Ross-Smith et al. 2016). GPS tags provide flight heights, but have low precision unless sampling at high frequencies (e.g. > 1 Hz) (Peschko et al. 2021). Barometric pressure loggers provide more reliable altitude estimates that can generate very different collision risk estimates compared with flight-height observations (Cleasby et al. 2015). Biologging is especially valuable for assessing displacement impacts in terms of movement and energetics (Heylen & Nachtsheim 2018, Williams et al. 2020). GPS tags and time-depth recorders are also valuable to assess impacts of other poorly studied MREIs such as tidal stream and wave energy installations (Grecian et al. 2010, Waggitt & Scott 2014). Finally, biologging may also be important for understanding any potential positive impacts of MREIs such as by creating roost sites, fish aggregating devices and protected areas at-sea (Inger et al. 2009).

Oil, gas and deep-sea mining platforms may also pose a threat to some seabirds. Yet, few studies have attempted to quantify seabird collision rates at these structures which may be illuminated at night (Ronconi et al. 2015, Miller et al. 2018a). Of the limited research in this area, overlap between platforms and birds tracked with geolocation loggers provide only course-scale information (Hedd et al. 2011, McFarlane Tranquilla et al. 2013, Fort et al. 2013) and cannot measure bird-platform interactions directly and at refined spatial scale (Ronconi et al. 2015, Bolton 2020).

1.3.4. Marine pollution

Pollution is a threat to some seabird populations, both on land (e.g. light pollution) and at-sea (e.g. oil, chemical pollutants and plastic), and tracking provides insight into these potential threats. For example, artificial light pollution may influence seabird mortality at night, especially for fledglings (Ainley et al. 2001, Rodríguez & Rodríguez 2009). Much of the information on birds killed or grounded annually are collected from rescue campaigns (Rodríguez et al. 2012), but key information such as the origin of birds attracted to lights, the drivers of attraction, and to what distances or light intensity thresholds seabirds are affected can only be obtained with tracking data (Rodríguez et al. 2015).

Movement information can be used to quantify the risk exposure to hydrocarbon pollution, such as oil spills, the distribution of plastics/microplastics or heavy metals. For example, tracking Black-vented shearwaters (*Puffinus opisthomelas*) and Cory's shearwaters (*Calonectris borealis*), combined with stable isotope analysis, pinpointed the areas of higher mercury contamination in the foraging ranges of both species during the breeding (Soldatini et al. 2020) and non-reeding periods (Gatt et al. 2020), respectively. Moreover, tracking can also provide information on the risk exposure to other pollutants such as oil (Montevecchi et al. 2012) and chemical additives used to produce plastic (Miller et al. 2020). Tracking studies together with contaminant studies are necessary to assess the risk exposure of seabirds to marine pollution (Mallory et al. 2010).

1.3.5. Marine protected areas (MPAs)

Seabird tracking is proving instrumental for marine spatial planning and for identifying protected areas at-sea (Le Corre et al. 2012, Krüger et al. 2017, Hays et al. 2019). This has become especially effective as there is a move towards multi-species, multi-colony projects across different institutions (Grecian et al. 2016, Fayet et al. 2017, Hindell et al.

2020).This is exemplified by BirdLife International's seabird tracking database, created in 2003, it is a major repository for seabird tracking data holding >14 million locations from >30 000 individual tracks of >130 species breeding at approximately 362 colonies. The increasing volume of tracking data compiled in seabird tracking database led to a major need to create standard methodological frameworks to analyse tracking data for multiple seabird species and colonies. To handle the dimension and complexity of the data compiled in the seabird tracking database, BirdLife International developed a generic protocol to identify important area for seabirds at regional and global scales (Lascelles et al. 2016). Several recent studies have used such methodologies to identify areas with higher conservation importance around important seabird colonies (Dias et al. 2018, 2019b, Steinfurth et al. 2020) and in pelagic waters (Dias et al. 2017, Heerah et al. 2019). Such collaborative projects that breakdown international barriers are crucial if we are to create protected areas for seabirds at-sea (Handley et al. 2021), especially on high seas (Beal et al. 2021).

1.4. Study area: eastern North Atlantic region

The study area included in this thesis extends in latitude from the South limit of the Celtic Sea (approximately 50° N) to the coast of Senegal (approximately 15° N). In longitude, it spans from the West coast of the Iberian Peninsula and the Northwest coast of Africa (approximately between 10° W to 15° W) to the Mid-Atlantic Ridge (approximately 30° W) (Fig. 1.5). This region encompasses a variety of oceanographic conditions, from sub-tropical to temperate mid-latitudes and from coastal upwelling areas to oceanic waters in the middle of the North Atlantic Ocean basin. This region is divided into three major systems based on local oceanography and bottom topography: (1) western Iberian upwelling system; (2) Canary upwelling system; and (3) Azores confluence zone (Fig. 1.5). Even though the western coast of the Iberian Peninsula includes the Northern section of the Canary upwelling system, it was decided to separate this large ecosystem into two distinct regions because of the little continuity in the flow between these two systems (Arístegui et al. 2009, Kämpf & Chapman 2016).

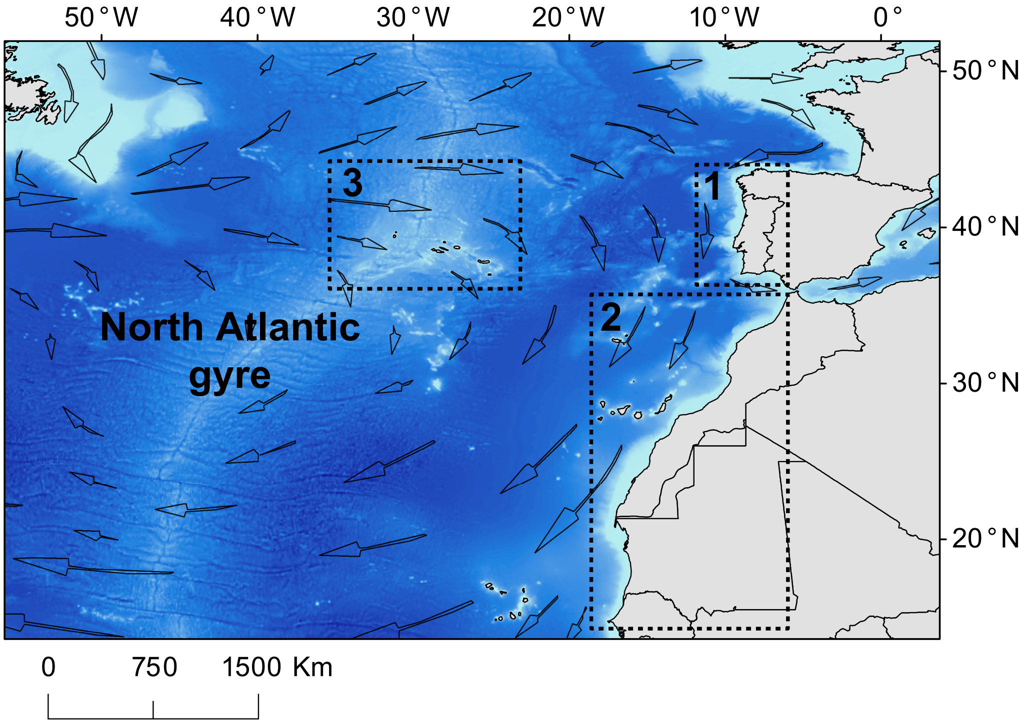

Figure 1.5: *Major circulation of the eastern North Atlantic region and main oceanographic systems: (1) western Iberian upwelling system; (2) Canary upwelling system; and (3) Azores confluence zone. Background displays bathymetry of the region (lighter to darker blue as depth increases). Map credit: Jorge M. Pereira.*

The main oceanographic characteristics of the western Iberian upwelling system are similar to those observed on other major coastal upwelling systems located in the eastern boundaries of large oceanic gyres (Bakun 1990, Chavez & Messié 2009, Sydeman et al. 2015). For instance, the Canary and Benguela upwelling systems in the South and North Atlantic Ocean, respectively, and the California and Humboldt upwelling systems in the Pacific Ocean. In terms of bottom topography, this region is characterised by a considerable large continental shelf and steep slope (Fig. 1.6). The dominant regional circulation pattern over the western Iberian upwelling system is attributed to the Portuguese Current (Pérez et al. 2001). This current is maintained by a deflected branch of the North Atlantic drift, in the eastern section of the North Atlantic gyre (Fig. 1.6). Mesoscale activity generated by these forces, together with the influence of bottom topography, are responsible for a moderate weak circulation that flows South-easterly towards the coast of Portugal (Relvas et al. 2007).

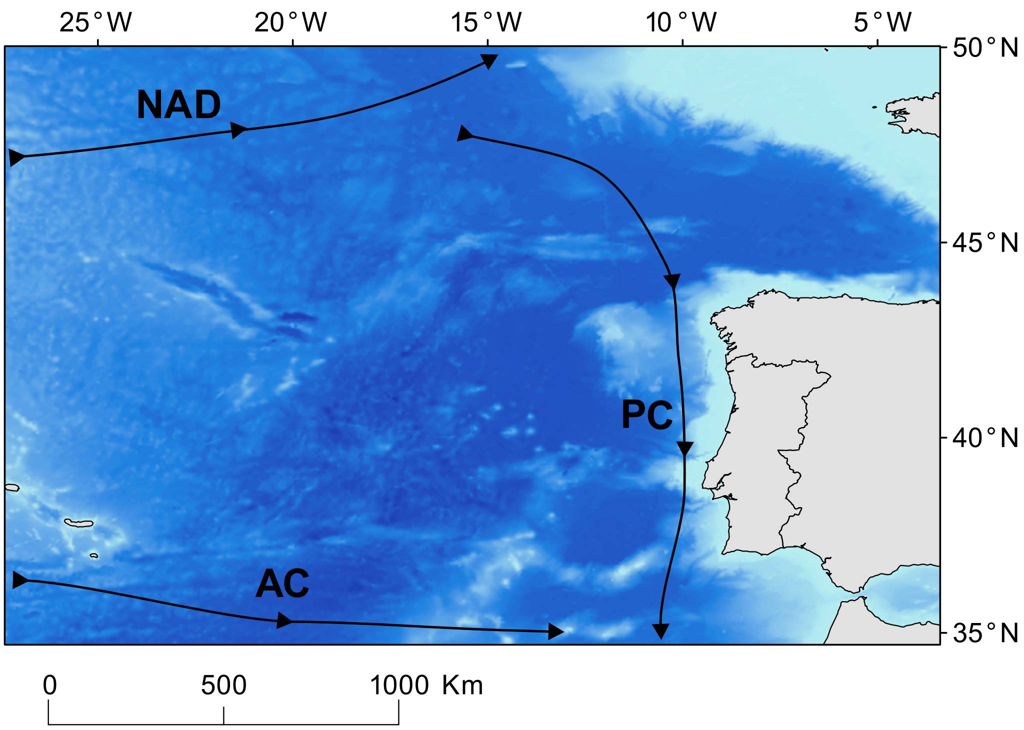

Figure 1.6. *Bathymetry of the western Iberian upwelling system (lighter to darker blue as depth increases) showing the bottom topography and highlighting the large continental shelf and steep slope. NAD- North Atlantic Drift; PC- Portuguese Current; and AC- Azores Current. Adapted from Kämpf & Chapman (2016). Map credit: Jorge M. Pereira.*

Local meteorological conditions also play a key role in the general circulation of this system and are responsible for large seasonal variations in the upwelling intensity (Fiúza et al. 1982). During the spring-summer months (i.e. from April to September) predominant North winds cause wind-driven persistent and intense upwelling along the Iberian Peninsula coast, providing optimal conditions for concentrations of large pelagic fish populations (Sousa et al. 2008). Altogether, local winds and bottom topography shape the upwelling intensity and primary productivity patterns in the western Iberian system.

1.4.2. Canary upwelling system

The Canary upwelling system is a vast region, spanning from the northern coast of Morocco to the coast of Senegal (Arístegui et al. 2009). This system is characterised by abrupt changes in coastal morphology and encompasses several large capes that favour the formation of intense mesoscale activity along its length (Van Camp et al. 1991, Santos et al. 2005). The major flow contribution to the Canary upwelling system comes from an eastward branch of the current of the Azores that ejects cold oceanic waters into the upwelling region (Fig. 1.7). In addition, it also receives a small contribution from the Portuguese current and the Mediterranean Sea at its northern limit (Hernández-Guerra et al. 2001). This long upwelling system displays a great geographical variability, which translates into different upwelling environments that can be classified into three main sub-regions: (1) almost permanent upwelling zone; (2) permanent upwelling zone; and (3) seasonal upwelling zone (Cropper et al. 2014). While the northern sub-regions of the Canary upwelling system exhibit a year-round upwelling, the southern sub-region starts to display some seasonality and is characterised by the strong winter upwelling movements followed by a downwelling period during the summer months (Marcello et al. 2011, Gómez-Letona et al. 2017). The major topographic feature in this long upwelling system is the Canary archipelago, which is located in a transition zone between coastal and oceanic domains (Barton et al. 1998). The abrupt topography of the Canary archipelago causes a major disturbance of the downstream flow of Canary upwelling current and generates intense mesoscale activity between the African continental shelf and the Canary archipelago (Fig. 1.7) (Arístegui et al. 1994, Pingree & Garcia-Soto 2004, Sangrà et al. 2009).

The enlargement of filaments and meanders coming from the intense mesoscale activity in this area is responsible to enhance prey availability by transporting fish larvae from the African shelf to offshore areas near the Canary archipelago (Basterretxea & Arístegui 2000, Rodríguez et al. 2004, Pelegrí et al. 2005). Nevertheless, the southern part of the Canary upwelling system is considered the most productive sub-region of this large ecosystem. While the northern sub-regions are influenced by lower primary productivity patterns from the North Atlantic Central Waters (NACW), the southern sub-regions benefit from higher nutrient concentrations of the South Atlantic Central Waters (SACW) (Gómez-Letona et al. 2017).

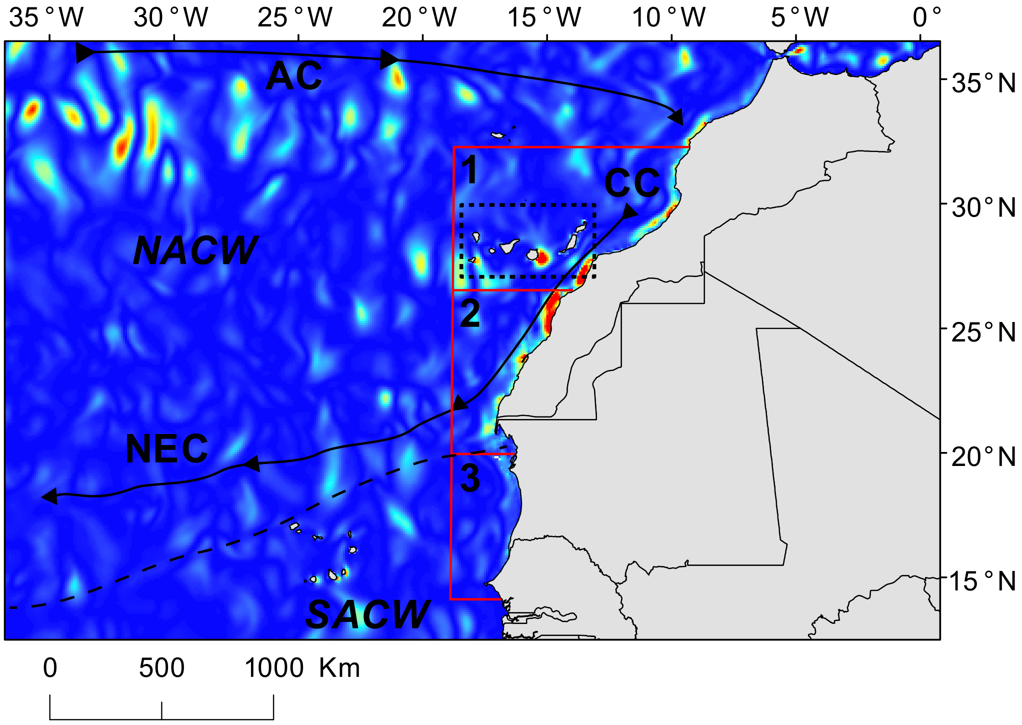

Figure 1.7. *Eddy Kinetic Energy (EKE) as a surrogate of mesoscale activity displayed over the Canary upwelling system. Intense mesoscale activity (warm colours) is depicted towards southern latitudes of the Canary archipelago. AC- Azores Current; CC- Canary Current; and NEC- North Equatorial Current. Black dashed square highlights the Canary archipelago. Red limits identify three main sub-regions of the Canary upwelling system where the upwelling intensity are reported to differently vary along the year: (1) almost permanent upwelling zone; (2) permanent upwelling zone; and (3) seasonal upwelling zone. Boundaries of sub-regions were adapted from Cropper et al. (2014). The black dashed line separates the regions of the ocean influenced by the North Atlantic Central Waters (NACW) and the South Atlantic Central Waters (SACW). Map credit: Jorge M. Pereira.*

1.4.3. Azores confluence zone

The Mid-Atlantic region of the Azores archipelago is greatly supplied by the western boundary of the North Atlantic gyre and is under the permanent influence of the Gulf Stream (Klein & Siedler 1989). This region has a particular oceanography due to the convergence of two large currents with contrasting characteristics: the Gulf Stream (a warm current flowing towards northern latitudes of the North Atlantic Ocean) and the Labrador Current (a cold current flowing from the Arctic Ocean to southern latitudes along the Canadian coast) (Mann 1967, Krauss et al. 1990). As a consequence, the region where these two large currents converge is characterised by intense water mixing and the prevalence of turbulent structures, such as eddies, meanders and filaments (Fig. 1.8). These structures have a major influence on the regional oceanography and biological activity on the waters around the archipelago of Azores, particularly on the western and central groups of the archipelago.

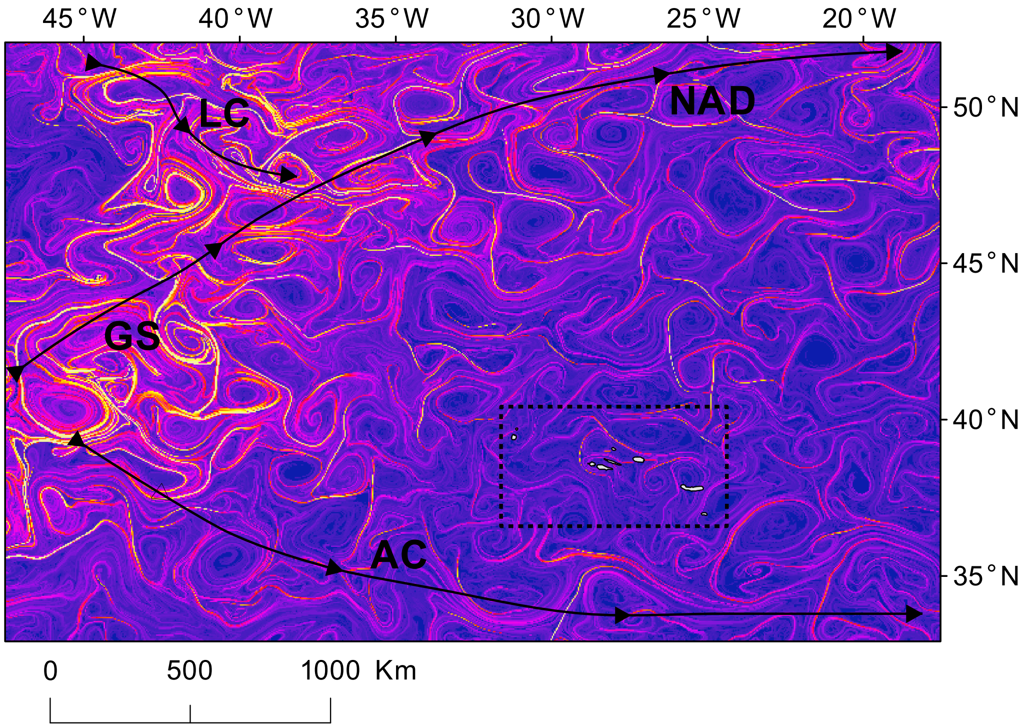

Figure 1.8. *Finite-Size Lyapunov Exponents (FSLE) as a surrogate of sub-mesoscale activity (i.e. eddies, meanders and filaments) displayed over the Azores confluence zone. Warm colours depict intense water mixing while cold colours denote low water mixing. GS- Gulf Stream; LC- Labrador Current; AC- Azores Current; and NAD- North Atlantic Drift. Black dashed square highlights the archipelago of Azores. Adapted from Caldeira & Reis (2017). Map credit: Jorge M. Pereira.*

Due to its positioning, the Azores archipelago is greatly influenced by mesoscale structures generated in the Gulf Stream, but the eastern group is particularly affected by propagating eddies from the Azores Current (Caldeira & Reis 2017). On the one hand, eddies generated in Gulf Stream are usually larger (up to 80 km radius), with higher longevity (approximately 51 days) and are responsible to boost primary productivity around the western and central groups of the archipelago of Azores. Plus, younger near-field eddies from the Azores Current are smaller and ephemeral (approximately between 2 and 10 days), making the eastern group the least productive of the archipelago (Caldeira & Reis 2017). Even though the Azores region is located in oligotrophic oceanic waters

(Amorim et al. 2017), this region is considered to be a hotspot of marine biodiversity in the North Atlantic Ocean, gathering large communities of fish and marine megafauna (Afonso et al. 2020). The phenomena known to boost primary productivity in this region can be related with the interplay of two mechanisms: (1) the “Island mass effect” (Doty & Oguri 1956) and the (2) “Sticky water effect” (Wolanski 1994). While the “Island mass effect” explains how the enhanced biological activity is upwelled to the surface given the abrupt topography of the islands and the numerous seamounts in the area (Morato et al. 2008), the “Sticky water effect” demonstrates that the disturbance of oceanic flow by the regional bottom topography generates an incoming flow within the archipelago, and increase the retention capacity close to islands and seamounts (Sala et al. 2016).

1.5. Study species: Cory’s shearwater

1.5.1. Population numbers and breeding locations

Cory’s shearwater (*Calonectris borealis*) is a long-lived and medium-sized Procellariiform that undertakes exceptionally long migrations from their breeding areas in the North Atlantic Ocean to the wintering areas in South America and South Africa coasts (González-Solís et al. 2007, Dias et al. 2011, Catry et al. 2011, Missagia et al. 2015). It is classified as a Least Concerned (LC) species according to the International Union for Conservation of Nature (IUCN) Red List of Threatened Species, with a global population estimated of approximately 500 000 mature individuals with more than 85% breeding in the archipelago of Azores and Madeira (BirdLife International 2020). The largest colony in the Azores is located on Corvo Island with an estimated population of 6000-10 000 breeding pairs (Oppel et al. 2014). The largest colony of Cory’s shearwaters is located on Selvagem Grande, archipelago of Madeira, with approximately 30 000 breeding pairs (Granadeiro et al. 2006). The remaining breeding population is distributed on small colonies along the coastline of the main islands of the Azores, Madeira, and Canary archipelagos, as well as islets in these regions and also on the Berlenga archipelago, close to mainland Portugal (Lecoq et al. 2011, Ramos et al. 2013).

1.5.2. Breeding biology

Adult shearwaters (Fig. 1.9 top left and top right panels) arrive at the colony annually by late February and early March, where they restore their energetic stocks depleted during migration (Monteiro et al. 1996). In early May, females initiate the pre-laying exodus for about 20 days, to fulfil nutritional requirements for the energetically costly production of an egg (Jouanin et al. 2001). At the same time, males remain near the colony to defend the nest until the partners arrive (Granadeiro et al. 1998b, Werner et al. 2014). In early June, females return to the colony and lay a large single egg, whereas males take the first incubation shift allowing females to recover their energetic body reserves lost during the pre-laying exodus (Ramos et al. 2003, Paiva et al. 2013b). The incubation period lasts for approximately two months and it is shared between males and females until the end of July and early August when the eggs hatch (Zino et al. 1987, Granadeiro 1991). During the long chick-rearing period (over two months), parents use a dual-foraging strategy by alternating between short foraging trips to regularly feed the chicks (Fig. 1.9 bottom right panel) and long foraging trips for self-maintenance, which allow them to restore their body condition (Weimerskirch et al. 1997, Magalhães et al. 2008, Paiva et al. 2010a). The regularity of chick provisioning decreases until the end of September when the adults leave the colony and initiate the wintering migration (Monteiro et al. 1996, Granadeiro et al. 1998b, Ramos et al. 2003). Consequently, chicks decrease their body size and fledge in early November (Mougin et al. 2000).

1.5.3. Diet and foraging ecology

The diet of Cory' shearwaters is largely composed by epi-mesopelagic fish and cephalopods (Granadeiro et al. 1998a, Paiva et al. 2010e, Xavier et al. 2011). However, previous studies suggest that populations breeding in neritic and oceanic colonies could differ in some of the prey choices. European pilchard (*Sardina pilchardus*), Atlantic horse mackerel (*Trachurus trachurus*) and garfish (*Belone belone*) dominate the diet of neritic populations of Cory's shearwaters (e.g. Berlenga Island) (Paiva et al. 2010e, Alonso et al. 2012). Moreover, blue jack mackerel (*Trachurus picturatus*), chub mackerel (*Scomber* *colias*), two-wing flying-fish (*Exocoetus volitans*), trumpetfish (*Macroramphosus* sp.) and boarfish (*Capros aper*) are also important prey for populations exploring oceanic environments in the mid-North Atlantic (archipelago of Azores) and subtropical North Atlantic (archipelago of Madeira) (Granadeiro et al. 1998a, Paiva et al. 2010e, Alonso et al. 2018).

Figure 1.9. *Breeding pairs of Cory's shearwaters from Berlenga Island, Portugal (top left panel), adult within the burrow during the breeding period (top right panel), adult equipped with a GPS device to the four central tail feathers (bottom left panel) and chick during the mid-chick-rearing period (bottom right panel). Photo credits: top left panel (Maria I. Laranjeiro), top right panel, bottom left panel and bottom right panel (Jorge M. Pereira).*

The overall distribution patterns of Cory's shearwaters are well understood, especially during the breeding period. Previous studies on Cory's shearwaters have shown that the at-sea distribution of adults tracked with GPS loggers (Fig. 1.9 bottom left panel) during the breeding period is shaped by the location of the breeding colony in relation to the closest major coastal upwelling system. In this sense, the main distribution patterns of

Cory's shearwaters during the breeding period may be classified as: (1) mainly coastal; (2) exclusively oceanic; or (3) a mixed strategy. Previous tracking studies showed that Cory's shearwaters breeding in Berlenga Island are extremely influenced by the major summer upwelling occurring along the western coast of the Iberian Peninsula (Paiva et al. 2010c). The vast majority of the shearwaters from this neritic population engage in short foraging trips searching for prey in coastal waters near the colony, especially during the chick-rearing period (Paiva et al. 2010b). Long foraging trips to offshore waters are only reported to occur during the early breeding period (Paiva et al. 2013b, Werner et al. 2014) or in scenarios of extreme low food conditions (Paiva et al. 2013a, 2017). On the contrary, Cory's shearwaters breeding in the archipelago of Azores forage exclusively over deep oceanic waters and never use areas of coastal upwelling given the distance of approximately 2000 km (Magalhães et al. 2008, Paiva et al. 2010a, Ceia et al. 2015). However, they are known to rely on structures of enhanced oceanic marine productivity, for instance from cold upwelled waters in the vicinity of seamounts and intense mesoscale activity coming from the Gulf Stream (Magalhães et al. 2008). In terms of distance to coastal upwelling, the Canary and Madeira archipelagos are located approximately 150 km and 600 km, respectively. Previous tracking studies showed that Cory's shearwaters breeding in different populations of these archipelagos exhibit a mixed foraging strategy. They spent most of the time foraging over the West African coast during both incubation and chick-rearing, yet short foraging trips are also verified around the breeding colony and nearby seamounts (Ramos et al. 2013, Avalos et al. 2017, Alonso et al. 2018).

1.6. Objectives and thesis outline

With this thesis I aim to: (1) investigate the influence of spatio-temporal environmental variability on at-sea foraging behaviour and foraging decisions of Cory's shearwaters across the North Atlantic Ocean; and (2) evaluate seabirds' exposure to human pressures and the importance to marine spatial planning within the Portuguese Exclusive Economic Zone (EEZ). This thesis is structured in 6 chapters, including an introductory review and a general discussion. With the exception of general discussion, the remaining chapters are prepared as scientific manuscripts and the introduction as part of a book chapter. These manuscripts are already published or submitted for review. More specifically:

In **Chapter 1**, I overview the recent advances in tracking devices commonly used to study at-sea distribution and behaviour of seabirds. I further describe some of the main applications of tracking data to tackle seabird major threats, and present some case studies in which conservation policy and marine spatial planning benefited from the integration of seabird tracking data. The combination of these topics as a book chapter aim to assist students, researchers and wildlife managers. In addition, the introductory review provides most of the background information supporting the reasoning behind the use of Cory's shearwaters as a model species for studies of movement and foraging ecology. It also describes the general oceanographic characteristics and marine productivity patterns of the eastern North Atlantic Ocean region (study area), as well as the population numbers, breeding biology and foraging ecology of Cory's shearwaters (study species).

In **Chapter 2**, I test for differences in foraging tactics, foraging habitats, trophic positions and chick growth data among sub-colonies of two *Calonectris* populations from two different environments in the North Atlantic Ocean, over two consecutive breeding seasons (2017-2018), during the chick-rearing period. For this, I use GPS tracking data of 52 Cory's shearwaters nesting in two proximate (separated by 800m) and comparatively small-sized sub-colonies (ca. 100 *vs* 30 breeding pairs) at Berlenga Island (Portugal) and 59 Cape Verde shearwaters (*Calonectris edwardsii*) nesting in two sub-colonies differing greatly in size (ca. 1800 *vs* 200 breeding pairs) and located on opposite sides (separated by 3 km) of Raso Islet (Cabo Verde). These conditions provide a suitable experimental design to investigate whether colony size, location of sub-colonies and resource distribution drive to within-colony differences in the foraging behaviour of these two populations of shearwaters.

In **Chapter 3**, I investigate how two populations of Cory's shearwaters breeding in distinct oceanographic domains respond to contrasting and extreme regional marine climate anomalies. Thus, I compare the foraging behaviour, habitat use, body condition and breeding performance of 78 Cory's shearwaters from a neritic and oceanic population, during the most negative (2010) and most positive (2015) phases of the North Atlantic

Oscillation (NAO) index reported in recent decades. These conditions allow investigating the effects of strong climate variability on two different populations of Cory's shearwaters, in a context where most scenarios for future climate change predict the increasing frequency and severity of extreme climate events.

In **Chapter 4**, I quantify the large-scale spatial overlap between foraging Cory's shearwaters and industrial fisheries operating within the EEZ of mainland Portugal. I further investigate the influence of intrinsic (individual boldness and sex) and external (breeding stage) drivers on the overlap between foraging seabirds and fisheries. For this, I combine tracking data of 72 Cory's shearwaters nesting close to the mainland coast of Portugal over five consecutive breeding seasons (2012-2016) with remotely sensed fishing effort from Global Fishing Watch for the same period. The coexistence between foraging shearwaters and industrial fisheries operating in the colony surroundings provides an ideal system for testing the occurrence of boldness and sex differences in the overlap with fisheries. This chapter is the first study quantifying the at-sea overlap between Cory's shearwaters and industrial fishing fleets in the North Atlantic Ocean, and one of the few addressing spatial overlap with fisheries in populations of shearwaters breeding outside the Mediterranean Sea.

In **Chapter 5**, I assemble 8-years of at-sea censuses (2004-2012) and generate habitat suitability maps of 30 breeding and non-breeding seabird species occurring within the mainland EEZ of Portugal. I use those maps to identify important areas for seabirds and to evaluate the potential influence of human pressures (e.g. fisheries, ship traffic and marine pollution) on seabird hotspots. Overall, this chapter aim to assist researchers and decision-makers with an effective methodology for designing management strategies in this area and similar upwelling regions elsewhere in the world.

Lastly, in **Chapter 6** I provide an integrative conclusion of all the ecological results presented in this thesis, and their pertinence and relevance to further understand the effects of environmental variability and human pressures on seabird populations. The limitations and implications of those findings are discussed in terms of seabird conservation and marine spatial planning. Topics for future research projects are also discussed in this chapter.

Chapter 2

The role of colony size and foraging cost in explaining within-colony spatial segregation in two shearwater species

This chapter is under review as:

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Abstract

Spatial foraging segregation is frequent in central-place foragers during the breeding season. But, while much research has focused on colonies separated by tens or hundreds of kilometres, few studies have investigated spatial foraging segregation between adjacent sub-colonies, especially in wide-ranging species. Here, we tested for within-colony differences in the at-sea distribution, habitat use, trophic ecology and chick growth data of two *Calonectris* populations differing in size and breeding in two different environments in the North Atlantic Ocean. For this, we GPS tracked 52 Cory's shearwaters (*Calonectris borealis*) nesting in two small sub-colonies at Berlenga Island (Portugal) and 59 Cape Verde shearwaters (*Calonectris edwardsii*) nesting in two sub-colonies differing greatly in size at Raso Islet (Cabo Verde), over two consecutive breeding seasons (2017-2018), during chick-rearing. Cory's shearwaters at Berlenga Island broadly overlapped in repeatedly used patches close to the colony. In contrast, Cape Verde shearwaters partially segregated foraging grounds at relatively close distance from the colony but overlapped at distant foraging areas off the west coast of Africa. Despite spatial segregation close to the colony, Cape Verde shearwaters from both sub-colonies departed in similar directions and exhibited mostly short trips within the archipelago of Cabo Verde. These results, corroborated with similar trophic ecology and chick growth rates between sub-colonies, support the idea that spatial segregation in the colony surroundings was not likely driven by density-dependent competition or directional biased. We suggest that individual-level information of resource distribution could be an important mechanism explaining spatial segregation in neighbouring colonies of central-place foragers.

Keywords: *Calonectris*, Central-place foraging, Individual-level information, Resource sharing, Sub-colony.

2.1. Introduction

There is growing evidence that variations in foraging strategies within a population can be larger than expected by chance, though we still lack a mechanistic understanding of the drivers of such variations (Bolnick et al. 2003). The majority of variation in the foraging strategies of individuals within populations is often explained by differences among morphologies, genders, age-classes and individual-level specialisations independent of these factors (Araújo et al. 2011). However, for colonial animals such as seabirds, differences in the foraging strategies may also emerge from the spatial distribution of nesting sites within breeding colonies, but these have been comparatively less studied (Hipfner et al. 2007).

Seabird colonies are not often defined entities (Jovani et al. 2008) and are generally composed by several discrete and isolated nesting aggregations or sub-colonies differing in a range of features, such as age, breeding density and geography (Kharitonov & Siegel-Causey 1988, Forbes et al. 2000, Coulson 2001). The location of nesting aggregations on land was previously reported to be sufficient to cause spatial segregation within colonies (Masello et al. 2010, Bogdanova et al. 2014, Ceia et al. 2015) and lead to differences in breeding success (Hipfner et al. 2007, Sánchez et al. 2018). Yet, differences in foraging behaviour between sub-colonies have received little attention because in most studies much of sampling efforts are usually focused only on one sub-colony, which is usually the most accessible and known site (Waggitt et al. 2014). Ignoring the differences between sub-colonies, and assuming that behaviours displayed by a single sub-colony are representative of the entire population or species (Soanes et al. 2013a), could have important implications in terms of conservation and our understanding of the ecological processes associated with colonial living (Bogdanova et al. 2014).

Foraging seabirds typically do not exhibit a territorial behaviour at-sea and should follow an ideal-free distribution (Fauchald 2009). According to this theory, all predators are equal competitors, free to relocate among habitat patches, have a perfect knowledge of the distribution of resources and exhibit similar intake rates (Fretwell 1969). However, related models focusing on the size and the proximity of colonies are important to explain seabird spatial foraging segregation (Bolton et al. 2019). For instance, Wakefield et al.

(2013) provided an example where Northern gannets (*Morus bassanus*), breeding in neighbouring colonies around Britain and Ireland, do not directly compete for food but rather occupy exclusive foraging areas in the colony surroundings to reduce the effects of competition. The model developed by Wakefield et al. (2013), termed the density-dependent hinterland (DDH) model, predicts that spatial segregation due to density-dependent competition will occur if potential competition is high, namely between neighbouring colonies, and between colonies differing in size and located in areas where prey is scarce and patchily distributed. Thus, distance between neighbouring colonies and their size, should determine the appearance of inter-colony competition and consequent spatial segregation (Bolton et al. 2019). More recently, individual-level memory of resource distribution has been proposed as another possible mechanism explaining the emergence of spatial segregation in the foraging ranges of colonial animals (Aarts et al. 2021). In the former study, authors argue that central-place foragers just need to memorise the quality of a prey patch within their foraging range to create spatial segregation between neighbouring colonies.

The majority of studies assessing spatial segregation in colonial seabirds have been conducted between colonies separated by tens or hundreds of kilometres (Wakefield et al. 2013, Dean et al. 2015, Corman et al. 2016, Gulka et al. 2020). Yet, studies testing spatial segregation between colonies located at short distances (as close as 5 km) or between adjacent sub-colonies were restricted to species with smaller foraging ranges, such as shags (Wanless & Harris 1993, Bogdanova et al. 2014, Evans et al. 2016), penguins (Masello et al. 2010, Sánchez et al. 2018, Ito et al. 2020) or gannets (Waggitt et al. 2014), and few were focused on wide-ranging seabirds (Ceia et al. 2015). Ceia et al. (2015) provided an example where Cory's shearwaters (*Calonectris borealis*) nesting as close as 2 km apart, on opposite sides of a densely populated colony in the mid-North Atlantic Ocean, partially segregated foraging areas in the vicinities of the colony. The authors suggested that such partial segregation was likely due to the location and orientation towards the sea of each breeding sub-colony. Nevertheless, they argued that despite spatial segregation, shearwaters from different sub-colonies concentrated their feeding activity in patches of similar oceanographic characteristics and prey.

Here, we tested for spatial segregation between sub-colonies located short distances apart, and investigated how spatial segregation relates to differences in habitat use, trophic ecology and chick growth rate in two populations of closely-related shearwaters. For this experiment we chose: (1) two proximate (separated by 800 m) and comparatively small sub-colonies (ca. 100 *vs* 30 breeding pairs) of Cory's shearwater breeding in a temperate upwelling area (Berlenga Island, Portugal); and (2) two sub-colonies differing in size (ca. 1800 *vs* 200 breeding pairs) and located on opposite sides (separated by 3 km) of Cape Verde shearwater (*Calonectris edwardsii*) nesting in a tropical oceanic area (Raso Islet, Cabo Verde). Previous tracking studies showed that Cory's shearwaters breeding at Berlenga Island are extremely influenced by the major summer upwelling occurring along the western coast of the Iberian Peninsula (Paiva et al. 2010c). The vast majority of the Cory's shearwaters from this neritic population engage in short foraging trips, searching for epipelagic prey in coastal waters near the colony, especially during the chick-rearing period (Paiva et al. 2010b e). During the chick-rearing, long foraging trips to offshore pelagic waters are rare and reported to occur mostly in scenarios of extreme low food conditions (Paiva et al. 2013a, Pereira et al. 2020). During the same period, Cape Verde shearwaters breeding at Raso Islet exploit the areas of comparatively low resource availability within the archipelago of Cabo Verde, at relatively close distance from the breeding colony (Paiva et al. 2015). At longer distances, Cape Verde shearwaters repeatedly target predictable and high-productive prey patches along the West African coast (Cerveira et al. 2020), which is also an area intensively exploited by international industrial fishing fleets (Gremillet et al. 2015).

Facing such conditions and based on the ideal-free distribution theory and DDH model predictions, we do not expect differences in trophic ecology and chick growth rates between shearwaters from sub-colonies located at short distances apart in both study sites. Yet, regarding the spatial distribution we made the following predictions: (1) Cory's shearwaters breeding in small sub-colonies located within a short distance of strong upwelling (i.e. high marine productivity) should overlap in repeatedly used patches close to the colony, with low foraging costs and higher foraging efficiency (Bolton et al. 2019); (2) Cape Verde shearwaters nesting in a large oceanic colony should partially segregate in their foraging grounds at relatively close distance from the colony, likely due to resource depletion (i.e. the "halo" effect) around the colony (Weber et al. 2021) or due to the location and orientation towards the sea of each breeding sub-colony (Ceia et al. 2015); however, (3) they should overlap in distant foraging patches along the West African coast, where prey depletion and the relative difference in foraging costs between sub-colonies would be comparably lower (Bolton et al. 2019).

2.2. Methods

2.2.1. Study areas

Fieldwork was conducted simultaneously on two sub-colonies of Cory' shearwaters at Berlenga Island (39°23' N, 9°36' W) and two sub-colonies of Cape Verde shearwaters at Raso Islet (16°36' N, 24°35' W) over two consecutive breeding seasons (2017-2018), during chick-rearing. In both study sites, we identified the sub-colonies as nest aggregations that were close to one another but separated by topographic features such as valleys or rocky cliffs. In this way, shearwaters from one sub-colony were not able to sight those from the other sub-colony while at their nest.

Berlenga is a small neritic island (ca. 0.7 km^2) located approximately 11 km off the West coast of Portugal and holds a small population of Cory's shearwater (ca. 300 breeding pairs) (Oliveira et al. 2020). Most of the nests are located in two discrete and relatively small sub-colonies separated only by 800 m (Fig. 2.1): Melreu (ML; ca. 100 breeding pairs) and Furado Seco (FS; ca. 30 breeding pairs) (Oliveira et al. 2016). In contrast, Raso (ca. 5.8 km^2) is an oceanic islet located in the Northern group of the Cabo Verde archipelago and approximately 900 km off the West African coast. Raso holds one of the most important populations of Cape Verde shearwater with an estimated population of ca. 6500 breeding pairs (Biosfera I, unpublished data). Contrary to Berlenga Island, the two sub-colonies studied at Raso Islet (Acampamento and Ribeira do Ladrão, hereafter AC and RL, respectively) are located in the extremes of the islet and separated by 3 km (Fig. 2.1). Moreover, they also differ in population size, with the sub-colony of RL having a much higher breeding density (ca. 1800 breeding pairs) than the sub-colony of AC (ca. 200 breeding pairs) (Fig.2.1).

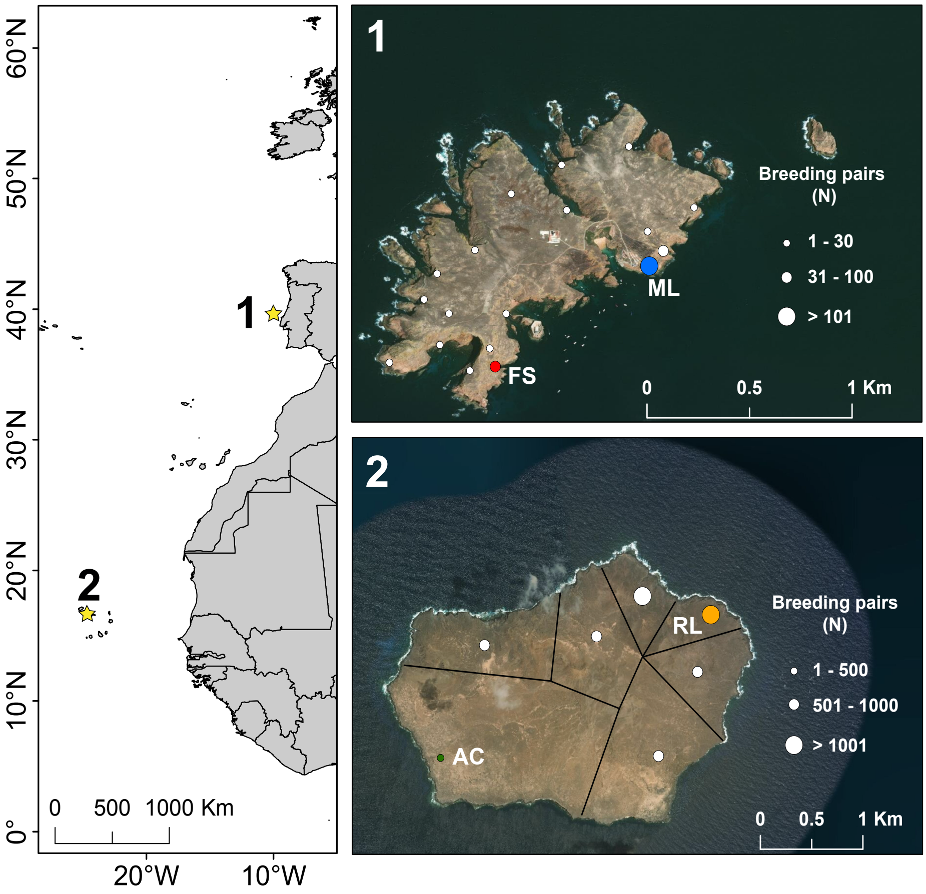

Figure 2.1: *Satellite images showing the location and geography of the breeding colonies of: (1) Cory's shearwaters (Calonectris borealis) at Berlenga Island (yellow star at approximately 11 km off the West coast of Portugal) and (2) Cape Verde shearwaters (Calonectris edwardsii) at Raso Islet (yellow star in the Cape Verde archipelago at approximately 900 km off West Africa). Location and estimated number of breeding pairs for each nesting sites are shown at Berlenga Island (Oliveira et al. 2016) and by sectors at Raso Islet (Biosfera I, unpublished data). Sub-colonies at Berlenga Island (ML: Melreu- blue) vs (FS: Furado Seco- red) and at Raso Islet (AC: Acampamento- green) vs (RL: Ribeira do Ladrão- orange) are marked with circles with different sizes according to the estimated number of breeding pairs (see legend).*

2.2.2. Bird instrumentation and GPS data processing

Over the two breeding seasons, we equipped 62 chick-rearing Cory' shearwaters from two sub-colonies at Berlenga Island (ML and FS) and 84 Cape Verde shearwaters from two sub-colonies at Raso Islet (AC and FS) with Global Positioning System (GPS) loggers (CatLog2; Perthold Engineering). Each device was attached to the tail feathers using TESA® tape, programmed to record positions at 10 min intervals and retrieved after several consecutive foraging trips (Table 2.1). Because Cape Verde shearwaters have comparatively lower body mass (mean ± SD: 431 ± 53.9 g) than Cory's shearwaters (845.3 ± 103.2 g), GPS loggers deployed on Cape Verde shearwaters were equipped with lighter batteries (weight of device = 15 g) when compared to those deployed on Cory's shearwaters (17 g). The weight of GPS loggers represented 2.6% and 2.8% of the body mass of the lightest Cory's shearwater and Cape Verde shearwater, respectively. Details on sample sizes and tracking data are given in Tables 2.1 and S2.1 in the Supplementary Information.

Tracking data were first filtered to remove positions within a 1 km radius of the colony to reduce the influence of rafting behaviour close to the colony (Weimerskirch et al. 2020b). It was also possible to identify individual foraging trips and calculate the trip duration (total time spent on a foraging trip in days), the maximum distance from the colony (distance from the distal location of the trip in relation to the breeding colony) and the departure direction (bearing angle between the breeding colony and the first location at 10 km distance in degrees, see Waggitt et al. 2014). Moreover, tracking datasets were partitioned in short (≤ 1 day, ≤ 100 km for Cory's shearwaters and ≤ 1 day, ≤ 250 km for Cape Verde shearwaters) and long trips (> 1 day, > 100 km for Cory's shearwaters and > 1 day, > 250 km for Cape Verde shearwaters) based on histograms of the frequency of occurrence of trip duration and maximum distance from colony reached on each foraging trip (See Fig. S2.1 in the Supplementary Information).

To characterise the foraging behaviour for each trip, we classified each GPS position as one of four behavioural states using the '*Expectation-Maximisation binary Clustering*' method implemented in the R package '*EMbC'* (Garriga et al. 2016). The four states were as follows: (1) travelling (high velocity, low tortuosity), (2) relocating (high velocity, high tortuosity), (3) intensive foraging (low velocity, high tortuosity) and (4) resting (low velocity, low tortuosity).

Table 2.1: *Colony size (estimated number of breeding pairs), fieldwork sampling and tracking details for Cory's shearwaters (Calonectris borealis) from two sub-colonies at Berlenga Island (FS- Furado Seco vs ML- Melreu) and for Cape Verde shearwaters (Calonectris edwardsii) from two sub-colonies at Raso Islet (AC- Acampamento vs RL- Ribeira do Ladrão), during the chick-rearing period (2017-2018).*

	Berlenga		**Raso**	
	FS	**ML**	**AC**	**RL**
Population size (breeding pairs)	ca. 30	ca. 100	ca. 200	ca. 1800
Experimental design				
Study period	11 Aug - 18 Sep 2017 16 Aug - 23 Sep 2018	10 Aug - 17 Sep 2017 17 Aug - 24 Sep 2018	14 Aug - 27 Sep 2017 09 Aug - 26 Sep 2018	28 Aug - 26 Sep 2017 18 Aug - 06 Sep 2018
N GPS deployed	31	31	47	37
N GPS recovered and with data	27	25	28	31
N blood samples for stable isotope analyses	22	18	28	30
N monitored chicks	27	25	31	15
Tracking details				
Tracking duration (days)	15.6 ± 8.8	15.8 ± 6.8	14.5 ± 6.3	13.0 ± 5.5
N of completed foraging trips	253	268	216	174
N of short trips	207	233	179	141
N of long trips	46	35	37	33

Kernel density estimates were generated for the positions in which tracked shearwaters engaged in "intensive foraging" behaviour using the *'adehabitatHR'* R package (Calenge 2006). We calculated the spatial overlap of 50% core foraging areas (hereafter foraging overlap) between each individual shearwater from one sub-colony with each shearwater from the neighbouring sub-colony in the same year using the Home Range (HR) overlap index (Kernohan et al. 2001). The most appropriate smoothing parameter (*h*) was determined following Lascelles et al. (2016) as the average value of area-restricted search (ARS) behaviour exhibited across short and long foraging trips within each year and sub-colony.

Lastly, we evaluated whether the core foraging areas of shearwaters from each sub-colony were representative of the whole population by bootstrapping 100 times the '*repAssess'* function of the BirdLife International R package *'track2KBA'* (Beal et al. 2020).

2.2.3. Oceanographic covariates

To characterise the oceanographic conditions which are associated with "intensive foraging" behaviour, we extracted (1) Sea depth (0.01° spatial resolution, m); and monthly averages for the chick-rearing period (August - September) of (2) sea surface temperature (SST, 0.08°, °C); (3) sea surface height (SSH, 0.08°, m); (4) zonal sea water velocity (0.08°, m s^{-1}); (5) meridional sea water velocity (0.08°, m s^{-1}); (6) biomass of zooplankton (0.08°, gr m^{2}); and (7) biomass of micronekton in the epipelagic layer (0.08°, g m^{-2}). Sea surface height anomaly (SSHA, 0.08°, cm) was obtained by calculating the difference between the average of SSH values for the chick-rearing period and the average for the same months along 25 years (1993-2018). Eddy kinetic energy (EKE, 0.08°, cm^{-2} s^{-2}) was computed following the equation: $\frac{1}{2}(U^2 + V^2)$, where U is the zonal sea water velocity and V is the meridional sea water velocity. Further details on environmental variables are shown in Table S2.2 and Fig. S2.2 in the Supplementary Information.

Regionally, SSHA and EKE play an important role in the vertical and horizontal transport of nutrients and are responsible to enhance prey aggregation in the open ocean (Stramma et al. 2013). On one hand, SSHA identifies the presence of mesoscale activity, with positive SSHA values denoting anticyclonic (warm-core) eddies and negative SSHA values depicting cyclonic (cold-core) eddies (McGillicuddy et al. 1998). Thus, we can expect comparably better foraging conditions/ higher availability to prey under positive SSHA and the opposite scenario under negative SSHA values. On other hand, EKE provides a measure of the relative intensity of ocean circulation or water mixing (Santora et al. 2017). SEAPODYM is a numerical model that uses physical (e.g. sea surface temperate and currents) and biological variables (e.g. primary productivity) to simulate the spatio-temporal distribution of zooplankton and micronekton (2-20 cm) at global scale (Lehodey et al. 2008, 2010). This model was previously used as a surrogate of the concentration of low and mid-trophic level prey (e.g. mid-water fish, cephalopods, crustaceans) of tuna (Lehodey et al. 2008), sea turtles (Abecassis et al. 2013), seabirds (Miller et al. 2018b) and marine mammals (Lambert et al. 2014, Green et al. 2020, Virgili et al. 2021).

2.2.4. Stable Isotope Analysis (SIA)

Over the two breeding seasons, we collected blood samples from 40 adults of Cory's shearwater and 58 adults of Cape Verde shearwaters (Table 2.1). Blood samples (0.5-1.0 ml) were collected from the tarsal or brachial vein of individual birds after logger retrieval. Within 2-3 hours from sampling, blood samples were separated into plasma and red blood cell (RBC) fractions using a centrifuge and frozen at -20 °C until preparation for SIA. In 2017, it was only possible to perform SIA for whole blood in Cape Verde shearwaters due to logistical issues during fieldwork. However, values of δ^{15}N and δ^{13}C in whole blood were considered to be comparable to those of RBC (Cherel et al. 2005). Whole blood and RBC have a turnover rate of a few weeks, which reflects in average the assimilated diet over the past 3-4 weeks prior to the sampling (and logger retrieval) and thus representative of the tracking period (Table 2.1). Laboratory procedures for SIA are shown in Supplementary Information 1.

2.2.5. Chicks' growth and body condition

Over the two breeding seasons, we collected biometric data from 52 chicks of Cory's shearwater and 46 chicks of Cape Verde shearwaters (Table 2.1). Chicks were weighed (to the nearest 5 g) and wing length (to the nearest 1 mm) was measured every two days during the linear growth period (See Figs. S2.3 and S2.4 in the Supplementary Information). Linear growth rate (LGR; g day^{-1}) of each chick was obtained from the slope of the regression line of chick body mass during the linear growth period, between 10 and 40 days of age for the chicks at Berlenga Island (Ramos et al. 2003), and between 20 and 50 days of age for the chicks at Raso Islet (Ramos et al. 2018). We also used body mass and wing length to estimate chicks' body condition index (BCI) during the linear growth period. Chicks' BCI was determined following the equation in Catry et al. (2013): BCI = $\frac{\text{residual OM}}{\text{PM}}$, where PM is the predicted mass calculated using the linear regression between body mass and wing length, and residual OM is the difference between the observed mass (OM) and predicted mass (PM). A BCI < 0 shows that the bird is lighter than expected by chance and thus in poor body condition, while a BCI > 0 shows that the bird is heavier than expected by chance and thus in better body condition. Chicks' LGR and BCI were not computed for one sub-colony at Raso Islet (Ribeira do Ladrão) in 2018 due to lack of data (See Table S2.1 in the Supplementary Information).

2.2.6. Statistical analysis

Generalised linear mixed models (GLMMs) were built separately for each study site to investigate the effect of sub-colony (ML *vs* FS at Berlenga Island and AC *vs* RL at Raso Islet) and year (2017 *vs* 2018) on: (1) foraging overlap; (2) habitat of foraging areas; (3) trophic ecology; and (4) chicks' growth and body condition (details on models' structure are in Tables S2.3 and S2.4 in the Supplementary Information). The influence of sub-colony and year on foraging overlap and habitat of foraging areas was tested separately for short and long trips in each study site. We next used the '*performance*' R package (Lüdecke et al. 2021) to evaluate model assumptions (i.e. linearity, homogeneity of variances, collinearity, normality of residuals and normality of random effects) and performance (i.e. Akaike's information criterion - AIC). Appropriate statistical distributions were fitted to the data and the best models were selected based on the lowest AIC values. Trip identity nested within individual ID was fitted as a random effect to account for multiple trips per individual. GLMMs were computed using the *'glmmTMB'* R package. We used circular ANOVAs (function '*aov.circular*') from the '*circular'* package (Lund et al. 2017) to test if shearwaters from different sub-colonies departed in different directions. All statistical analyses were conducted within the R environment v. 4.0.3 (R Core Team 2019). All data are presented as mean ± SD (standard deviation). Differences were considered statistically significant at *p*-value ≤ 0.05.

2.3. Results

2.3.1. Sample sizes

Over the two breeding seasons, we retrieved data from a total of 911 complete foraging trips made by 52 adult Cory's shearwaters (521 trips) and 59 adult Cape Verde shearwaters (390 trips) from the two sub-colonies in each study site (Fig. 2.2). From those, both Cory's shearwaters and Cape Verde shearwaters engaged mostly in short foraging trips (84.5% and 82.1%, respectively) and to a lesser extent in long foraging trips (15.5% and 17.9%, respectively). Tracking duration was similar between study sites ($\chi^2_{1, 109} = 2.42$, *p*-value = 0.13) and between sub-colonies (Berlenga Island: $\chi^2_{1, 50} = 0.01$, *p*-value = 0.95; Raso Islet: $\chi^2_{1, 57} = 1.14$, *p*-value = 0.29).

The tracking datasets used in this study represented more than 95% of the core foraging areas used by Cory's shearwaters at Berlenga Island (ML= 99%; FS= 97.2%) and more than 80% of the core foraging areas used by Cape Verde shearwaters at Raso Islet (AC= 93.6%; RL= 83.3%) (See Fig. S2.5 in the Supplementary Information). Therefore, we are confident that the number of tracked shearwaters in each sub-colony was sufficient to represent the core foraging areas for the whole population.

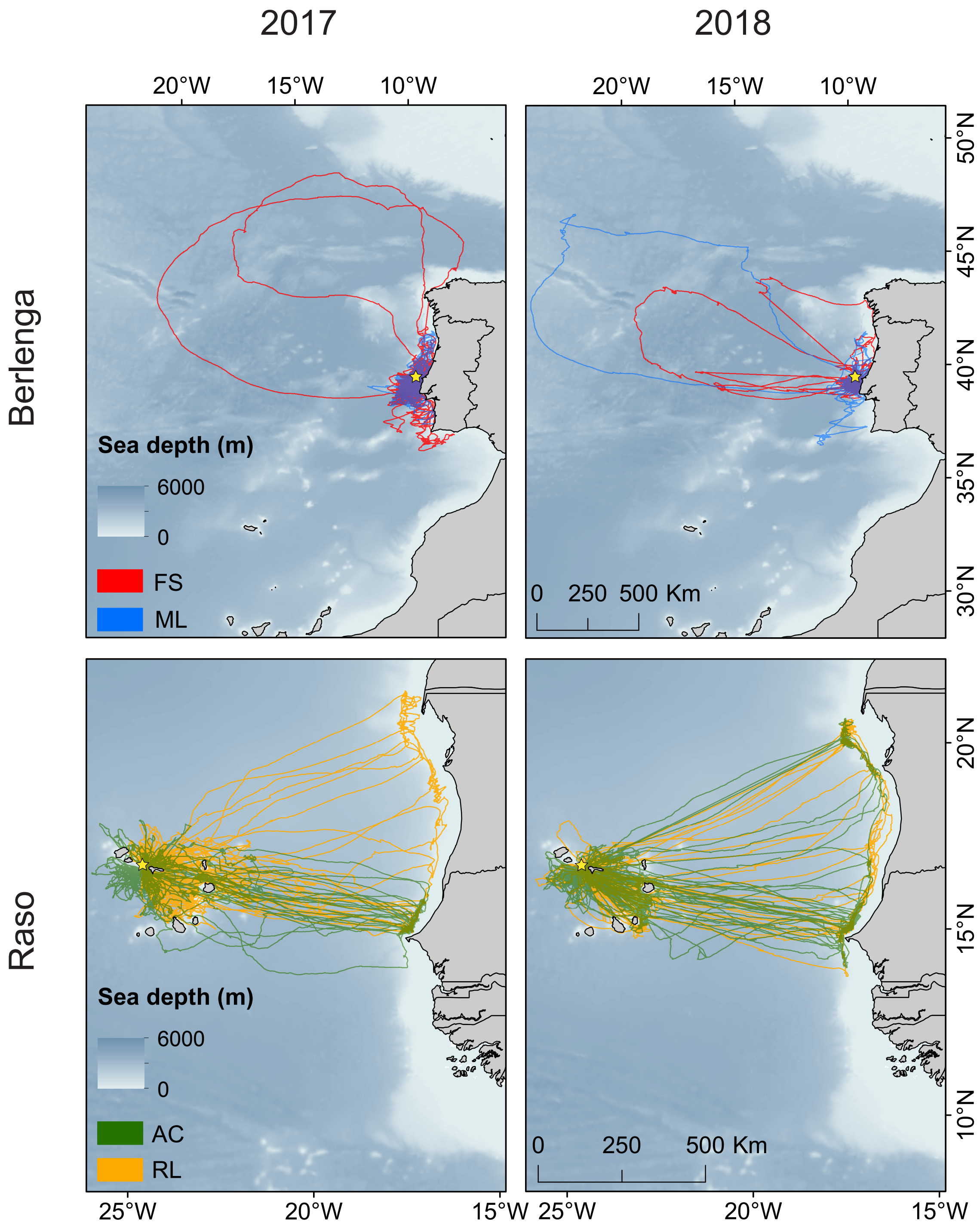

Figure 2.2: *Overall foraging trips made by Cory's shearwaters from two sub-colonies at Berlenga Island (ML- Melreu vs FS- Furado Seco) and Cape Verde shearwater from two sub-colonies at Raso Islet (AC- Acampamento vs RL- Ribeira do Ladrão) during the chick-rearing period (2017-2018), overlaid on the sea depth of the region. The location of each breeding colony is marked with a yellow star.*

2.3.2. Foraging overlap and habitat use

Foraging overlap and habitat of foraging areas showed high inter-annual variation in both study sites during short and long trips (See Tables S2.5 and S2.6 in the Supplementary Information), but consistent patterns emerged between sub-colonies. We found that Cory's shearwaters from the two small sub-colonies at Berlenga Island departed in similar directions (ML: 206.6 ± 62.1° *vs* FS: 206.7 ± 73.0°, angular variance = 0.80, $\chi^2_{1,\,512} = 0.05$, *p*-value = 0.83; See Fig. S2.6 in the Supplementary Information). Moreover, foraging overlap between Cory's shearwaters from neighbouring sub-colonies was high during both short (52.7 ± 26.2%) and long (48.7 ± 36.5%) trips ($\chi^2_{1,\,957} = 2.42$, *p*-value = 0.12; Figs. 3 and 4). In terms of foraging habitats, we found that shearwaters from FS foraged in areas of higher EKE (i.e. areas of intense water mixing) during short trips (FS: 1.4 ± 1.1 m s^{-1} *vs* ML: 1.1 ± 1.7 m s^{-1}; $\chi^2_{1,\,418} = 5.36$, *p*-value = 0.02; Fig. 2.5) and in areas with relatively higher biomass of micronekton in the epipelagic layer during long trips (FS: 2.4 ± 0.6 g m^{-2} *vs* ML: 2.5 ± 0.6 g m^{-2}; $\chi^2_{1,\,418} = 4.76$, *p*-value = 0.05; Fig. 2.5) when compared to shearwaters from ML.

Cape Verde shearwaters from the two sub-colonies differing in size and located in opposite sides at Raso Islet departed in different bearing angles (AC: 142.6 ± 67.0° *vs* RL: 104.1 ± 49.4°, angular variance = 0.86, $\chi^2_{1,\,384} = 36.19$, *p*-value < 0.001), but headed in similar directions (to Southwest; See Fig. S2.6 in the Supplementary Information). Foraging overlap among Cape Verde shearwaters from both sub-colonies during long trips (55.4 ± 33.4%) was on average 2 times higher than during short (27.7 ± 26.5%) trips ($\chi^2_{1,\,1634} = 23.46$, *p*-value < 0.001; Fig. 2.4). The core foraging areas where Cape Verde shearwaters from both sub-colonies overlapped during long trips were located off the West coast of Africa, especially between Cap Blanc (Mauritania) and Cap-Vert (Dakar, Senegal) (Fig. 2.3). In terms of foraging habitats, we found that shearwaters from RL foraged in shallower water topographies during short trips (AC: 2472.0 ± 1131.3 m *vs* RL: 2215.7 ± 848.7 m; $\chi^2_{1,\,318} = 8.14$, *p*-value = 0.001; Fig. 2.5) and in relatively colder waters during long trips (AC: 27.6 ± 1.3 °C *vs* RL: 27.2 ± 0.6 °C; $\chi^2_{1,\,318} = 4.45$, *p*-value = 0.04; Fig. 2.5) when compared to shearwaters from AC.

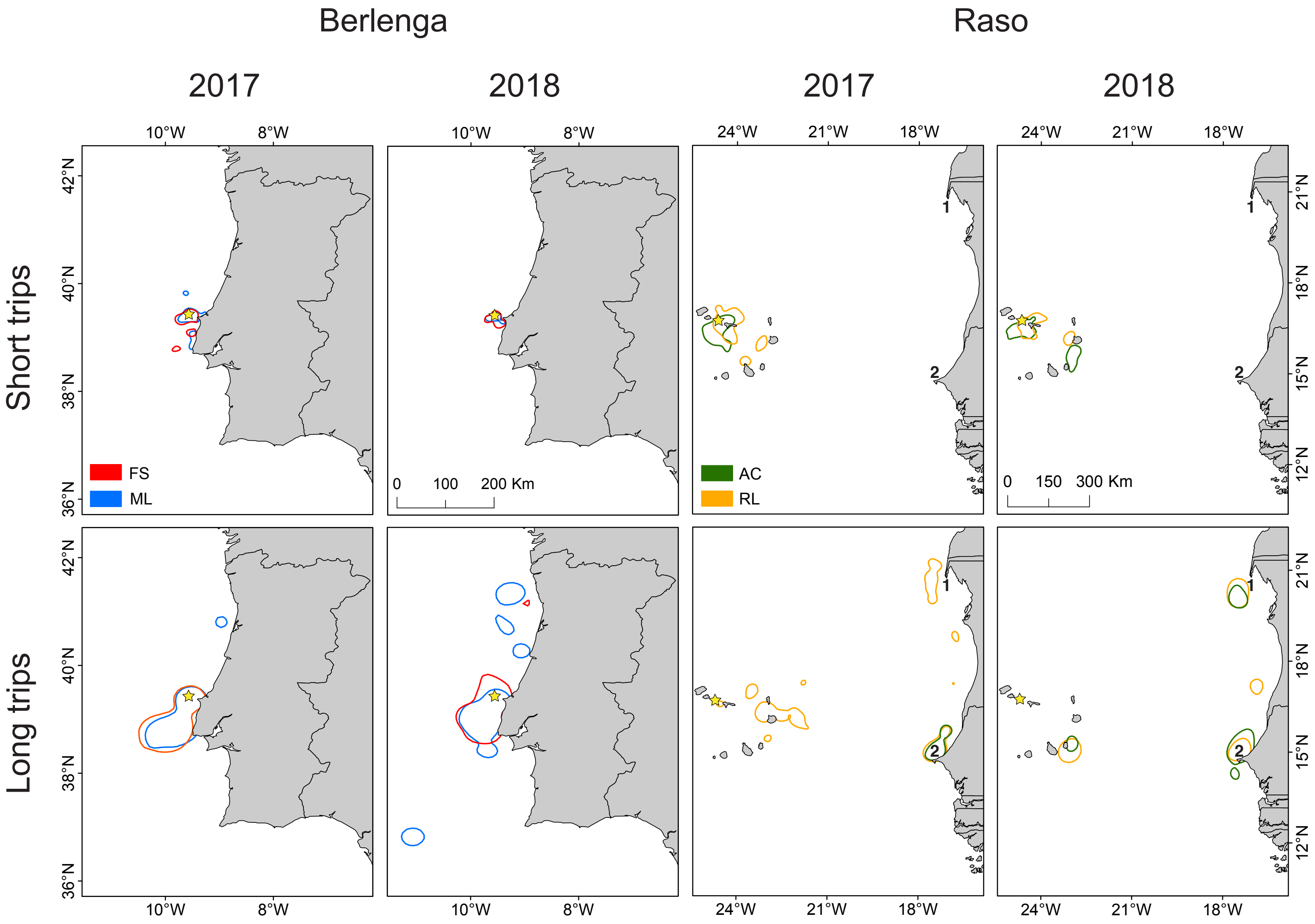

Figure 2.3: *50% core foraging areas of Cory's shearwaters from two sub-colonies at Berlenga Island (ML- Melreu vs FS- Furado Seco) and Cape Verde shearwaters from two sub-colonies at Raso Islet (AC- Acampamento vs RL- Ribeira do Ladrão) during short and long trips, over two consecutive breeding seasons (2017-2018). (1) Cap Blanc (Mauritania) and (2) Cap-Vert (Dakar, Senegal).*

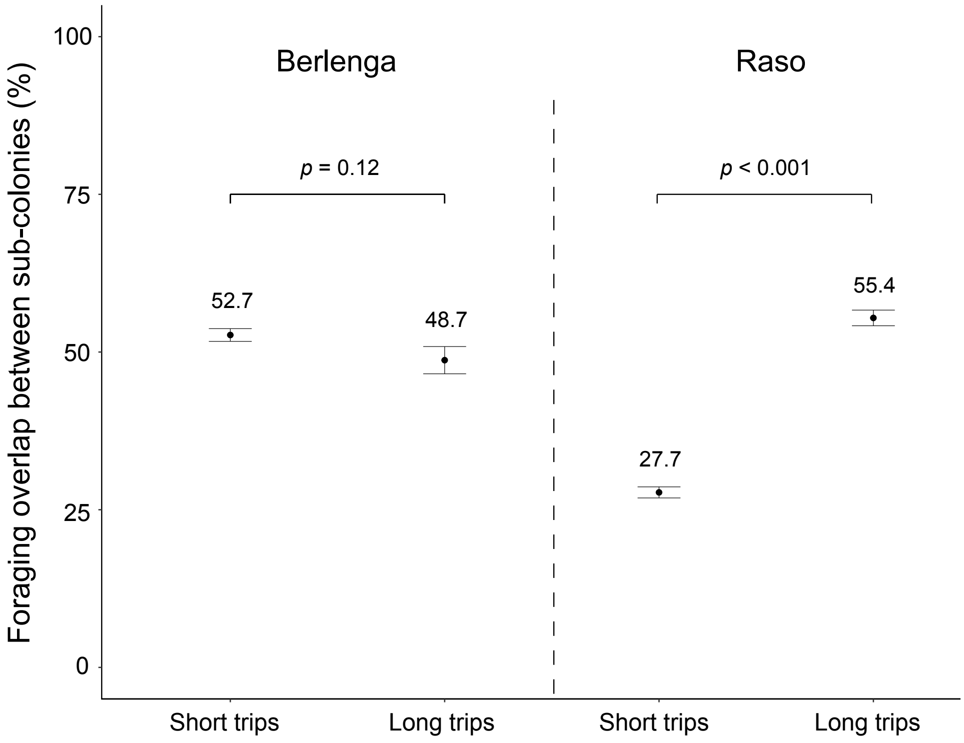

Figure 2.4: *Mean percentage of foraging overlap (50% of core foraging areas) and standard error (SE) between shearwaters from different sub-colonies at Berlenga Island and Raso Islet during short and long trips.*

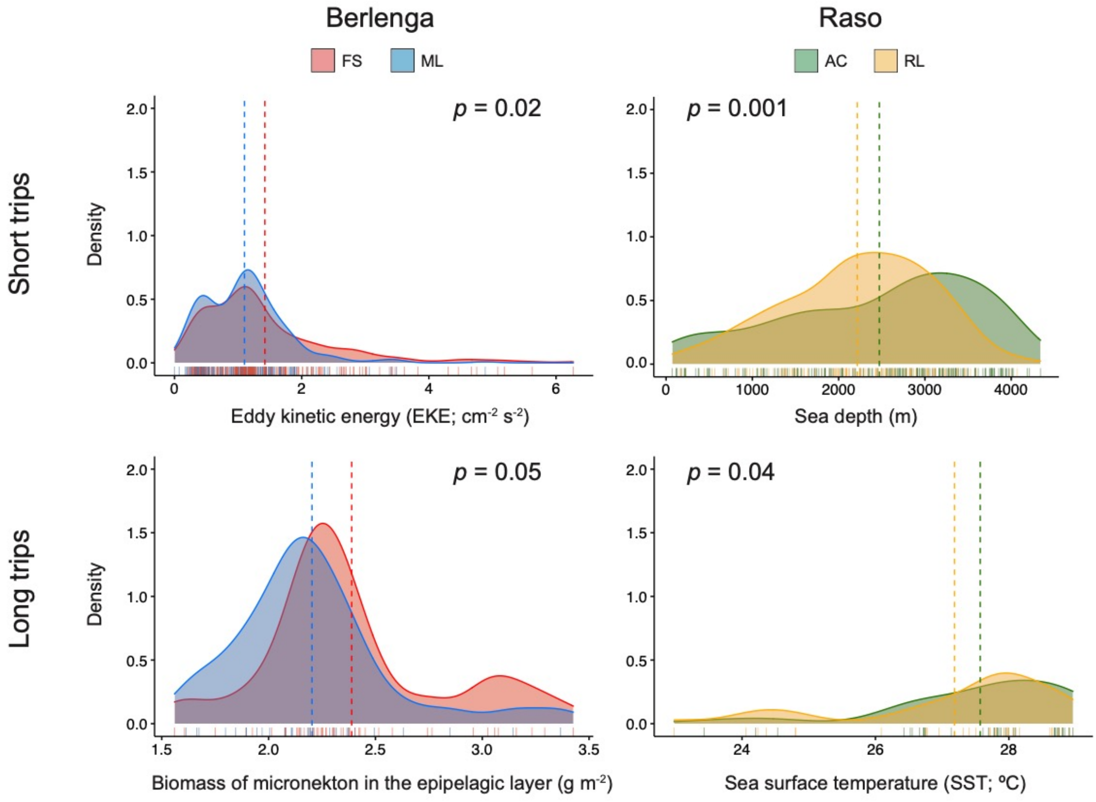

Figure 2.5: *Density plots of the foraging habitats used by Cory's shearwaters from different sub-colonies at Berlenga Island (ML- Melreu vs FS- Furado Seco) and by Cape Verde shearwaters at Raso Islet (AC- Acampamento vs RL- Ribeira do Ladrão) during short and long trips. Dashed lines indicate the average value of environmental variables for each sub-colony.*

2.3.3. Trophic ecology

Mean δ^{13}C and δ^{15}N whole blood/RBC values by sub-colony and year are shown in Table S2.7 of Supplementary Information for each study site. Despite the high inter-annual variation in the mean δ^{13}C and δ^{15}N whole blood/RBC values in both study sites (Table S2.7), no significant differences were found among shearwaters from different sub-colonies both at Berlenga Island (δ^{13}C: $\chi^2_{1,38} = 0.02$, *p*-value= 0.85; δ^{15}N: $\chi^2_{1,38} = 0.04$, *p*-value= 0.88) and at Raso Islet (δ^{13}C: $\chi^2_{1,56} = 1.88$, *p*-value= 0.17; δ^{15}N: $\chi^2_{1,56} = 0.70$, *p*-value= 0.40).

2.3.4. Chicks' growth and body condition

Mean values of chicks' LGR and BCI by sub-colony and year are shown in Table S2.7 of Supplementary Information for each study site. Despite the high inter-annual variation in the mean chicks' LGR and BCI (Table S2.7), no significant differences were found among chicks from different sub-colonies at Berlenga Island (LGR: $\chi^2_{1,50} = 2.60$, *p*-value= 0.11; BCI: $\chi^2_{1,50} = 1.50$, *p*-value= 0.22) and at Raso Islet (LGR: $\chi^2_{1,24} = 0.94$, *p*-value= 0.33; BCI: $\chi^2_{1,24} = 2.27$, *p*-value= 0.13).

2.4. Discussion

In this study, we tested for differences in at-sea spatial distribution, habitat use, trophic ecology and chick growth among sub-colonies of a small (ca. 300 breeding pairs) neritic colony of Cory's shearwater and a large (ca. 6500 breeding pairs) oceanic colony of Cape Verde shearwater over two consecutive breeding seasons (2017-2018), during the chick-rearing period. Shearwaters from neighbouring sub-colonies did not differ in trophic ecology, chick growth rates and body condition in both study sites, but differ in the foraging overlap. While Cory's shearwaters from two small sub-colonies (ca. 100 *vs* 30 breeding pairs) broadly overlapped in repeatedly used patches close to the colony, Cape Verde shearwaters from two sub-colonies differing in size (ca. 1800 *vs* 200 breeding pairs) partially segregated foraging grounds at relatively close distance from the colony. However, at longer distances, Cape Verde shearwaters from the different sub-colonies broadly overlapped in repeatedly visited patches along the West African coast. Below we discuss the potential mechanisms behind our results.

2.4.1. Prediction 1: Cory' shearwaters nesting in a small neritic colony will overlap in repeatedly used patches close to the colony

As expected, we found that Cory's shearwaters nesting in two small sub-colonies (separated only by 800 m) at Berlenga Island broadly overlapped in repeatedly used patches close to the colony. Although we found marginal differences in the habitat used by Cory's shearwaters from the different sub-colonies, birds exhibited similar isotopic signatures, chick growth rates and body condition. Similar patterns were previously reported by Waggitt et al. (2014) that found no differences in foraging behaviour and trophic ecology among Northern gannets from 7 sub-colonies separated by only 200 m, during chick-rearing. Findings of shared foraging areas between individuals from small colonies were also observed for other seabirds, particularly in species with smaller foraging ranges, such as penguins (Ainley et al. 2004) and shags (Evans et al. 2016). For instance, Evans et al. (2016) showed that European shags (*Gulosus aristotelis*) from two small colonies located only 4 km apart, extensively overlapped foraging ranges in predictable prey patches near the colony, suggesting an absence of inter-colony competition. This appears to be also the case in our study, as the travel costs are similar between neighbouring sub-colonies, and foraging efficiency is higher close to the colony, where spatial overlap naturally occurs (Bolton et al. 2019).

2.4.2. Prediction 2: Cape Verde shearwaters nesting in a large oceanic colony will partially segregate foraging locations close to the colony

As expected, we found that Cape Verde shearwaters nesting in two sub-colonies differing greatly in size at Raso Islet partially segregated foraging grounds at relatively close distance from the colony. The areas surrounding large colonies of tropical seabird populations are likely to become resource-depleted (Ashmole 1963) and increasing colony size is expected to result in faster resource depletion, as recently demonstrated by Weber et al. (2021). Despite spatial segregation close to the colony, Cape Verde shearwaters from both sub-colonies performed mostly short trips within the Cabo Verde archipelago. Under the optimal foraging theory this means that the number of foragers close to the colony should not be high enough to create a prey-depleted halo around the colony (Ashmole 1963, Bolton et al. 2019, Weber et al. 2021). This could suggest that foraging grounds around the colony are still attractive to these birds, because foraging costs are lower, and therefore it is unlikely that density-dependent competition would eventually trigger foraging segregation behaviours between Cape Verde shearwaters from different sub-colonies at Raso Islet. The absence for within-colony competition could also be supported by the similar isotopic signatures, chick growth rates and body condition between Cape Verde shearwaters from both sub-colonies. Evidence for spatial segregation around the colony between sub-colonies located in opposite sides of a densely populated colony were also reported by Ceia et al. (2015). The authors showed that Cory's shearwaters from two neighbouring sub-colonies, in the mid-North Atlantic Ocean, partially segregated foraging areas at relatively close distance from the colony but concentrated their feeding activity in patches of similar habitat and prey during the chick-rearing. However, the authors suggested that such partial segregation could be mediated by directional bias, whereby shearwaters departed on a bearing consistent with the location and orientation of each breeding sub-colony. This was not the case in our study, as Cape Verde shearwaters from neighbouring sub-colonies at Raso Islet headed in similar directions and make it unlikely that spatial segregation can be directional biased.

Individual-level memory of resource distribution has recently been proposed as an alternative mechanism to explain the emergence of spatial segregation in the foraging ranges of colonial animals (Aarts et al. 2021). The authors argued that central-place foragers just need to memorise the quality of a prey patch within their foraging range to create spatial segregation between neighbouring colonies. Our results suggest that density-dependent competition and directionality of the sub-colonies are not likely the mechanisms underpinning spatial segregation between neighbouring sub-colonies of Cape Verde shearwaters. Besides spatial segregation, we show that Cape Verde shearwaters also differed in the habitat of foraging areas at relatively close distance from the colony. Shearwaters from the larger sub-colony (RL) foraged more in shallower water topographies, possibly reflecting the seamounts in the area, than those from the smaller sub-colony (AC). Our results seems to support the theory proposed in Aarts et al. (2021), where memory-based foraging movements can lead to spatial segregation between neighbouring central-place foragers in the areas close to the colony.

2.4.3. Prediction 3: Cape Verde shearwaters will overlap in repeatedly visited patches along the West African coast

Spatial segregation around seabird colonies has been reported in a variety of species (Bolton et al. 2019) however, very few studies demonstrated aggregation of central-place foragers at more distant foraging grounds. In this study, we suggest that memory-based foraging movements can lead to the emergence of spatial segregation in the areas close to the colony. However, as expected, foraging grounds between different sub-colonies of Cape Verde shearwaters overlapped at greater distances along the West African coast, where depletion is less and instantaneous intake rate is expected to be higher (Bolton et al. 2019). Our results of shared foraging areas between sub-colonies at distant foraging patches are supported by previous research. For instance, Ramos et al. (2013) found that Cory's shearwaters from different colonies in the subtropical North Atlantic Ocean exhibited substantial spatial segregation in their oceanic foraging grounds but consistently overlapped in high-productivity areas along the Canary Current. Aggregation of birds from different colonies at distant foraging patches are also documented to occur in enhanced marine productivity near frontal systems (Dean et al. 2013, 2015) and areas of intense mesoscale activity (Paredes et al. 2014). These studies suggest that areas of local enhanced marine productivity might also be attractive for birds from other more distant colonies, hence creating overlap between central-place foragers from different colonies.

2.4.4. Conclusion

Our findings highlight the importance of understanding within-colony differences in seabirds' at-sea foraging distributions and their consequences for the colonial living. We suggest that within-colony differences in at-sea foraging behaviour may be frequent when seabird colonies are spatially structured in breeding sites differing in size or location, leading to site-specific. Moreover, we suggest that individual-level memory of resource availability can be sufficient to cause spatial segregation in central-place foragers. High productivity areas might also be attractive for birds from other more distant colonies, hence creating overlap between central-place foragers from different colonies. We argue that assessing more than one breeding site is necessary to capture the foraging behaviour variability within a colony, providing meaningful knowledge on marine spatial usage to obtain accurate population assessments and to incorporate into conservation strategies.

2.5. Supplementary Information

Supplementary Information 1: Laboratory procedures for Stable Isotope Analysis (SIA)

Prior to stable isotope analysis, samples were defrosted, homogenised and dried overnight at 60 ºC. Approximately 0.3 mg of each sample was weighted in a tin capsule using an ultra-microbalance. Values of $\delta^{15}N$ and $\delta^{13}C$ were determined using a Continuous Flow Isotope Ratio Mass Spectrometer (Delta V™ Advantage - Thermo Scientific®) with an organic elemental analyser (Flash™ EA 1112 - Thermo Scientific®). Results are expressed in delta (δ) notation as parts per thousand (‰) and calculated using the equation $\delta X = (R_{sample} – R_{standard} – 1) x 1000$, where X is N or C and R the ratio between $^{15}N/^{14}N$ and $^{13}C/^{12}C$. Atmospheric N_2 and Vienna-Pee Dee Belemnite Limestone were use as standard for N and C, respectively. Acetanilide (Thermo Scientific®) was used as reference material to measure machine intern errors (<0.3‰ for $\delta^{15}N$ and <0.1‰ for $\delta^{13}C$).

Table S2.1: *Fieldwork sampling and tracking details conducted in two neighbouring sub-colonies of Cory's shearwaters (Calonectris borealis) at Berlenga Island (ML: Melreu vs FS: Furado Seco) and for two neighbouring sub-colonies of Cape Verde shearwaters (Calonectris edwardii) at Raso Islet (AC: Acampamento vs RL: Ribeira do Ladrão) over the 2017-2018 breeding seasons, during chick-rearing. It was only possible to obtain chick biometrics from both sub-colonies at Raso Islet in 2017, but just for one sub-colony (AC) in 2018.*

	Berlenga				**Raso**			
	2017		**2018**		**2017**		**2018**	
	FS	**ML**	**FS**	**ML**	**AC**	**RL**	**AC**	**RL**
Experimental details								
Study period	11 Aug - 18 Sep	10 Aug - 17 Sep	16 Aug - 23 Sep	17 Aug - 24 Sep	14 Aug - 27 Sep	28 Aug - 26 Sep	09 Aug - 26 Sep	18 Aug - 06 Sep
Duration of tracking period (days)	30	29	13	15	23	22	27	22
N GPS deployed	15	15	16	16	20	20	27	17
N GPS recovered and with data	13	13	14	12	11	16	17	15
N blood samples for stable isotope analyses	8	8	14	10	11	16	17	14
N monitored chicks	13	13	14	12	11	15	20	-
Tracking details								
N total foraging trips	172	178	81	90	85	118	131	56
N of short trips	137	150	70	83	70	99	109	42
N long trips	35	28	11	7	15	19	22	14

Table S2.2: *Details of the environmental variables used to model the foraging habitats of chick-rearing Cory's shearwaters and Cape Verde shearwaters. With the exception of Sea depth that was downloaded from the ETOPO1 Global Relief Model (https://www.ngdc.noaa.gov/mgg/global/global.html), all the remaining environmental variables were downloaded from the Copernicus website (http://marine.copernicus.eu/services-portfolio/access-to-products/).*

Variable	Unit	Spatial resolution	Temporal resolution	Source
Sea depth	m	0.01°	-	ETOPO1 Global Relief Model
Biomass of zooplankton	$g\ m^{-2}$	0.08°	Month	GLOBAL_MULTIYEAR_BGC_001_033
Biomass of micronekton in the epipelagic layer	$g\ m^{-2}$	0.08°	Month	GLOBAL_MULTIYEAR_BGC_001_033
Eddy kinetic energy (EKE)	$cm^{-2}s^{-2}$	0.08°	Month	$EKE = 1/2 * (U^2 + V^2)$
Meridional sea water velocity (V)	$m\ s^{-1}$	0.08°	Month	GLOBAL_ANALYSIS_FORECAST_PHY_001_024
Sea surface height (SSH)	m	0.08°	Month	GLOBAL_ANALYSIS_FORECAST_PHY_001_024
Sea surface height anomaly (SSHA)	cm	0.08°	Month	$SSHA = SSH_{(chick\text{-}rearing)} - SSH_{(1993\text{-}2018)}$
Sea surface temperature (SST)	°C	0.08°	Month	GLOBAL_ANALYSIS_FORECAST_PHY_001_024
Zonal sea water velocity (U)	$m\ s^{-1}$	0.08°	Month	GLOBAL_ANALYSIS_FORECAST_PHY_001_024

Table S2.3: *Sample size, model structure and performance (Akaike information criterion - AIC) of generalised linear mixed models (GLMMs) used to test the effect of trip type (short vs long trips), sub-colony (ML: Melreu vs FS: Furado Seco) and year (2017 vs 2018) on (1) spatial overlap (50% core foraging areas) and habitat of foraging areas, (2) trophic ecology and (3) chick growth and body condition of Cory's shearwaters* breeding at Berlenga Island.

	Trip type	N observations	Fixed effect	Random Effect	Family	Transformation	AIC
Spatial overlap and habitat of foraging areas							
Foraging overlap between sub-colonies (%)		960	Trip type	Ring	Beta_family (link = "logit")	Arcsine (Sqrt)-transformed	732.1
Sea depth (m)	Short trips	440	Sub-colony + Year	Ring/Trip	Gaussian (link = "identity")	Log-transformed	1272.9
	Long trips	81	Sub-colony + Year	Ring/Trip	Gaussian (link = "identity")	Log-transformed	263.2
Biomass of zooplankton (g m^{-2})	Short trips	320	Sub-colony + Year	Ring/Trip	Gaussian (link = "identity")		739.2
	Long trips	70	Sub-colony + Year	Ring/Trip	Gaussian (link = "identity")		42.9
Biomass of micronekton in the epipelagic layer (g m^{-2})	Short trips	440	Sub-colony + Year	Ring/Trip	Gaussian (link = "identity")		63.1
	Long trips	81	Sub-colony + Year	Ring/Trip	Gaussian (link = "identity")	Log-transformed	102.0
Eddy kinetic energy (EKE; cm^{-2}s^{-2})	Short trips	440	Sub-colony + Year	Ring/Trip	Gaussian (link = "identity")	Log-transformed	73.8
	Long trips	81	Sub-colony + Year	Ring/Trip	Gaussian (link = "identity")	Log-transformed	62.0
Sea surface height anomaly (SSHA; cm)	Short trips	440	Sub-colony + Year	Ring/Trip	Gaussian (link = "identity")		509.6
	Long trips	81	Sub-colony + Year	Ring/Trip	Gaussian (link = "identity")		219.3
Sea surface temperature (SST; °C)	Short trips	440	Sub-colony + Year	Ring/Trip	Gaussian (link = "identity")		251.1
	Long trips	81	Sub-colony + Year	Ring/Trip	Gaussian (link = "identity")		692.3
Trophic ecology							
Whole blood/ RBC δ^{13}C (‰)		40	Sub-colony + Year	Ring	Gaussian (link = "identity")		44.6
Whole blood/ RBC δ^{15}N (‰)		40	Sub-colony + Year	Ring	Gaussian (link = "identity")		40.5
Chick growth and body condition							
Linear chick growth rate (LGR; g day^{-1})		52	Sub-colony + Year	Ring	Gaussian (link = "identity")	Log-transformed	11.2
Chicks' body condition index (BCI)		52	Sub-colony + Year	Ring	Gaussian (link = "identity")	Log-transformed	60.9

Table S2.4: *Sample size, model structure and performance (Akaike information criterion - AIC) of generalised linear mixed models (GLMMs) used to test the effect of trip type (short vs long trips), sub-colony (AC: Acampamento vs RL: Ribeira do Ladrão) and year (2017 vs 2018) on (1) spatial overlap (50% core foraging areas) and habitat of foraging areas, (2) trophic ecology and (3) chick growth and body condition of Cape Verde shearwaters breeding at Raso Islet.*

	Trip type	N observations	Fixed effect	Random Effect	Family	Transformation	AIC
Spatial overlap and habitat of foraging areas							
Foraging overlap between sub-colonies (%)		1636	Trip type	Ring	Beta_family (link = "logit")	Arcsine (Sqrt)-transformed	719.4
Sea depth (m)	Short trips	320	Sub-colony + Year	Ring/Trip	Gaussian (link = "identity")		143.3
	Long trips	70	Sub-colony + Year	Ring/Trip	Gaussian (link = "identity")	Log-transformed	126.4
Biomass of zooplankton (g m^{-2})	Short trips	320	Sub-colony + Year	Ring/Trip	Gaussian (link = "identity")	Log-transformed	367.3
	Long trips	70	Sub-colony + Year	Ring/Trip	Gaussian (link = "identity")	Log-transformed	18.8
Biomass of micronekton in the epipelagic layer (g m^{-2})	Short trips	320	Sub-colony + Year	Ring/Trip	Gaussian (link = "identity")	Log-transformed	143.3
	Long trips	70	Sub-colony + Year	Ring/Trip	Gaussian (link = "identity")	Log-transformed	7.1
Eddy kinetic energy (EKE; $cm^{-2}s^{-2}$)	Short trips	320	Sub-colony + Year	Ring/Trip	Gaussian (link = "identity")	Log-transformed	136.9
	Long trips	70	Sub-colony + Year	Ring/Trip	Gaussian (link = "identity")	Log-transformed	217.3
Sea surface height anomaly (SSHA; cm)	Short trips	320	Sub-colony + Year	Ring/Trip	Gaussian (link = "identity")		883.3
	Long trips	70	Sub-colony + Year	Ring/Trip	Gaussian (link = "identity")	Log-transformed	372.9
Sea surface temperature (SST; °C)	Short trips	320	Sub-colony + Year	Ring/Trip	Gaussian (link = "identity")		125.3
	Long trips	70	Sub-colony + Year	Ring/Trip	Gaussian (link = "identity")	Sqrt-transformed	94.0
Trophic ecology							
Whole blood/ RBC $\delta^{13}C$ (‰)		58	Sub-colony + Year	Ring	Gaussian (link = "identity")	Log-transformed	13.4
Whole blood/ RBC $\delta^{15}N$ (‰)		58	Sub-colony + Year	Ring	Gaussian (link = "identity")		108.4
Chick growth and body condition							
Linear chick growth rate (LGR; g day^{-1})		26	Sub-colony	Ring	Gaussian (link = "identity")	Log-transformed	11.5
Chicks' body condition index (BCI)		26	Sub-colony	Ring	Gaussian (link = "identity")	Sqrt-transformed	53.5

Table S2.5: *Foraging overlap (50% core foraging areas) and habitats visited by foraging shearwaters from neighbouring sub-colonies at Berlenga Island (FS- Furado Seco vs ML- Melreu) and Raso Islet (AC- Acampamento vs RL- Ribeira do Ladrão) over the 2017-2018 breeding seasons, during chick-rearing. Summary statistics were obtained for short and long trips based on histograms of the frequency of trip duration (days) and maximum distance from colony reached on each foraging trip (km) (see Fig. S2.1). All values are mean ± standard deviation (SD).*

	Berlenga				**Raso**			
	Short trips		**Long trips**		**Short trips**		**Long trips**	
	(≤ 1 day and ≤ 150 km)		**(> 1 day and > 150 km)**		**(≤ 1 day and ≤ 250 km**		**(> 1 day and > 250 km)**	
	FS	**ML**	**FS**	**ML**	**AC**	**RL**	**AC**	**RL**
Spatial overlap and foraging habitats								
Foraging overlap between sub-colonies (%)	52.7 ± 26.2		48.7 ± 36.5		27.7 ± 26.5		55.4 ± 33.4	
Sea depth (m)	255 ± 330.7	237.7 ± 401.5	1216.2 ± 1034.3	1126.1 ± 1231.4	2472.0 ± 1131.3	2215.7 ± 848.7	1344.7 ± 840.8	1439.2 ± 840.1
Biomass of zooplankton (g m^{-2})	3.7 ± 0.5	3.5 ± 0.6	2.5 ± 0.7	2.7 ± 0.9	0.7 ± 0.2	0.6 ± 0.2	1.0 ± 0.6	1.2 ± 0.8
Biomass of micronekton in the epipelagic layer (g m^{-2})	2.4 ± 0.6	2.5 ± 0.6	2.4 ± 0.4	2.2 ± 0.4	3.0 ± 0.9	2.7 ± 0.8	4.6 ± 1.0	4.9 ± 1.0
Eddy kinetic energy (EKE; $cm^{-2}s^{-2}$)	1.4 ± 1.1	1.1 ± 0.7	1.7 ± 1.5	2.3 ± 1.6	2.9 ± 2.8	1.7 ± 2.9	1.9 ± 2.1	1.8 ± 2.2
Sea surface height anomaly (SSHA; cm)	0.8 ± 1.7	0.7 ± 1.8	0.9 ± 1.7	0.9 ± 1.7	-2.3 ± 1.0	-2.4 ± 1.1	-1.0 ± 1.7	-1.2 ± 1.9
Sea surface temperature (SST; °C)	17.7 ± 0.6	17.6 ± 0.6	18.3 ± 1.1	18.0 ± 1.2	27.0 ± 0.7	27.4 ± 0.7	27.6 ± 1.3	27.2 ± 1.6

Table S2.6: *Results of Generalised linear mixed models (GLMMs) testing the effect of sub-colony at Berlenga Island (ML- Melreu vs FS- Furado Seco) and at Raso Islet (AC- Acampamento vs RL- Ribeira do Ladrão) on the habitats visited by chick-rearing shearwaters during short and long trips. Each model included trip identity nested within the individual as a random effect. GLMMs were also used to test the effect of trip type (short vs long trips) on the foraging overlap (50% core foraging areas) between shearwaters from different sub-colonies at Berlenga Island and Raso Islet. Differences were considered to be statistically significant at p-value ≤ 0.05 (**in bold**).*

	Berlenga				**Raso**			
	Short trips (≤ 1 day and ≤ 100 km)		**Long trips (≤ 1 day and ≤ 100 km)**		**Short trips (≤ 1 day and ≤ 250 km)**		**Long trips (> 1 day and > 250 km)**	
	GLMM	***p*-value**	**GLMM**	***p*-value**	**GLMM**	***p*-value**	**GLMM**	***p*-value**
Spatial overlap and habitat of foraging areas								
Foraging overlap between sub-colonies (%)	$\chi^2_{1, 957}$= 2.42; *p*-value = 0.12				$\chi^2_{1, 1634}$= 23.46; *p*-value **< 0.001**			
Sea depth (m)	$\chi^2_{1, 418}$= 0.89	0.32	$\chi^2_{1, 79}$= 1.69	0.19	$\chi^2_{1, 318}$= 8.14	**0.001**	$\chi^2_{1, 68}$= 0.20	0.66
Biomass of zooplankton (g m^{-2})	$\chi^2_{1, 418}$= 1.26	0.26	$\chi^2_{1, 79}$= 0.68	0.41	$\chi^2_{1, 318}$= 2.49	0.12	$\chi^2_{1, 68}$= 3.81	0.06
Biomass of micronekton in the epipelagic layer (g m^{-2})	$\chi^2_{1, 418}$= 1.76	0.18	$\chi^2_{1, 79}$= 4.76	**0.05**	$\chi^2_{1, 318}$= 0.04	0.85	$\chi^2_{1, 68}$= 0.93	0.34
Eddy kinetic energy (EKE; cm^{-2}s^{-2})	$\chi^2_{1, 418}$= 5.36	**0.02**	$\chi^2_{1, 79}$= 2.01	0.15	$\chi^2_{1, 318}$= 2.58	0.11	$\chi^2_{1, 68}$= 2.39	0.12
Sea surface height anomaly (SSHA; cm)	$\chi^2_{1, 418}$= 0.01	0.96	$\chi^2_{1, 79}$= 0.58	0.45	$\chi^2_{1, 318}$= 1.13	0.29	$\chi^2_{1, 68}$= 1.58	0.21
Sea surface temperature (SST; °C)	$\chi^2_{1, 418}$= 0.62	0.43	$\chi^2_{1, 79}$= 2.20	0.14	$\chi^2_{1, 318}$= 0.34	0.56	$\chi^2_{1, 68}$= 4.45	**0.04**

Table S2.7: *Characteristics of adults' trophic ecology and chick growth and body condition of Cory's shearwaters from neighbouring sub-colonies at Berlenga Island and of Cape Verde shearwaters from neighbouring sub-colonies at Raso Islet over the 2017-2018 breeding seasons, during chick-rearing. RBC- Red Blood Cells. Values are mean ± SD. (2) Results of generalised linear mixed models (GLMMs) testing the effects of sub-colony (Berlenga: FS- Furado Seco vs ML- Melreu; Raso: AC- Acampamento vs RL- Ribeira do Ladrão) and year (2017 vs 2018) on adults' trophic ecology and chicks' growth and body condition. Each model included individual as a random effect. Differences were considered statistically significant when p-value ≤ 0.05 (**in bold**).*

Berlenga			**Sub-colony**		**Year**	
	FS	**ML**	**GLMM**	***p*-value**	**GLMM**	***p*-value**
Trophic ecology						
Whole blood/ RBC δ^{13}C (‰)	-18.9 ± 0.6	-18.1 ± 0.9	$\chi^2_{1, 38}= 0.04$	0.85	$\chi^2_{1, 38}= 12.46$	**< 0.001**
Whole blood/ RBC δ^{15}N (‰)	16.5 ± 4.1	15.3 ± 4.9	$\chi^2_{1, 38}= 0.02$	0.88	$\chi^2_{1, 38}= 13.05$	**< 0.001**
Chick growth and body condition						
Linear chick growth rate (LGR; g day^{-1})	16.6 ± 4.1	15.3 ± 4.9	$\chi^2_{1, 50}= 2.60$	0.11	$\chi^2_{1, 50}= 13.97$	**< 0.001**
Chicks' body condition index (BCI)	-0.10 ± 0.32	-0.08 ± 0.12	$\chi^2_{1, 50}= 1.50$	0.22	$\chi^2_{1, 50}= 1.26$	0.26

Raso			**Sub-colony**		**Year**	
	AC	**RL**	**GLMM**	***p*-value**	**GLMM**	***p*-value**
Trophic ecology						
Whole blood/ RBC δ^{13}C (‰)	-16.3 ± 0.9	-16.2 ± 1.1	$\chi^2_{1, 56}= 1.88$	0.17	$\chi^2_{1, 56}= 29.40$	**< 0.001**
Whole blood/ RBC δ^{15}N (‰)	11.7 ± 0.6	11.5 ± 0.7	$\chi^2_{1, 56}= 0.70$	0.40	$\chi^2_{1, 56}= 11.63$	**< 0.001**
Chick growth and body condition						
Linear chick growth rate (LGR; g day^{-1})	8.8 ± 1.3	9.4 ± 1.8	$\chi^2_{1, 24}= 0.94$	0.33		
Chicks' body condition index (BCI)	-0.01 ± 0.06	0.07 ± 0.19	$\chi^2_{1, 24}= 2.27$	0.13		

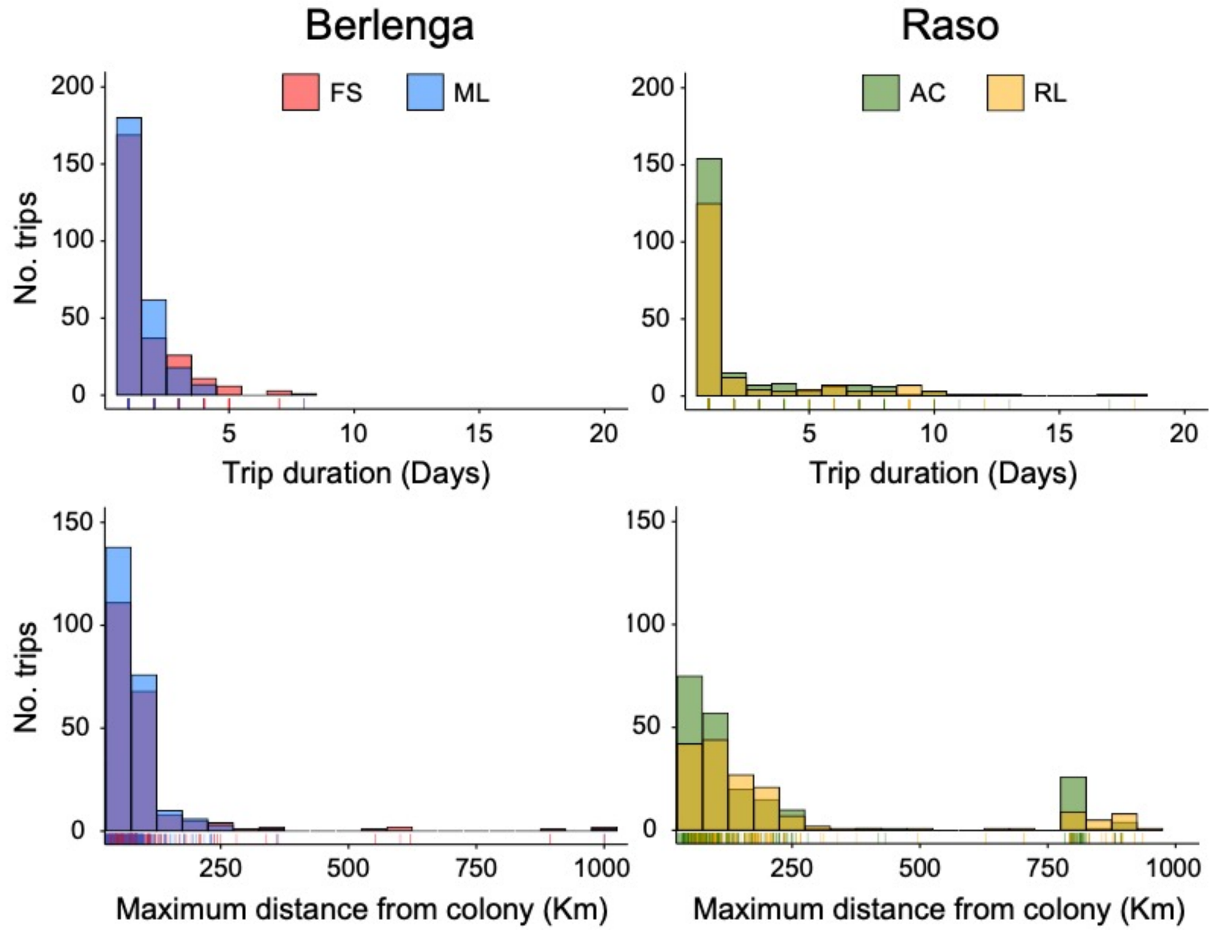

Figure S2.1: *Frequency distributions of trip duration (days) and maximum distance from the colony (km) for 521 trips made by Cory's shearwaters (Calonectris borealis) at Berlenga Island and 390 trips made by Cape Verde shearwaters (Calonectris edwardsii) at Raso Islet over two breeding seasons (2017-2018), during chick-rearing. Cory's shearwater sub-colonies at Berlenga Island are shown in blue (ML- Melreu) and red (FS- Furado Seco) and Cape Verde shearwater sub-colonies at Raso Islet are shown in green (AC- Acampamento) and orange (RL- Ribeira do Ladrão). For Cory's shearwaters at Berlenga Island, short trips were defined as ≤ 1 day and ≤ 100 km and long trips as > 1 day and > 100 km and for Cape Verde shearwaters at Raso Islet short trips were defined as ≤ 1 day and ≤ 250 km and long trips as > 1 day and > 250 km.*

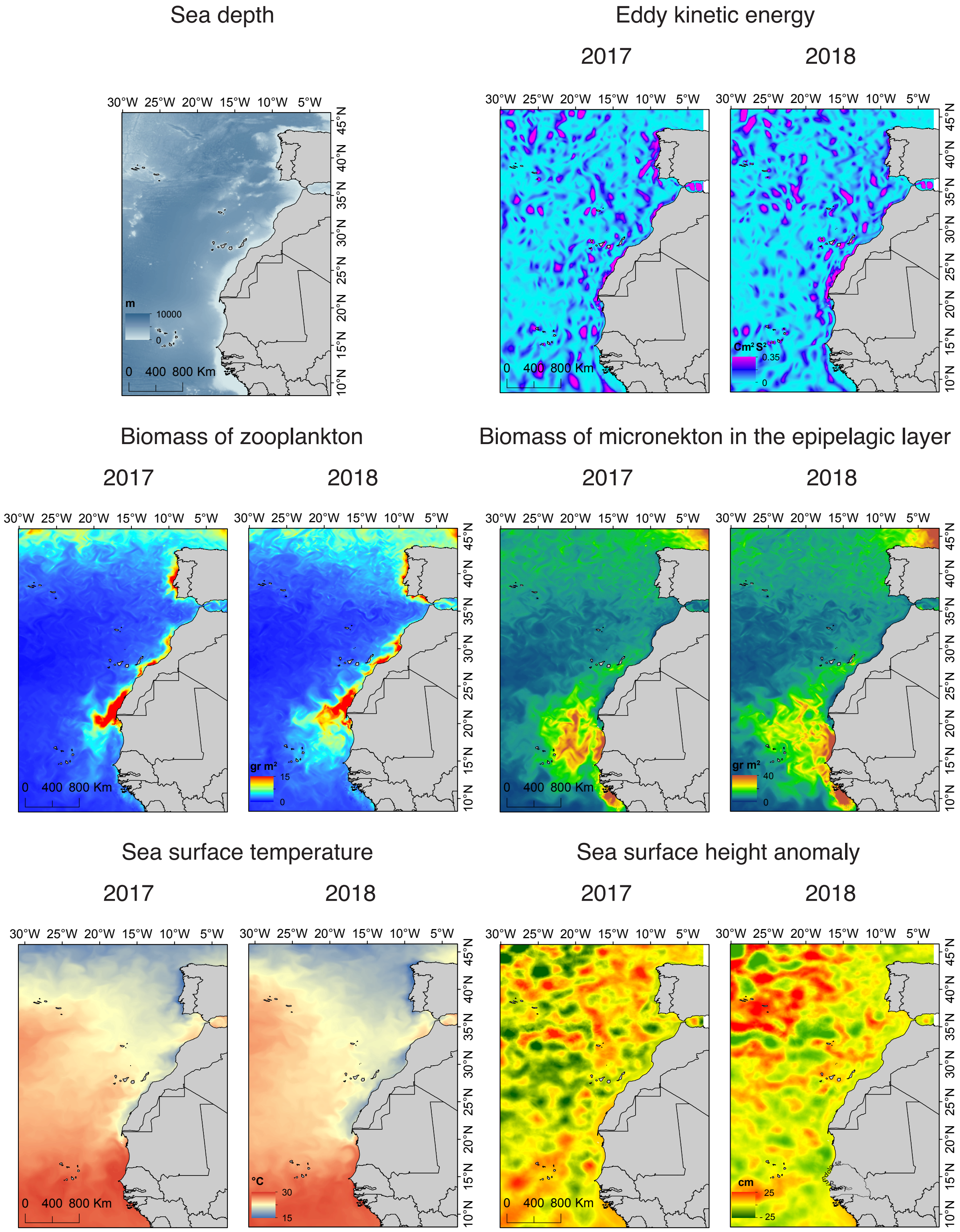

Figure S2.2: *Sea depth and monthly averages of oceanographic conditions (i.e. eddy kinetic energy, biomass of zooplankton, biomass of micronekton in the epipelagic layer, sea surface temperature and sea surface height anomaly) for the chick-rearing period (August-September) used to model the foraging habitats of Cory's shearwaters and Cape Verde shearwaters during two consecutive breeding seasons (2017-2018).*

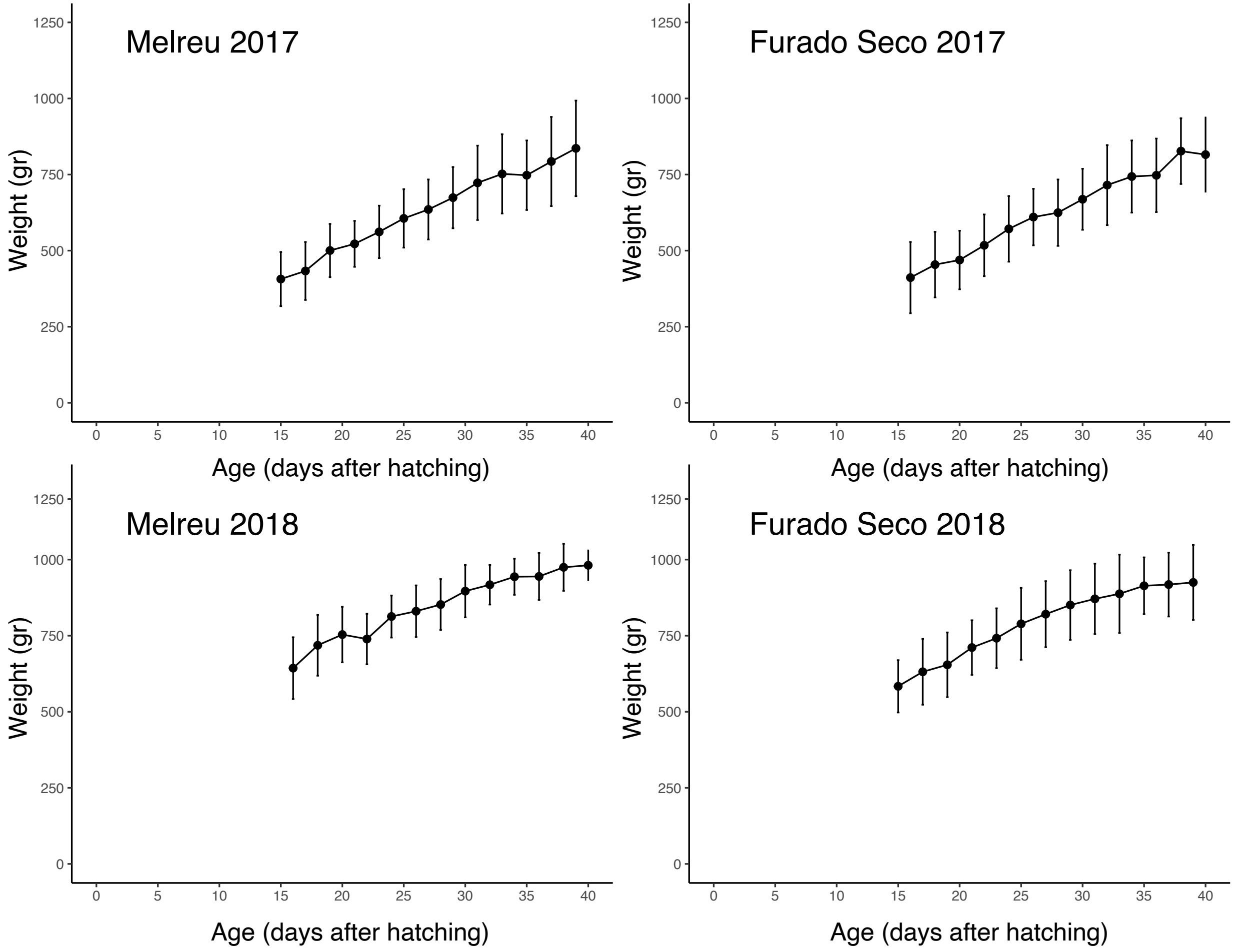

Figure S2.3: *Growth curve of Cory's shearwater chicks at Berlenga Island during the linear growth rate (LGR) period for each sub-colony (Melreu vs Furado Seco) in each study year (2017 and 2018).*

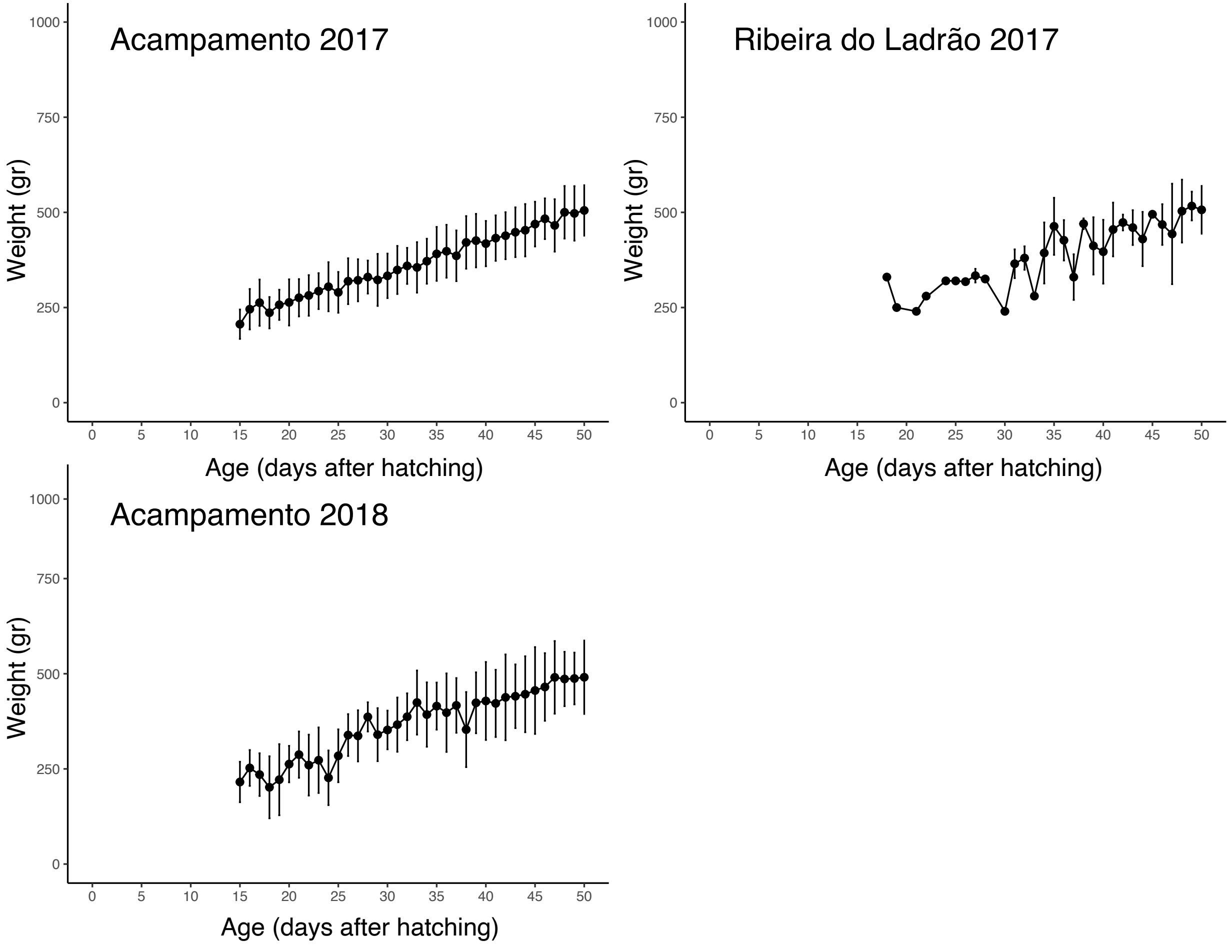

Figure S2.4: *Growth curve of chicks of Cape Verde shearwater chicks during the linear growth rate (LGR) period for each sub-colony (Acampamento vs Ribeira do Ladrão) in each study year (2017 and 2018).*

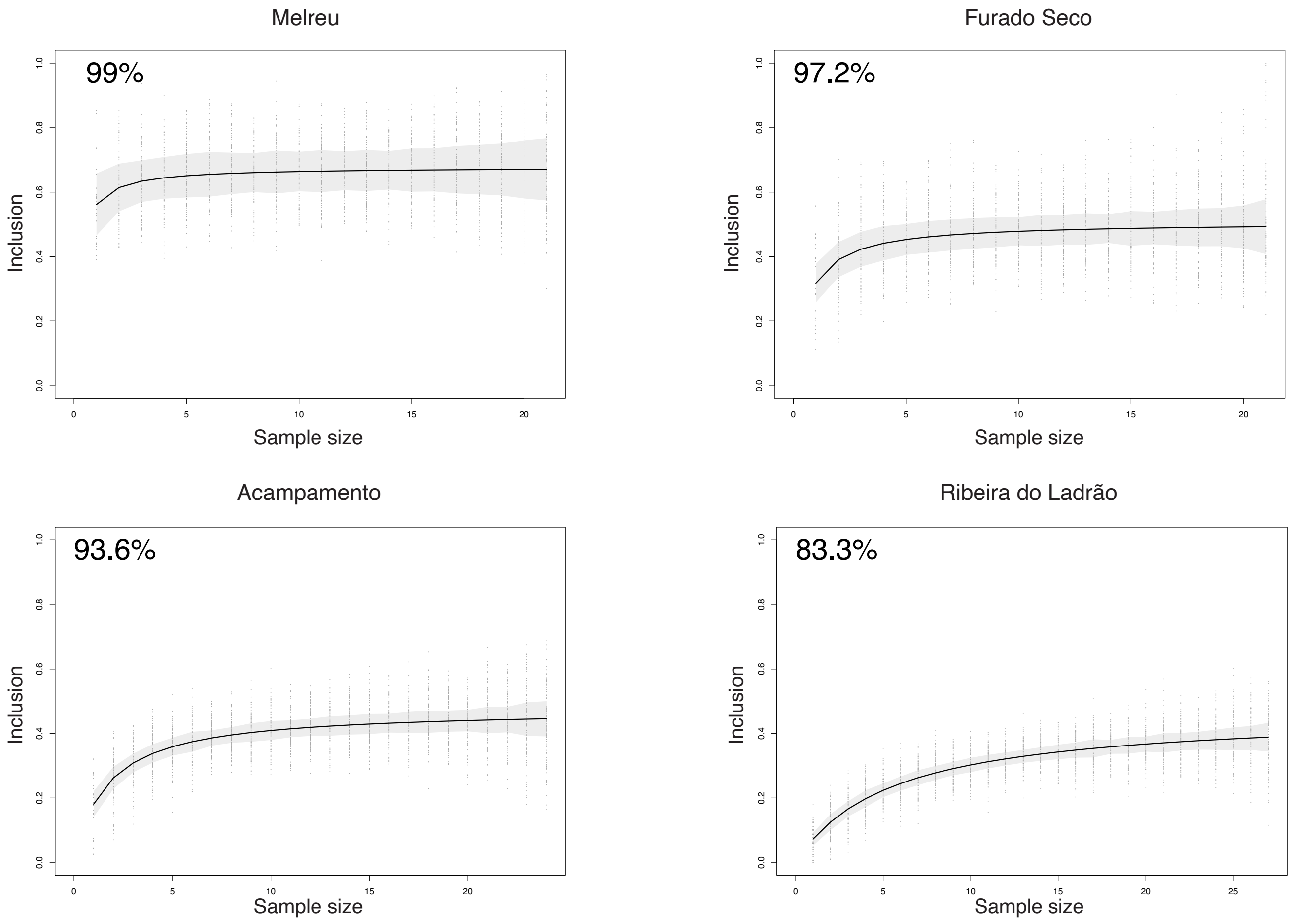

Figure S2.5: *Estimated percentage of representativeness sample sizes for sub-colonies of Cory's shearwaters at Berlenga Island (Melreu and Furado Seco) and Cape Verde shearwaters at Raso Islet (Acampamento and Ribeira do Ladrão).*

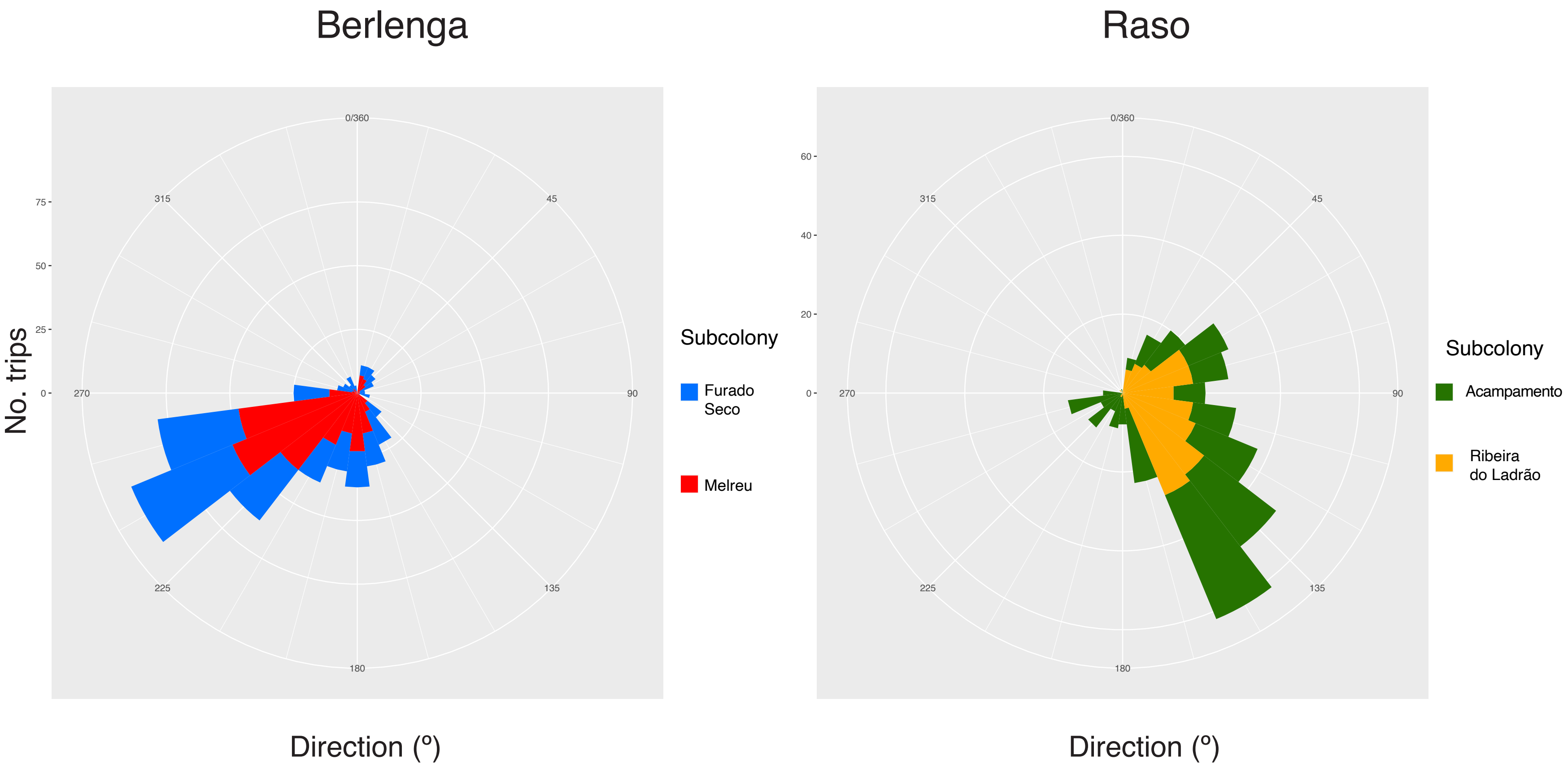

Figure S2.6: *Circular histograms of the departure direction of Cory's shearwaters from two neighbouring sub-colonies at Berlenga Island (Melreu vs Furado Seco) and for two neighbouring sub-colonies of Cape Verde shearwaters at Raso Islet (Acampamento vs Ribeira do Ladrão) during chick-rearing over the 2017-2018 breeding seasons.*

Chapter 3

Facing extremes: Cory's shearwaters adjust their foraging behaviour differently in response to contrasting phases of North Atlantic Oscillation

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Abstract

Climate projections predict increases in the frequency and severity of extreme climate events over the next decades. Hence, phases of extreme climatic indices are emerging as one of the most dangerous effects of climate change, though their impacts on wildlife populations are still poorly understood. Here, we studied the foraging behaviour, body condition and breeding performance of a neritic (Berlenga Island) and oceanic (Corvo Island) population of Cory's shearwaters (*Calonectris borealis*) in the mid-North Atlantic, during the two most positive and negative phases of North Atlantic Oscillation (NAO) reported in recent decades. We showed that during an extreme negative NAO phase, birds from Berlenga Island spent less time foraging and provided less food to their chicks, which subsequently grew more slowly and were in poorer body condition. In contrast, the opposite pattern was found during the strong positive NAO phase in this population. Interestingly, during the same extreme negative NAO phase, birds from Corvo Island were more successful in terms of their foraging and breeding performance, taking advantage of the enhanced productivity associated with the cyclonic eddies (negative sea surface height anomalies) which occurred close to the colony. However, when anticyclonic eddies (positive sea surface height anomalies) were prevalent near the colony during the strong positive NAO phase, birds travelled longer distances, which negatively impacted their own body condition and that of their chicks. Our study shows that populations breeding in neritic and oceanic areas of the eastern North Atlantic Ocean make contrasting foraging behavioural decisions in response to climate extremes and highlights the importance of mesoscale eddies for oceanic populations of pelagic seabirds.

Keywords: Body condition, Climate extreme, Foraging plasticity, Mesoscale eddies, Seabird, Sea surface height anomalies.

3.1. Introduction

Climate change is now recognised as a global threat to biodiversity, which has already led to considerable changes in the structure and functioning of ecosystems (Walther et al. 2002, Araújo & Rahbek 2006, Sydeman et al. 2015). Hence, how climate change affects wildlife species is a major concern in ecology (Jenouvrier et al. 2003, Sandvik & Einar Erikstad 2008). Several studies have shown that climate change is altering species' breeding phenology, foraging behaviour and demographic traits such as breeding success and adult survival, with consequences at different scales ranging from individuals to entire ecosystems (Hoegh-Guldberg & Bruno 2010, Shackell et al. 2010, Amélineau et al. 2019). Most scenarios for future climate change predict that increasing environmental variability will lead to intensification in the frequency and amplitude of extreme climatic anomalies (Easterling 2000, Frederiksen et al. 2008, Bailey & van de Pol 2016). Therefore, phases of extreme climatic indices are emerging as one of the most dangerous effects of climate change (Jentsch et al. 2007). However, relatively few studies have quantified their effects on wildlife populations, mostly because they are by definition episodic and their study is mainly opportunistic (Descamps et al. 2015). These events play an important role in shaping species' life-history traits (Moreno & Møller 2011, Bailey & van de Pol 2016, Chevin & Hoffmann 2017) and it is important to understand their impacts on population reproductive and foraging parameters.

In marine ecosystems, oceanographic processes are closely linked with inter-annual variations of large-scale atmospheric phenomena, such as the El-Niño Southern Oscillation (ENSO) or the North Atlantic Oscillation (NAO) indices (Stenseth et al. 2003). Consequently, perturbations in the dynamics of these large-scale phenomena could result in adverse effects for the mesoscale ocean circulation (Ummenhofer & Meehl 2017, Caesar et al. 2018, Thornalley et al. 2018). In oceanic areas, mesoscale features (e.g. eddies) play a critical role in ocean circulation and biogeochemistry (Stramma et al. 2013). These large (approximately 10-100 km), ephemeral (hours) and persistent (weeks) features are responsible for the transport of nutrients and enhance primary productivity in oceanic areas (Oschlies & Garçon 1998, José et al. 2014, Uchiyama et al. 2017). The eddy-pumping hypothesis suggest that cyclonic eddies (counter-clockwise rotation in the Northern

Hemisphere) are associated with divergent surface flow movements that boost deep, cold and nutrient-rich waters towards the euphotic zone, enhancing the primary production (Falkowski et al. 1991, McGillicuddy et al. 2007, Klein & Lapeyre 2009). Conversely, in anticyclonic eddies (clockwise rotation in the Northern Hemisphere), nutrients are pushed farther away from the euphotic zone, which leads to a decrease in productivity (Martin 2003). Mesoscale eddies also provide potential foraging opportunities for a wide range of marine taxa (Ferraroli et al. 2004, Woodworth et al. 2012, Abrahms et al. 2018, Braun et al. 2019), including seabirds (Nel et al. 2001, Cotté et al. 2007, Weimerskirch et al. 2010, Jaquemet et al. 2014).

Particularly, seabirds have been shown to be sensitive indicators of the extent and severity of environmental variation in the marine environment (Grémillet & Boulinier 2009, Thorne et al. 2016), and respond to variation namely by changing their life-history traits (Jenouvrier et al. 2018). For example, in response to extreme high sea ice concentrations, Antarctic seabirds increased their foraging effort, foraging further from the colony, which ultimately had negative effects on their breeding performance (Barbraud et al. 2015). However, some of the most drastic effects of climate extremes on seabirds have been reported for tropical oceanic environments (reviewed by Şekercioĝlu et al. 2012), given their lower marine productivity and more unpredictable and patchily distributed food resources (Morel et al. 2010). Several studies have shown that during major El-Niño years, tropical seabirds drastically reduce their breeding success and are more likely to show a null breeding success or even skip reproduction altogether (Ramos et al. 2002, Zavalaga et al. 2008, Cubaynes et al. 2011). Despite the reported evidence that extreme climate events influence the life-history traits of seabirds, most studies have focused on analysing the indirect effects of these events on reproductive measures at the colony level (e.g. Morrison et al. 2011; Descamps et al. 2015; Ropert-Coudert et al. 2015) and few have analysed the direct influence on adults' foraging behaviour and the subsequent implications on their body condition (a proxy of fitness) and offspring growth rates (e.g. Jenouvrier et al. 2015).

In this study, we investigated the foraging behaviour of two populations of Cory's shearwaters (*Calonectris borealis*) breeding in two different environments in the North Atlantic Ocean, separated by approximately 2000 km: (1) a neritic zone (Berlenga Island) and (2) an oceanic zone (Corvo Island), during the most positive and most negative phases of NAO index reported in recent decades (i.e. 2010 and 2015). In addition, we quantified the consequences of adult foraging behaviour and habitat use on their fitness measures (body condition) and those of their chicks (linear growth rate and body condition). Cory's shearwaters are one of the most abundant and studied seabird species breeding in the eastern North Atlantic Ocean (Ramos et al. 2013) and are an important indicator of environmental anomalies for this region (Paiva et al. 2010c, 2013a). These conditions provide an ideal framework for a "natural experiment" to test how populations of shearwaters breeding in different environments respond to contrasting climatic conditions (based on extreme phases of NAO index) and thus simulating the effects of climate change. Facing such conditions, we made the following predictions: (1) both populations should respond in situations of lower prey availability, particularly during years of negative NAO index, by increasing their foraging effort and exploring distant foraging grounds (Paiva et al. 2013a, Avalos et al. 2017); (2) the increase in foraging effort may translate into lower adult and chick body condition and negatively affect chick growth rates; however, (3) the severity of these effects should vary between populations, with birds from Corvo showing lower fitness parameters than birds from Berlenga, because marine resources are more patchily distributed in large pelagic oceanic regions than in predictable upwelling systems with higher prey availability.

3.2. Methods

3.2.1. Study area and fieldwork

We studied the foraging behaviour of Cory's shearwaters on Berlenga (39°23′ N, 9°36′ W) and Corvo Islands (39°40′ N, 31°06′ W) during two breeding seasons (1 August 2010 to 31 August 2010, and 14 August 2015 to 11 September 2015; hereafter referred to as study years 2010 and 2015, respectively). Berlenga is a coastal island located within the Portuguese continental shelf, where a seasonal upwelling system occurs between April and September and provides optimal conditions for concentrations of large pelagic fish populations (Sousa et al. 2008). These favourable conditions benefit a number of marine predators, including several seabird species that are known to exploit this area both during the summer and the winter periods (Pereira et al. 2018). In contrast, Corvo is an oceanic island in the middle of the North Atlantic Ocean and the farthest western known colony of Cory's shearwaters (Magalhães et al. 2008).

To record the at-sea movements of Cory's shearwaters, global positioning system (GPS) loggers (IgotU GT-120; Mobile Action Technology Inc., Taiwan) were attached to the back feathers of breeding adults using TESA® tape following Wilson et al. (1997). Each device was sealed with heat-shrink tubing to waterproof and programmed to record positions at 5-min intervals. The weight of each device, together with the heat-shrink tubing, was approximately 17 g, representing less than 3% of the birds' body mass, the threshold under which several studies have reported no deleterious effects on seabirds (Phillips et al. 2003). Evaluation of the effect of loggers during short-term studies has already been tested in prior research on Cory's shearwaters (Igual et al. 2005, Villard et al. 2011), namely in the populations from Berlenga (Paiva et al. 2010b c) and Corvo (Paiva et al. 2010a). These studies found no differences in the body mass change, hatching or fledging success of birds that were equipped with GPS devices and a randomly selected subset of birds without devices.

3.2.2. Body condition and chick growth

Birds were ringed during capture and weighed (to the nearest 5 g) at both capture and recapture, using a Pesola spring balance. In addition, for all adults equipped with a GPS logger, wing length, tarsus length, culmen length and height of the bill at the base and at the gonys was measured using a calliper (to the nearest 1 mm) to calculate the Body Condition Index (BCI). This index was calculated following Paiva et al. (2017) by including body biometrics (except body mass) in a Principal Component Analysis (PCA) and using the PC1 scores as a measure of structural body size. We obtained the BCI from the residuals of a linear regression of body mass on PC1 scores. BCI is also a proxy of survival in Procellariforms (Chastel et al. 1995, Labocha et al. 2014). Similarly, BCI was also determined for chicks of tracked adults following Catry et al. (2013), using daily measures of body mass and wing length taken from the time GPS loggers were equipped in the adults until their recovery. A BCI < 0 indicates that the bird is lighter than expected by chance and thus in poor body condition, while a BCI > 0 shows that the individual is in better body condition (Catry et al. 2013). Linear growth rate (g day^{-1}) was estimated for each chick and defined as the slope of the regression line of chick mass (weighed daily to the nearest 5 g) during the linear growth period, between 10 and 40 days of age following Ramos et al. (2003).

3.2.3. Foraging behaviour

We used the '*Expectation-Maximization binary Clustering*' (EMbC) R package to classify the different foraging behaviours adopted by each tracked bird (Garriga et al. 2016). The EMbC is a non-supervised multivariate clustering algorithm that labels each GPS position based on the estimated velocity and turning angle (reviewed by Garriga et al. 2016). Before clustering analysis, a built-in smoother function was applied to account for the temporal association in each behavioural state. Each position was classified into 4 movement categories: (1) High velocity/Low turning angles- HL; (2) High velocity/ High turning angles- HH; (3) Low velocity/ Low turning angles- LL; and (4) Low velocity/ High turning angles- LH (See Fig. S3.1 in the Supplementary Information). Different biological interpretations were assigned to each movement category following Louzao et al. (2014). GPS positions characterised by high velocity rates, such as the HL and HH labels, were associated with flying and extensive search, respectively (Mendez et al. 2017). The LL label refers to when birds are drifting passively on the water surface, which is associated with resting behaviour (de Grissac et al. 2017). Decreases in velocity and abrupt changes in bird trajectory (LH label) were interpreted as intensive search behaviour and related to Area-Restricted Search (ARS) zones according to the definition of Fauchald and Tveraa (2003).

3.2.4. Regional and local-scale environmental conditions

We used the annual North Atlantic Oscillation (hereafter referred to as NAO) index to represent the large-scale climatic conditions for the North Atlantic Ocean (Hurrell 1995), downloaded from https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based. This index is characterised by the oscillation in atmospheric mass between the subtropical high-pressure zone of the Azores and the low-pressure zone of Iceland (Stenseth et al. 2003) and is considered one of the most robust proxy of climate dynamics for the North Atlantic Ocean (Stenseth 2002). A positive NAO index is characterised by an intense pressure difference between the Icelandic Low pressure and the Azores High pressure, which results in the increased frequency and intensity of winter storms crossing the Atlantic Ocean to northern latitudes. In contrast, the reduced pressure gradient of negative NAO phases leads to fewer and weaker winter storms occurring on a West-East zonal circulation (Ottersen et al. 2001).

To characterise the oceanographic conditions that are associated with intensive search behaviour in Cory's shearwaters, we extracted: (1) Bathymetry (BAT, 0.01° spatial resolution, m); (2) Chlorophyll-*a* concentration (CHL, 0.08°, mg m^{-3}); (3) Sea surface temperature (SST, 0.08°, °C); (4) Sea surface height (SSH, 0.08°, cm); and (5) Wind speed (WS, 0.13°, m/s^{-1}).

BAT was downloaded from https://www.ngdc.noaa.gov/mgg/global/global.html, while CHL, SST, SSH and WS were extracted from http://marine.copernicus.eu. Monthly averages for the chick-rearing period (August - September) were used for variables 2, 3, 4 and 5. SST and SSH anomalies (SSTA and SSHA, respectively) were computed by calculating the difference between the average of the variable for the chick-rearing period and the long-term climatology for the same months (i.e. 1993-2015).

Satellite altimetry has been widely used to study large-scale changes in ocean circulation and is considered to be an efficient strategy to map mesoscale activity along vast oceanic regions (Fu et al. 2010, Mason et al. 2014). Therefore, in this study we used SSHA to identify the presence of mesoscale eddies along the study area, with positive SSHA values denoting anticyclonic eddies and negative SSHA depicting cyclonic eddies (McGillicuddy et al. 1998).

3.2.5. Statistical analysis

We used linear mixed models (LMMs) to evaluate the colony (Berlenga *vs* Corvo) and year (2010 *vs* 2015) effect on (1) trip characteristics (i.e. tracking period, trip duration, time spent on long foraging trips and maximum distance from the colony); (2) behaviour within foraging trips (i.e. time spent flying, time spent in intensive search, time spent in extensive search and time spent resting); and (3) foraging area habitat (i.e. BAT, CHL, SSHA, SSTA and WS). All LMMs included trip identity nested within the individual ID as a random term to account for pseudo-replication problems since most individuals performed multiple trips. Short and long foraging trips were distinguished based on histograms of the frequency of occurrence of: (1) trip duration (days); and (2) maximum distance from the colony reached for each foraging trip (km). During 2010, long trips were considered for Berlenga as being > 1 day and > 90 km, and for Corvo, > 1 day and > 100 km. During 2015 for Berlenga this was > 1 day and > 60 km, and for Corvo > 3 days and > 40 km (See Fig. S3.2 and Fig. S3.3 in the Supplementary Information).

Prior to statistical analysis, all data were visually inspected for normality (Q-Q plots) and homogeneity (Cleveland dotplots) (Zuur et al. 2010). Trip characteristics and habitat variables were log-transformed, while percentages of time spent performing each foraging behaviour and time spent on long trips were arcsin-transformed to meet parametric assumptions when necessary. Additionally, linear models (LMs) were used to test for differences between the two populations for each study year, in terms of: (1) sex-differences in the tracking period; (2) environmental conditions within a 200 km radius of the colony (i.e. SSHA and SSTA); and (3) fitness parameters (i.e. adults' and chicks' BCI, and linear chick growth rate). LMs and LMMs were computed using functions of the '*lme4*' (Bates et al. 2015) and '*lmerTest*' R packages (Kuznetsova et al. 2017). All statistical analyses were conducted within the R environment v. 3.4.4 (R Core Team 2019). All data are presented as mean ± SD (standard deviation). Differences were considered as statistically significant when *p*-value ≤ 0.05.

Lastly, Kernel Utilization Distributions (KUDs) were generated for the positions in which all the individuals of each population engaged in intensive search behaviour, using the '*adehabitatHR*' R package (Calenge 2006). The most appropriate smoothing parameter (*h*) was set at 0.10° for the complete dataset and then applied on a 0.13° grid (to match with the environmental variables). We considered 95% and 50% kernel UD boundaries to represent home ranges and core foraging areas, respectively.

3.3. Results

3.3.1. Changing patterns of colony productivity

The average of the annual NAO index indicated a contrasting pattern in climatic conditions over the North Atlantic during 2010 and 2015: 2010 was strongly negative (-5.96) and 2015 was strongly positive (+4.09) (Fig. 3.1). This drastic variation in regional climatic conditions was expressed by a switch in ocean productivity, as shown by the SSTA for the North Atlantic region (Fig. 3.2). In terms of local-scale conditions, the negative NAO index for 2010 was related to significant increases in SSTA (i.e. warmer waters) for both colonies, but warmer waters were registered around Corvo than Berlenga (Fig. 3.2). In contrast, the positive NAO index for 2015 was associated with colder waters, particularly in Corvo (Table 3.1). In addition, differences in mesoscale ocean circulation patterns were also found among colonies for each year. Specifically, during 2010, waters within 200 km of Corvo had negative values of SSHA, which denote the presence of cyclonic eddies, while the waters surrounding Berlenga were characterised by moderate positive SSHA values (Tables 3.1 and 3.2). In contrast, during 2015 waters within 200 km of both Berlenga and Corvo were characterised by a prevalence of intense anticyclonic water masses depicted by positive SSHA anomalies, which were particularly intense around Corvo (Tables 3.1 and 3.2).

3.3.2. Divergent foraging behaviour and habitat use

Over the two breeding seasons, we collected tracking data from 419 foraging trips made by 78 adult Cory's shearwaters (2010= 50 birds/307 trips and 2015= 28 birds/112 trips). A similar proportion of males and females were tracked between years and colonies (Berlenga 2010: 13 *vs* 16; Corvo 2010: 10 *vs* 11; Berlenga 2015: 10 *vs* 8; Corvo: 5 *vs* 5, respectively). In addition, no sex differences were found in tracking duration between Berlenga and Corvo for 2010 (8.2 ± 2.4 days and 9.4 ± 3.1 days, respectively; $F_{1,48}$= 0.43; *p*-value= 0.51) and 2015 (12.4 ± 4.2 days and 7.2 ± 3.5 days, respectively: $F_{1,26}$= 0.44; *p*-value=

0.65). Overall, the distribution and foraging behaviour of individuals from Berlenga and Corvo differed substantially between contrasting climatic scenarios (Fig. 3.3). During the extreme negative NAO year, individuals from Berlenga had significantly longer foraging excursions, within which they decreased the time allocated to foraging behaviour and spent significantly more time resting on the sea-water surface when compared with birds from Corvo (Tables 3.1 and 3.2). In contrast, the foraging behaviour adopted by each population during the year of strong positive NAO index showed the reverse trend. During this positive NAO year, birds from Corvo spent more time on each foraging trip; travelling significantly farther from the breeding colony and increasing their resting behaviour, while birds from Berlenga spent less time at-sea and performed shorter foraging trips, remaining close to the colony (Tables 3.1 and 3.2).

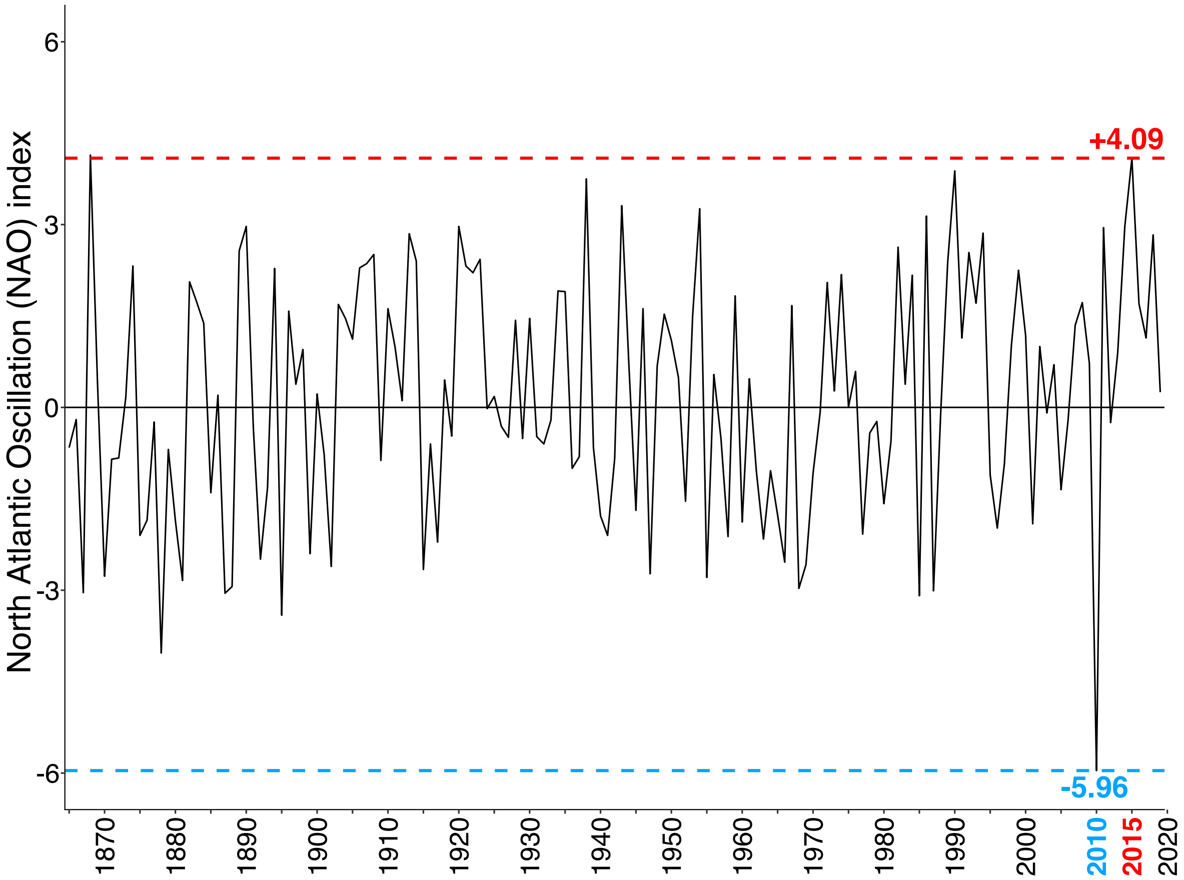

Figure 3.1: *Historical annual North Atlantic Oscillation (NAO) index displayed from 1865 to 2020 as computed by Hurrell et al. (2003). Study years are highlighted as the most negative (2010 in blue) and most positive (2015 in red) phases of NAO index reported in recent decades.*

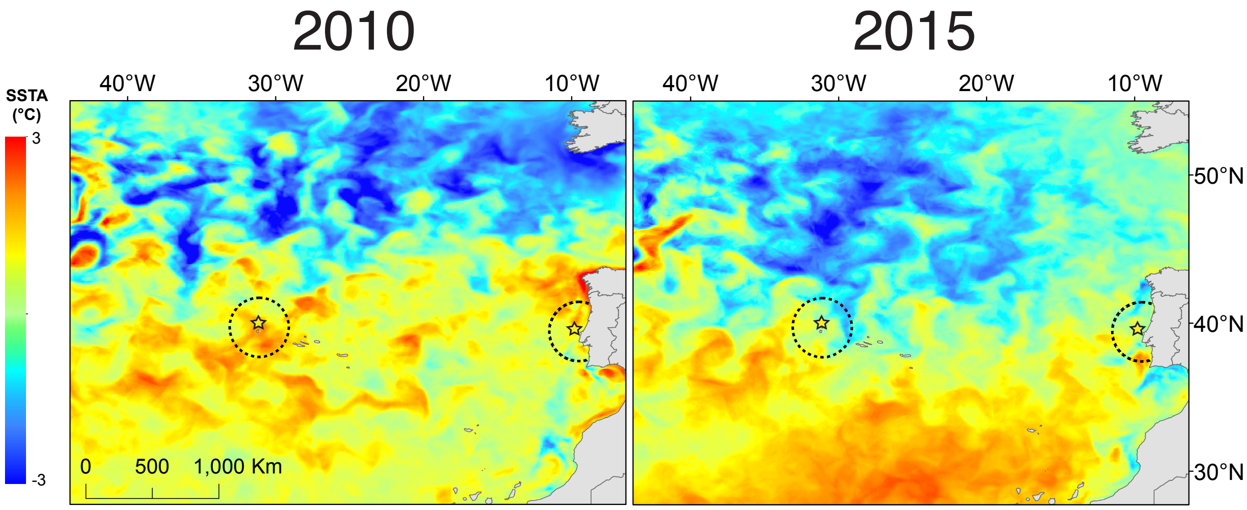

Figure 3.2: *Mean Sea surface temperature anomaly (SSTA) displayed for the study area and showing contrasting environmental conditions during extreme negative (2010) and extreme positive (2015) phases of North Atlantic Oscillation (NAO) index. SSTA was calculated for the tracking period according to a long-term monthly climatology (August-September) from 1993 to 2015. The dotted circles illustrate a radius of 200 km surrounding each colony as a proxy for local environmental conditions with colonies marked with yellow stars.*

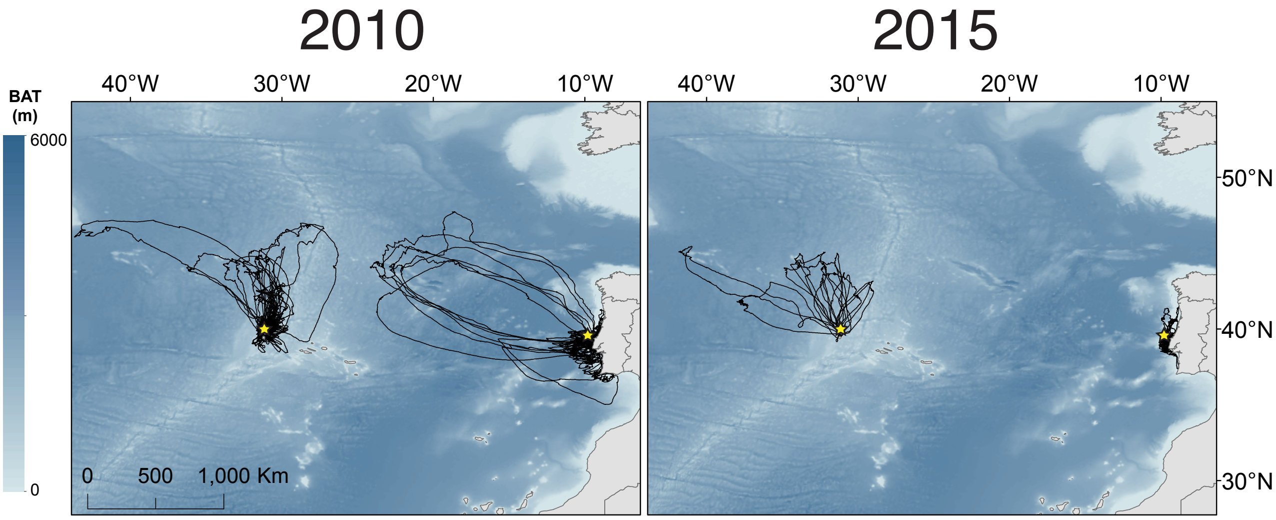

Figure 3.3: *Overall tracking data for populations of Cory's shearwaters (Calonectris borealis) from Berlenga (yellow star near continental Portugal) and Corvo (yellow star in the middle of the Ocean) during 2010 and 2015, overlaid on bathymetry of the region (BAT).*

Table 3.1: *Large-scale climate and habitat characteristics within 200 km of Berlenga and Corvo during 2010 and 2015. Trip characteristics, foraging behaviour, habitat of foraging areas and fitness parameters of both adults and chicks. The Annual North Atlantic Oscillation (NAO) index was extracted from https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based. Environmental predictors characterising the colony surroundings (200km) and individual foraging areas were extracted for the tracking period of each study year (August-September). Values are mean ± SD (standard deviation).*

	2010		**2015**	
	Berlenga	**Corvo**	**Berlenga**	**Corvo**
NAO index	-5.96		4.09	
N birds (N trips)	29 [127]	21 [180]	18 [91]	10 [21]
Habitat of colony surroundings (200 km)				
Sea surface height anomaly (SSHA; cm)	0.6 ± 1.4	-3.5 ± 2.9	2.8 ± 2.0	4.9 ± 2.6
Sea surface temperature anomaly (SSTA; °C)	0.2 ± 0.3	0.5 ± 0.3	-0.3 ± 0.6	-0.6 ± 0.6
Trip characteristics				
Tracking period (days)	8.2 ± 2.4	9.4 ± 3.1	12.4 ± 4.2	7.2 ± 3.5
Trip duration (days)	2.2 ± 2.1	1.4 ± 1.4	1.5 ± 0.9	3.1 ± 2.6
Time spent in long foraging trips (%)	37.8 ± 35.9	29.3 ± 24.9	43.5 ± 31.3	76.2 ± 39.3
Maximum distance from the colony (km)	137.8 ± 259.0	131.1 ± 171.0	47.0 ± 49.2	333.1 ± 303.0
Foraging behaviour				
Time spent flying (%)	24.9 ± 11.1	26.1 ± 15.5	42.9 ± 13.7	38.7 ± 9.9
Time spent in intensive search (%)	17.5 ± 6.2	21.6 ± 6.8	36.7 ± 13.5	20.2 ± 7.1
Time spent in extensive search (%)	24.9 ± 8.4	20.5 ± 8.7	18.8 ± 11.5	15.1 ± 7.6
Time spent resting (%)	32.7 ± 11.2	16.6 ± 6.0	16.7 ± 5.7	25.9 ± 17.1
Habitat of foraging areas				
Bathymetry (BAT; m)	472.2 ± 956.6	1360.2 ± 693.8	173.1 ± 269.0	1761.3 ± 1477.9
Chlorophyll-*a* concentration (CHL; mg m^{-3})	0.80 ± 0.49	0.14 ± 0.02	1.35 ± 0.84	0.18 ± 0.05
SSHA (cm)	0.7 ± 1.1	-4.3 ± 1.9	1.8 ± 0.3	0.5 ± 3.2
SSTA (°C)	0.2 ± 0.1	0.6 ± 0.3	-0.6 ± 0.2	-1.1 ± 0.7
Wind speed (WS; m/s^{-1})	5.1 ± 1.3	5.9 ± 0.4	5.9 ± 0.4	8.9 ± 0.9
Fitness parameters				
Adults' body condition index (BCI)	-1.0 ± 0.6	1.3 ± 0.3	1.1 ± 0.2	-0.2 ± 0.4
N chicks	23	18	13	6
Chicks' body condition index (BCI)	-0.9 ± 0.6	1.0 ± 0.3	1.0 ± 0.3	-0.2 ± 0.3
Linear chick growth rate (g day^{-1})	10.0 ± 3.0	22.8 ± 6.3	28.0 ± 5.0	12.1 ± 1.8

Table 3.2: *Results of linear mixed models (LMM) testing the differences between colonies (Berlenga vs Corvo) and years (2010 vs 2015) on habitat of colony surroundings, trip characteristics, foraging behaviour, habitat of foraging areas and fitness parameters of both adults and chicks. Each model included trip identity nested within the individual ID as a random effect. Differences were considered as statistically significant when p-value ≤ 0.05 (in* ***bold****).*

	2010				**2015**			
	β ± SE	***t*-test**	***p*-value**	**Effect**	**β ± SE**	***t*-test**	***p-value***	**Effect**
NAO Index			–				–	
N birds (N trips)			–				–	
Habitat of colony surroundings (200 km)								
Sea surface height anomaly (SSHA; cm)	-0.40 ± 0.01	42.27	**<0.001**	COR < BER	0.15 ± 0.01	22.73	**<0.001**	COR > BER
Sea surface temperature anomaly (SSTA; °C)	0.17 ± 0.01	18.38	**<0.001**	COR > BER	-0.12 ± 0.01	11.59	**<0.001**	COR < BER
Trip characteristics								
Tracking period (days)	1.19 ± 0.79	1.51	13.7		-5.19 ± 0.57	3.30	**0.001**	COR < BER
Trip duration (days)	-1.23 ± 0.44	2.83	**0.01**	COR < BER	2.39 ± 0.69	2.45	**0.001**	COR > BER
Time spent in long foraging trips (%)	0.05 ± 0.15	0.31	0.76		0.85 ± 0.18	4.78	**<0.001**	COR > BER
Maximum distance from the colony (km)	-0.20 ± 0.21	0.98	0.33		1.76 ± 0.38	4.64	**<0.001**	COR > BER
Foraging behaviour								
Time spent flying (%)	0.01 ± 0.03	0.30	0.76		-0.05 ± 0.04	1.31	0.20	
Time spent in intensive search (%)	0.21 ± 0.02	10.56	**<0.001**	COR > BER	-0.01 ± 0.02	0.80	0.43	
Time spent in extensive search (%)	-0.04 ± 0.01	2.79	**0.001**	COR < BER	-0.04 ± 0.03	1.47	0.15	
Time spent resting (%)	-0.17 ± 0.01	12.42	**<0.001**	COR < BER	0.11 ± 0.03	3.71	**0.001**	COR > BER

Habitat of foraging areas								
Bathymetry (BAT; m)	2.47 ± 0.30	8.29	**<0.001**	COR > BER	2.43 ± 0.31	7.76	**<0.001**	COR > BER
Chlorophyll-*a* concentration (CHL; mg m^{-3})	-1.91 ± 0.13	15.26	**<0.001**	COR < BER	-1.43 ± 0.14	10.54	**<0.001**	COR < BER
SSHA (cm)	-0.47 ± 0.02	19.02	**<0.001**	COR < BER	-0.34 ± 0.12	2.78	**0.001**	COR < BER
SSTA (°C)	0.13 ± 0.01	10.72	**<0.001**	COR > BER	-0.36 ± 0.10	3.71	**0.001**	COR < BER
Wind speed (WS; m/s^{-1})	0.17 ± 0.04	4.01	**<0.001**	COR > BER	0.30 ± 0.05	6.46	**0.001**	COR > BER
Fitness parameters								
Adults' body condition index (BCI)	2.13 ± 0.14	15.08	**<0.001**	COR > BER	-1.54 ± 0.12	12.48	**<0.001**	COR < BER
N chicks								
Chicks' body condition index (BCI)	1.92 ± 0.17	11.29	**<0.001**	COR > BER	-1.22 ± 0.15	8.42	**<0.001**	COR < BER
Linear chick growth rate (g day^{-1})	12.82 ± 1.50	8.57	**<0.001**	COR > BER	-15.98 ± 2.13	7.51	**<0.001**	COR < BER

In terms of foraging habitat, during 2010 birds from Corvo concentrated their foraging effort over specific oceanographic features, namely using areas associated with the presence of mesoscale cyclonic eddies that were intense near the colony (Fig. 3.4). Whereas birds from Berlenga used distant foraging grounds to locate productive oceanic areas (Fig. 3.4). In contrast to 2010, during 2015 individuals from Corvo travelled longer distances into oceanic waters that were colder and windier, and did not rely on cyclonic eddies as main foraging grounds because anticyclonic eddies were particularly intense near the colony (Tables 3.1 and 3.2). On the other hand, and also in contrast to 2010, individuals from Berlenga concentrated their foraging effort near the colony and along the Portuguese continental shelf where the coastal upwelling is stronger (Fig. 3.4).

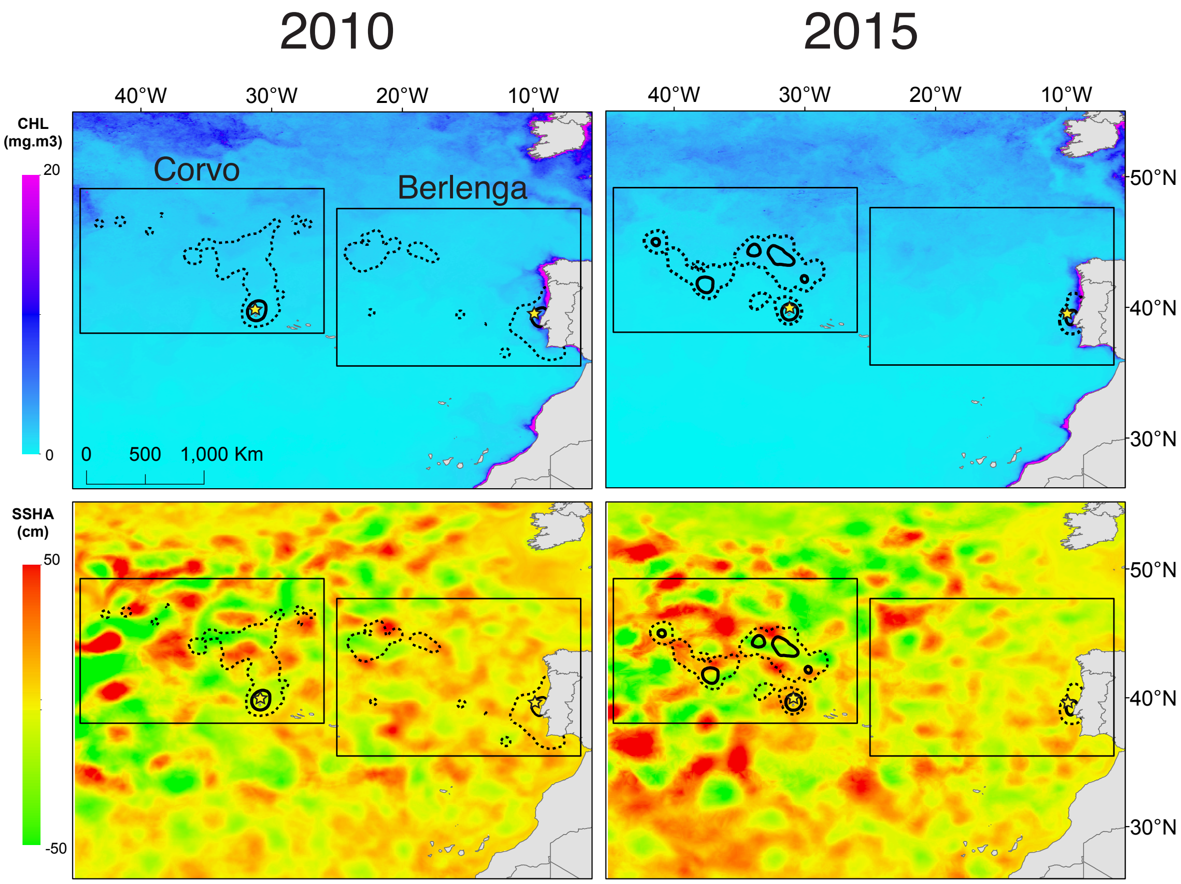

Figure 3.4: *Cory's shearwaters' home ranges (95% kernel UD; dotted lines) and core foraging areas (50% kernel UD; filled lines), overlaid on Chlorophyll-a concentration (CHL) and Sea surface height anomaly (SSHA) for Berlenga and Corvo populations during 2010 and 2015. SSHA was calculated for the tracking period according to a long-term monthly climatology (August-September) from 1993 to 2015. Yellow stars indicate the location of breeding colonies.*

3.3.3. Differential effects of foraging behaviour on adults' fitness and chicks' growth

Over the two breeding seasons, we collected biometric data from 60 chicks (41 and 19 for 2010 and 2015, respectively) of the 78 tracked adult Cory's shearwaters. When analysing the influence of adult foraging behaviour on their own body condition and chick growth, our results indicated that birds from Berlenga were particularly affected by the adverse conditions caused by the extreme negative event, while birds from Corvo were mostly affected by the strong positive NAO index (Tables 3.1 and 3.2). Facing a strong negative NAO index, adult shearwaters from Berlenga were in poorer body condition than birds from Corvo, which presumably limited the amount of food they provided to their chicks, and thus negatively affected their body condition and growth (Fig. 3.5). In contrast, during 2015 adults from Berlenga attained a higher body condition than birds from Corvo, which led to higher chick growth and body condition (Fig. 3.5)

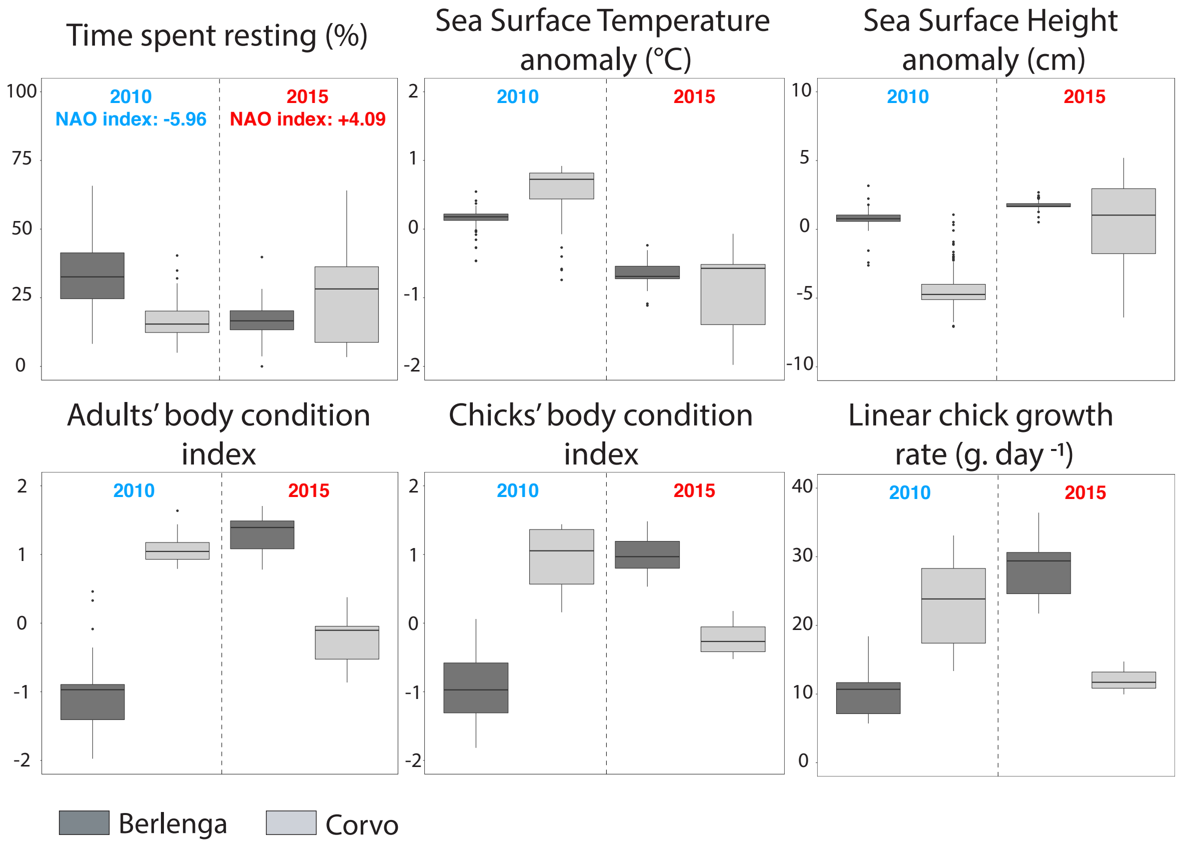

Figure 3.5: *Examples of boxplots showing the shifts in foraging behaviour, habitat use and fitness parameters of Cory's shearwaters from Berlenga (dark grey) and Corvo (light grey) in response to extreme and contrasting phases of North Atlantic Oscillation (NAO) index. Values of NAO index for each study year are shown at the top-left plot.*

3.4. Discussion

In this study, we examined how two populations of Cory's shearwaters (Berlenga *vs* Corvo) breeding in two different environments of the Atlantic Ocean (neritic *vs* oceanic) and separated by approximately 2000 km, responded to extreme and contrasting climatic conditions (the most positive *vs* the most negative phases of NAO index for recent decades). In addition, we evaluated how these events influenced adults' at-sea foraging decisions and ultimately their body condition and that of their chicks. We showed that during an extreme negative phase of NAO, birds breeding at Berlenga spent more time during each foraging excursion, but decreased the time allocated to foraging behaviour, which prejudiced their body condition and limited the amount of food delivered to their chicks. In contrast, individuals from Corvo performed shorter trips and invested more time foraging in association with cyclonic eddies near the colony. Interestingly, during a strong positive anomaly of the NAO index, foraging behaviour and fitness conditions of both populations reversed. The ecological interpretation of the tracking results, corroborated with data on adult body condition and chick growth rates, gives support to the idea that species or populations breeding in neritic and oceanic areas of the eastern North Atlantic Ocean may adjust the foraging behaviour differently in response to climate extremes, as already documented for opposing areas of the Pacific Ocean in response to major ENSO events (Duffy 1990).

That seabirds are able to respond to climate change by adjusting some of their key life-history traits is widely supported by the literature (Frederiksen et al. 2004, Moe et al. 2009, Weimerskirch et al. 2012, Jenouvrier et al. 2018). However, most previous studies have evaluated the effects of climate variability on breeding measures at the colony level and few tried to understand the interplay between these parameters and the individuals' at-sea behaviour or body condition. Our results are in line with Paiva et al. (2013a), confirming that individuals from Berlenga respond to decreased food availability caused by a record-breaking negative NAO (Osborn 2011), by reducing their foraging effort and spending more time at sea, with some individuals foraging in areas typically used during the initial stages of the breeding season (Paiva et al. 2013b). This decision carried a cost for themselves (poorer body condition), but also for their offspring (poorer body condition and chick linear growth rate). Interestingly, during the strong positive NAO year, individuals from the same population reversed their foraging behaviour and foraged in shallower, productive waters near the colony which led to an increased breeding performance. Positive relationships between enhanced local food availability motivated by favourable upwelling conditions and high breeding success are broadly documented for seabird species breeding in coastal upwelling systems (e.g. Simeone et al. 2002; Becker et al. 2007; Sherley et al. 2013).

Similar adverse impacts on demography and survival in response to major ENSO events have been previously demonstrated for several seabird species breeding in Indian (Ramos et al. 2006, Monticelli et al. 2007, Surman et al. 2012), Pacific (Bertram et al. 2005, Ancona et al. 2011, Champagnon et al. 2018) and Southern Oceans (Guinet et al. 1998, Inchausti et al. 2003, Le Bohec et al. 2008). In addition to variations in large-scale climatic indices, unusual extra-tropical climate events can also negatively affect seabirds' foraging behaviour and breeding performance. For example, when sea ice extent was unprecedently low in the Antarctica shelf, due to the high SST in the region, chick-rearing Southern fulmars (*Fulmarus glacialoides*) were forced to perform longer distance foraging trips in order to forage near the sea-ice edge and consequently provisioned less food to their growing offspring, which were shown to fledge in poor body condition (Jenouvrier et al. 2015). Likewise, towards northern latitudes an unusual atmospheric blocking in the Gulf of Alaska resulted in poor upwelling-favourable winds and increased SST in the California Current System, causing an unprecedented breeding failure in planktivorous Cassin's auklets (*Ptychoramphus aleuticus*) populations (Sydeman et al. 2006).

The contrasting differences in foraging behaviour and associated fitness measures, for the two areas (one neritic and one oceanic) of the Atlantic Ocean separated by approximately 2000 km is particularly relevant. Facing the same historical negative NAO event, birds from the oceanic area (Corvo) seemed to be more successful in their foraging and breeding than those from the neritic area (Berlenga). Birds from Corvo seemed to benefit from this event by investing more time foraging closer to the colony and taking advantage of the cyclonic eddies that were intense there. A similar pattern was reported for Cassin's auklets breeding in the Pacific Ocean, which exhibited high reproductive success in years of low SSH values within the birds' maximum foraging range (Wolf et al. 2009). Mesoscale eddies play an important role in the vertical and horizontal transport of nutrients in the open ocean (Stramma et al. 2013) and are important oceanographic features for marine predators and their prey (Braun et al. 2019). In particular, cyclonic eddies are known to be good indicators of oceanic upwelling since they boost primary productivity in oceanic waters by “injecting” deep-water nutrients into the euphotic zone, leading to enhanced localised biological activity in oligotrophic regions of the oceans (i.e. eddy pumping hypothesis) (Falkowski et al. 1991, McGillicuddy et al. 2007, Klein & Lapeyre 2009). Our results are in agreement with the literature suggesting that these features are used as potential foraging grounds by several marine vertebrates (Tynan 1997, Bailleul et al. 2010, Massie et al. 2016), including seabirds (Nel et al. 2001, Hyrenbach et al. 2006, Jaquemet et al. 2014).

Interestingly, in response to the strong positive NAO index, both populations of Cory’s shearwaters seemed to reverse their foraging behaviour, benefiting from the opposite regimes described before. While birds from Berlenga foraged in productive areas near the colony, individuals from Corvo travelled longer distances further North to locate their prey, which ultimately negatively affected their body condition and the growth rate of their chicks, in contrast to what was observed under the effect of an extreme negative NAO index. In the North Atlantic, anticyclonic eddies are predominantly associated with negative chlorophyll anomalies and thus low surface productivity (Gaube et al. 2014). Contrary to cyclonic eddies, in the anticyclonic circulation the nutrients are pushed farther away from the sea surface, leading to a reduction in productivity in the region (Martin 2003). The prevalence of an intense anticyclonic ocean circulation around Corvo during 2015 may explain why individuals decided to forage farther from the breeding colony, presumably looking for hotspots of marine productivity associated with cyclonic eddies which were located at northern latitudes. As cyclonic eddies are known to be favourable foraging habitats, we can hypothesise that the reason behind the use of these features may be related to the fact that zooplankton and micronekton tend to concentrate with cyclonic eddies, so they attract underwater marine predators such as tuna and cetaceans (Sabarros et al. 2009, Tew Kai & Marsac 2010, Tussadiah et al. 2018). Given that some seabirds rely heavily on associations with underwater marine predators to catch their prey, these features gain particular importance as preferential prey patches for facilitated foraging (Jaquemet et al. 2014), as already reported for Cory’s shearwaters foraging in the Azores (Martin 1986, Monteiro et al. 1996). These drastic differences verified for the population of Corvo when facing contrasting climatic scenarios, highlight the importance of ephemeral and unpredictable marine productivity for oceanic regions where the nutrients are usually more scarce and patchy distributed than in coastal areas, as already demonstrated for some seabird populations breeding in oceanic areas (Monticelli et al. 2007, Surman et al. 2012).

3.4.1. Conclusions

Overall, our results provide evidence of the ecological impacts of extreme climate events in shaping key life-history traits of pelagic seabirds and confirm the foraging plasticity of Cory's shearwaters when facing adverse environmental conditions (Paiva et al. 2013a, Avalos et al. 2017). Our results are particularly important as recent climate change modelling projections predict increases in the frequency and severity of extreme climate events in the next decades, which is likely to have negative impacts on marine predators and ecosystems (Ummenhofer & Meehl 2017, Sillmann et al. 2017). Future work should investigate the mechanisms of spatio-temporal plasticity for different seabird populations when facing extreme environmental changes. In addition, understanding why some populations, but not others, are strongly affected by variations in large-scale climatic anomalies would allow us to predict how climate change might drive population dynamics and the extinction risk of wild species (Morrison et al. 2011). Cory's shearwaters, which are wide-ranging and one of the most abundant seabird species breeding in the North Atlantic, are a suitable indicator of the global environmental changes occurring in the eastern North Atlantic, particularly in the Macaronesian biogeographical region.

3.5. Supplementary Information

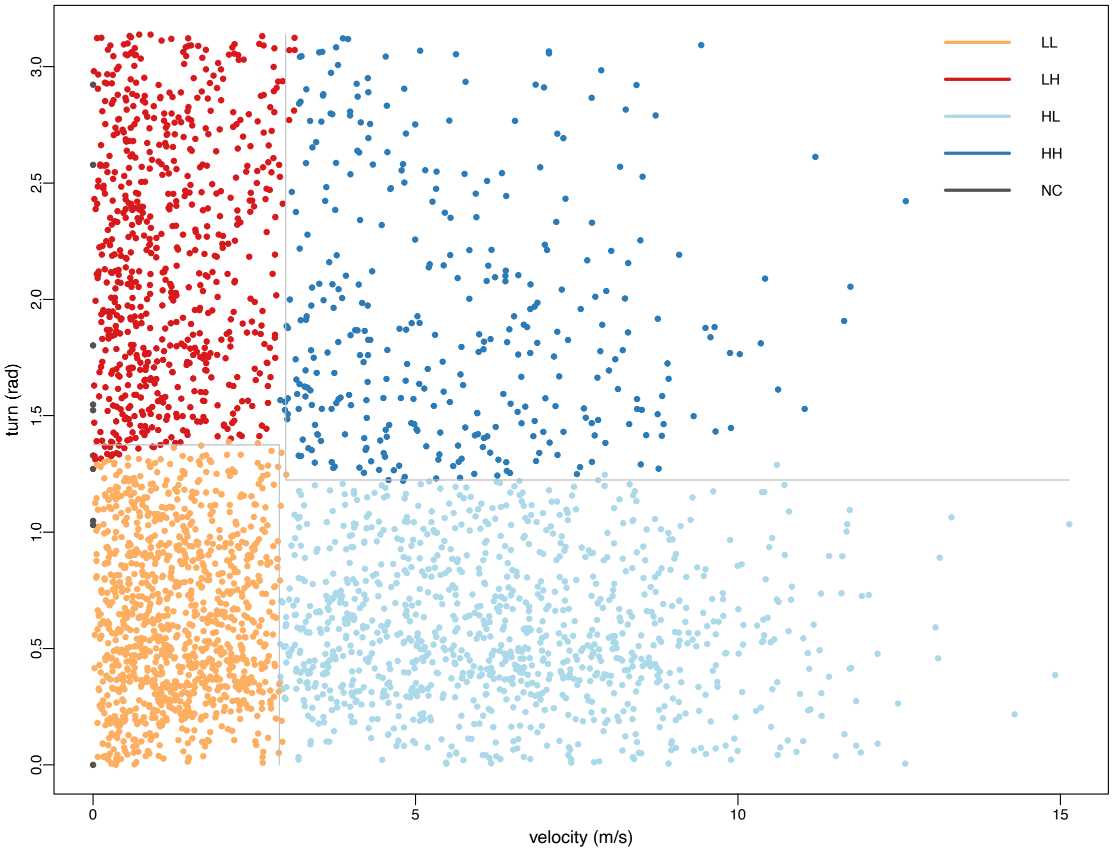

Figure S3.1: *Scatterplot of GPS positions showing the 'Expectation-Maximization binary Clustering' (EMbC) clusters in different colours: (1) (High velocity/Low turning angles [flying] – light blue; (2) High velocity/ High turning angles [extensive search] – dark blue; (3) Low velocity/ Low turning angles [resting] – yellow; and (4) Low velocity/ High turn [intensive search] – red). In addition, it is also shown the delimiters of each clustering region (light grey lines).*

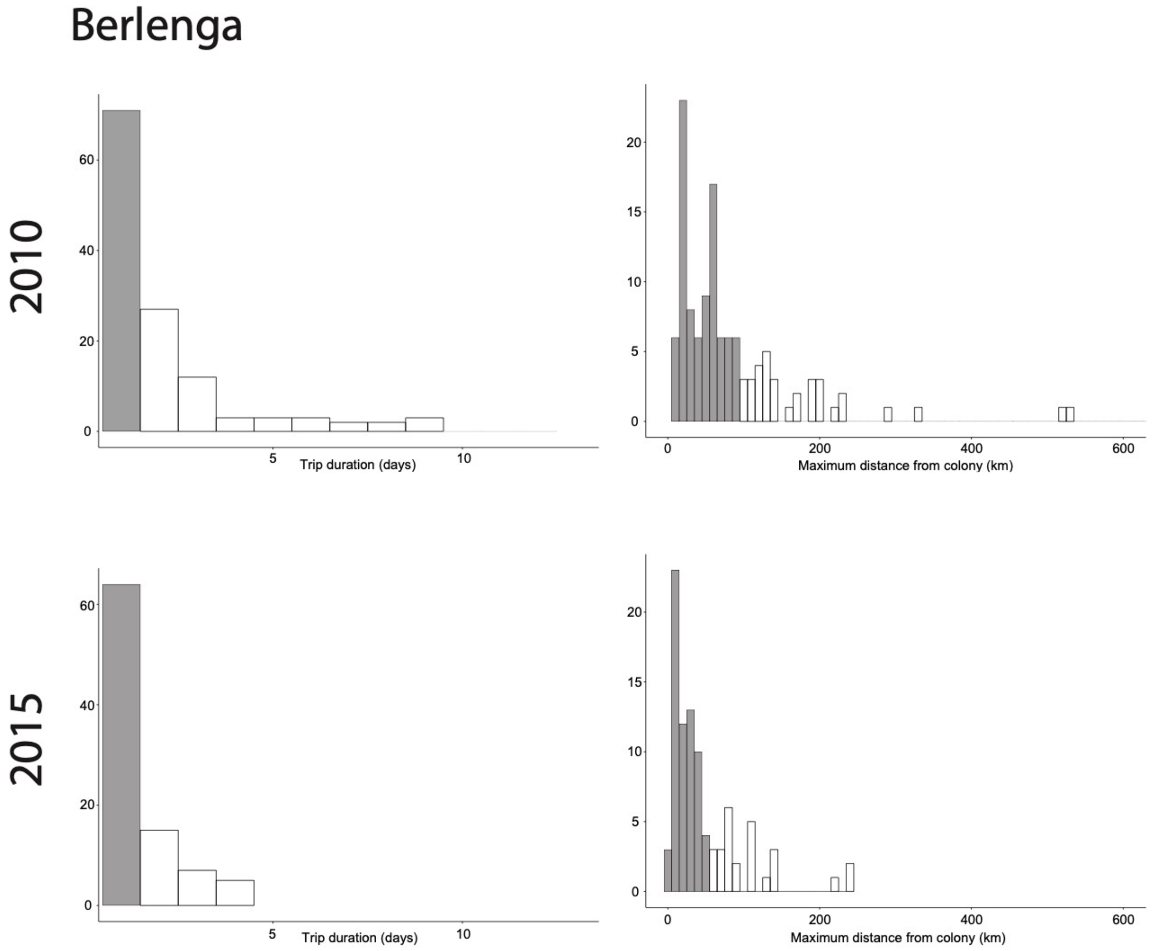

Figure S3.2: *Frequency of occurrence (counts) of trip duration (days) for birds from Berlenga, identifying short trips (≤ 1 day; grey colour) and long trips (> 1 day; white colour) during 2010 and 2015. Frequency of occurrence (counts) of maximum distances from the colony, depicting short trips (≤ 90 km; grey colour) and long trips (> 90 km; white colour) during 2010 and short trips (≤ 60 km; grey colour) and long trips (> 60 km; white colour) during 2015.*

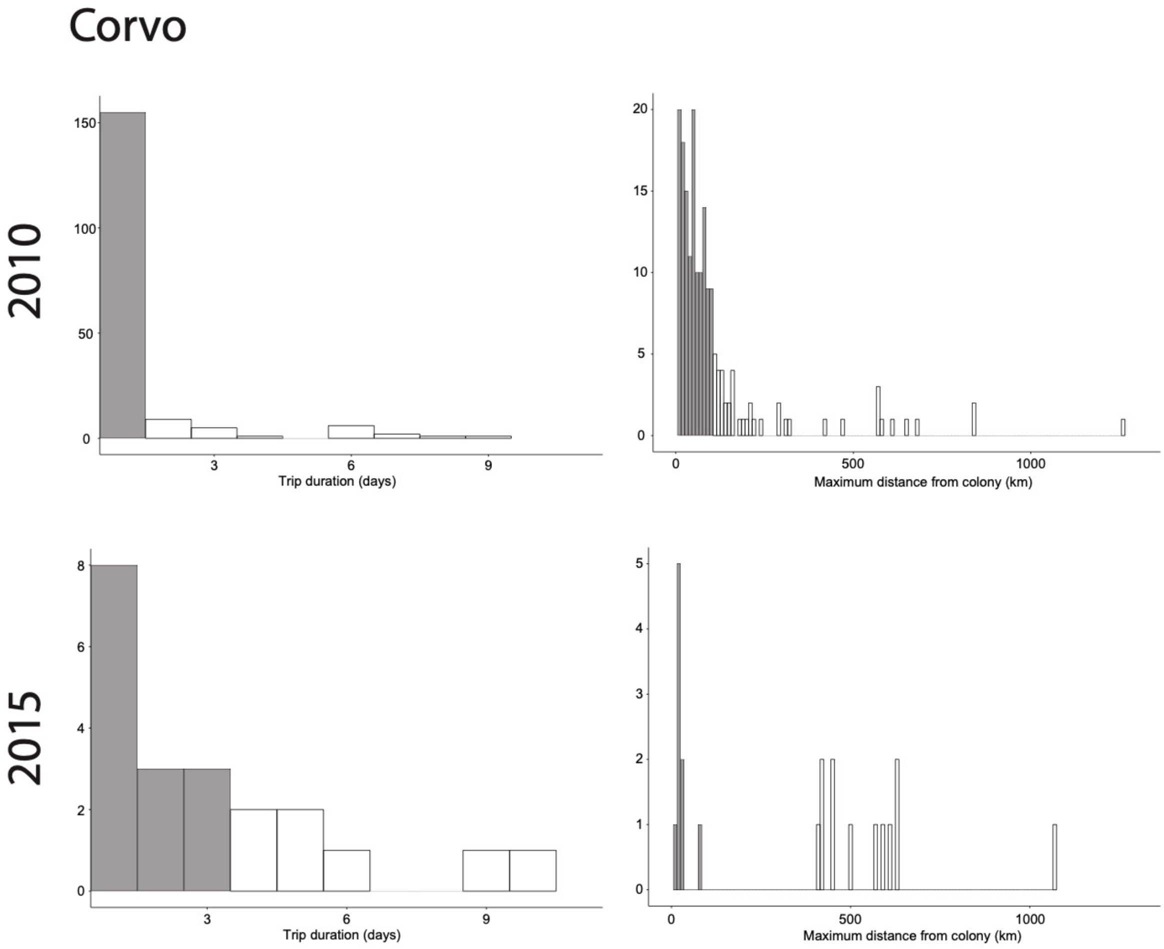

Figure S3.3: *Frequency of occurrence (counts) of trip duration (days) for birds from Corvo, identifying short trips (≤ 1 day; grey colour) and long trips (> 1 day; white colour) during 2010 and short trips (≤ 3 day; grey colour) and long trips (> 3 day; white colour) during 2015. Frequency of occurrence (counts) of maximum distances from the colony, depicting short trips (≤ 100 km; grey colour) and long trips (> 100 km; white colour) during 2010 and short trips (≤ 40 km; grey colour) and long trips (> 40 km; white colour) during 2015.*

Chapter 4

Low spatial overlap between foraging shearwaters during the breeding season and industrial fisheries off the West coast of Portugal

This chapter is published as:

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Abstract

Fisheries have impacted seabird populations worldwide, either via bycatch mortality or resource depletion. Understanding the overlap between seabird distributions and fisheries is an important element for bycatch risk assessment, though the drivers of variation in seabird–fishery overlap are not well understood for some seabird populations. Here, we quantified the spatial overlap between foraging Cory's shearwaters (*Calonectris borealis*) during the breeding season and industrial fisheries operating within the mainland Exclusive Economic Zone (EEZ) of Portugal. In addition, we evaluated whether overlap varied as a function of an individual's boldness, sex or breeding stage. For this, we GPS tracked 361 foraging trips by 72 Cory's shearwaters nesting at Berlenga Island, Portugal, over 5 consecutive breeding seasons (2012-2016). Simultaneously, we used fishing effort data from Global Fishing Watch detailing the distribution of industrial fisheries within the temporal and spatial range of Cory's shearwater tracks. Although fishing vessels were present during 88.1% of foraging trips, Cory's shearwaters spent only on average 13.3% of the time foraging in the same areas as fisheries. Such low spatial overlap is likely driven by high prey availability near the colony and suggests low direct competition for resources. We also found variation in overlap with fisheries across the breeding period, with Cory's shearwaters spending approximately 11% more time foraging in the same areas as fixed gear and purse seine vessels during pre-laying than during chick-rearing. Surprisingly, no sex or boldness-related differences were found in the overlap with any fishing gear. Our findings have implications for understanding within-population variations in the overlap between fisheries and seabirds and, in turn, bycatch risk.

Keywords: Boldness, Bycatch risk, Cory's shearwater, *Calonectris borealis*, Global fishing watch, Fixed gear, Purse seine, Seabird.

4.1. Introduction

Seabirds and fisheries have coexisted for centuries (Coleridge 1895). Long before industrial fisheries, seabirds provided fishermen with visual cues of fish aggregation (Coleridge 1895, Le Bot et al. 2018) and also fed on food subsidies generated during fishing operations (Garthe et al. 1996, Votier et al. 2004, Bicknell et al. 2013, Sherley et al. 2020). Such interactions make seabirds susceptible to becoming bycatch (Furness 2003, Anderson et al. 2011), although risk varies both among and within species (Torres et al. 2011, Votier et al. 2013, Granadeiro et al. 2014, Patrick et al. 2015, Collet et al. 2017, Genovart et al. 2018).

Studies of seabird−fishery overlap reveal much intra-population variation, such as by sex and age (reviewed in Gianuca et al. 2017), but this overlap may also vary depending on other life-history traits for which we lack a mechanistic understanding, such as individual ‘personality’ or boldness (Patrick & Weimerskirch 2014, Patrick et al. 2015). Boldness is an important individual behavioural trait, measured by whether and how individuals consistently respond to stimuli, which has important evolutionary and ecological consequences (Wolf & Weissing 2012). Boldness has previously been shown to be consistent within individuals (Dingemanse et al. 2002, Bell et al. 2009) and heritable in a variety of taxa (Sinn et al. 2006, Dochtermann et al. 2015, Winney et al. 2018), including pelagic seabird species (Patrick et al. 2013). Recent research shows that a significant amount of variation in seabird distribution and foraging behaviour can be explained by individual boldness (Patrick & Weimerskirch 2014, Krüger et al. 2019, Harris et al. 2020). For instance, shy seabirds may be more ‘explorative’, dispersing farther from the colony to forage after being displaced by bold individuals which remain close to the colony (Patrick & Weimerskirch 2014).

To our knowledge, only one study has addressed the influence of seabird individual boldness on overlap with fisheries, reporting no effect of boldness on overlap with longline fisheries operating in the Indian Southern Ocean in Black-browed albatrosses (*Thalassarche melanophris*) (Patrick & Weimerskirch 2014). However, the authors suggest boldness may impact overlap in populations where fishing activity and seabirds co-occur in the colony surroundings, which was not the case in their study. Thus, we may expect that overlap with fisheries should increase with increasing boldness, because competition for food resources may be particularly intense near fishing vessels or in areas of high fishing activity (Arcos et al. 2001). Understanding whether bolder individuals are more likely to be exposed to bycatch risk could be important in the context of quantifying the impacts of fisheries on demography and reproductive measures. This is particularly relevant if increasing boldness is associated with higher parental investment and offspring survival, which has been shown for a variety of species (Smith & Blumstein 2008, Patrick & Weimerskirch 2015).

Procellariiformes may be particularly threatened by fisheries (Tasker et al. 2000, Croxall et al. 2012). In the western Mediterranean, shearwaters are at high risk of becoming bycatch on longline fishing vessels (Cortés et al. 2017), especially Scopoli's shearwaters (*Calonectris diomedea*) (Belda & Sánchez 2001, Barcelona et al. 2010, Báez et al. 2014). This species is known to follow fishing vessels (Soriano-Redondo et al. 2016), and to attend trawlers and longline fishing vessels in higher numbers than expected by chance (Louzao et al. 2011a), particularly adult males during the breeding period (Laneri et al. 2010, Genovart et al. 2017, Cortés et al. 2018). However, in contrast to the western Mediterranean, this species was recently shown to exhibit limited interaction with fishing vessels in the central Mediterranean (Cianchetti-Benedetti et al. 2018). Furthermore, our understanding of the overlap between *Calonectris* populations breeding outside the Mediterranean and fisheries is limited, including for the abundant Cory's shearwater (*Calonectris borealis*) populations in the Atlantic Ocean. Previous studies have demonstrated that few Cory's shearwaters attend fishing vessels or are caught in fishing gear during breeding off the West Iberian Peninsula (Valeiras 2003, Oliveira et al. 2015, Calado et al. 2020), or the non-breeding period in the Southwest Atlantic (Bugoni et al. 2008, 2010). However, these studies relied almost exclusively on onboard observations from artisanal fishing vessels operating in nearshore waters (up to 20 km off the coast), and little is known about the at-sea overlap of Cory's shearwaters with industrial fishing fleets.

Here, by combining fine-scale data from bird- borne GPS trackers with data on the spatial distribution of gear-specific fishing effort, we were able to quantify the extent to which Cory's shearwaters overlap with fisheries of different gear types during the pre-laying and chick-rearing periods over 5 breeding seasons (2012−2016). Spatial overlap does not necessarily imply interaction, but it is commonly used as a proxy for potential exposure to fishing gear and increasing bycatch risk (Le Bot et al. 2018). In addition, we also explored the extent to which such spatial overlap is influenced by boldness, breeding stage and sex. We made the following predictions: (1) because Cory's shearwaters exhibit shorter foraging trips during chick-rearing (Paiva et al. 2010c, Ceia et al. 2014b), we expected higher overlap with coastal fisheries during this stage than during pre-laying, when the species usually has a more pelagic range (Paiva et al. 2013b); and (2) because fishing activity and breeding seabirds co-occur close to the colony in our study area, we expect males and bolder individuals to overlap more with coastal fisheries independent of breeding stage, as they may be able to outcompete females and shy individuals for fishery-related resources (Paiva et al. 2017, Krüger et al. 2019).

4.2. Methods

4.2.2. GPS tracking and data preparation

We used global positioning system (GPS) loggers (IgotU GT-120, Mobile Action Technology) to track foraging trips of Cory's shearwaters breeding at Berlenga Island, Portugal (39°23′ N, 9°36′ W) during pre-laying (April−May) and chick-rearing (August−September) periods from 2012 to 2016. The period of deployment was similar across years: between 5 May and 7 June for pre-laying and between 31 August and 21 September for chick-rearing. Each device was sealed with heat-shrink tubing to make it waterproof and programmed to record positions at 5 min intervals. GPS devices with heat-shrink tubing weighed approximately 17 g, which was 2.9% of the body mass of the lightest bird tagged. Previous studies found no effects of similar GPS devices on foraging behaviour, body mass change or fledging success in breeding Cory's shearwaters (Passos et al. 2010, Paiva et al. 2010b c, Villard et al. 2011). GPS loggers were attached using TESA® tape to the bird's back feathers following Wilson et al. (1997). Birds were captured on their nests at night and individually identified by their ring numbers. Each bird was sexed according to bill measurements and vocalisations (Granadeiro 1993). The handling process did not exceed 10 min and birds were released back into the breeding burrow to minimise stress.

Details of sample sizes and tracking period for each stage of breeding and study year are given in Table 4.1.

Tracking data were first filtered to remove positions within a 1 km radius of the colony. This buffer was used to reduce the influence of rafting behaviour close to the colony, which often occurs at sunset before the birds return to their nests at night (Weimerskirch et al. 2020b). In addition, by using this buffer we were able to identify individual foraging trips and calculate the following metrics: (1) trip duration; (2) cumulative distance travelled between all position (hereafter trip length); (3) maximum distance from the colony; and (4) percentage of short trips *vs* percentage of long trips. Short and long trips were distinguished based on histograms of the frequency of occurrence of (1) trip duration (days) and (2) maximum distance from the colony on each foraging trip (km). During both pre-laying and chick-rearing, short trips were defined as ≤1 day and ≤100 km and long trips as >1 day and >100 km (Fig. 4.2).

4.2.2. Behavioural classification

To characterise the foraging behaviour for each trip, we classified each GPS position as one of 4 behavioural states using the *'Expectation-Maximization binary Clustering'* method implemented in the R package EMbC (Garriga et al. 2016). The 4 states were as follows: (1) travelling (high velocity, low turning angles); (2) extensive search (high velocity, high turning angles); (3) intensive search (low velocity, high turning angles); and (4) resting (low velocity, low turning angles) (Louzao et al. 2014). This technique has previously been used to interpret ecologically meaningful behaviours from movement data in a variety of Procellariforms (de Grissac et al. 2017, Clay et al. 2019a, De Pascalis et al. 2020), including exploring behavioural differences between different populations of shearwaters (Weimerskirch et al. 2020b, Pereira et al. 2020). We further calculated the percentage of time individuals spent in each behavioural state during each foraging trip.

4.2.3. Boldness tests and analysis

Boldness of individual Cory's shearwaters was measured as the degree of response and/or aggression of individuals towards a novel object (2015-2018). This methodology has been used effectively in other seabirds (Grace & Anderson 2014, Patrick & Weimerskirch 2014, Harris et al. 2020), including Cory's shearwaters (Krüger et al. 2019). The novel object (an LED headlamp, 6.2 × 4.0 × 3.5 cm, ~70 g; Lighting EVER®) attached to a Campark Action HD waterproof camera (6.0 × 2.5 × 4.0 cm, ~77 g; Campark®) was placed in the nest entrance for approximately 2 min and the bird's response filmed (See Fig. S4.1 in the Supplementary Information). Because boldness can be influenced by the presence of another bird, tests were conducted when only one adult was present. After the test was complete, birds were taken from the nest to be identified by ring number.

Repeated tests were conducted on different days whenever possible, for a total of 314 videos of 124 individuals: 49 individuals were tested once, 22 were tested twice, 33 were tested 3 times, 7 were tested 4 times, 7 were tested 5 times, 4 were tested 6 times and 2 were tested 8 times. The full field protocol for boldness tests and video analysis is described in detail by Krüger et al. (2019). We applied non-metric multidimensional scaling (NMDS) to assign the recorded behaviours (See Table S4.1 in the Supplementary Information) along a boldness/shyness gradient using the R package *'vegan'* (Oksanen et al. 2013). To obtain a single estimate of boldness per individual we used scores from the first NMDS axis (See Table S4.2 in the Supplementary Information). Individuals were characterised as bold (lower values on the first NMDS axis) or shy (higher values on the first NMDS axis) based on the behaviours displayed (See Fig. S4.2 in the Supplementary Information). Fewer movements or non-aggressive behaviour to the object (e.g. twitching, moving head or blinking eyes) indicated shyer individuals, whereas agitated behaviours and more interactions with the object (e.g. pecking, protecting the egg or the chick, moving towards the object) indicated bolder individuals. Boldness was previously shown to be consistent within individuals and not influenced by sex in our study population of Cory's shearwaters Krüger et al. (2019).

4.2.4. Overlap of foraging shearwaters and fisheries

Raster files detailing the daily distribution of fishing effort (in hours) were downloaded from Global Fishing Watch (http://globalfishingwatch.org/) at a 0.01° grid cell resolution (approximately 1 km) for every day during 2012-2016. Global Fishing Watch is an open access global database that uses remote sensing and convolutional neural networks to classify the activity of vessels larger than 15 m as fishing or not fishing (Kroodsma et al. 2018). We downloaded data on 3 fishing gear types: (1) fixed gear; (2) purse seiners; and (3) trawlers. Fixed gear encompasses pots and traps, set gillnets and set longlines.

To quantify the spatial overlap of fisheries with tracked birds, we only included fishing effort data collected from the temporal and spatial extent of Cory's shearwater tracking data. Secondly, we grouped the subset of daily rasters as the mean fishing effort at a 10 × 10 km grid resolution within the study area. This grid cell size was chosen following the methodological considerations used in previous studies quantifying the large-scale overlap between fishing effort and foraging shearwaters during the breeding season (Waugh et al. 2016, Carle et al. 2019), and because this resolution allows fishing effort data to be grouped without losing much spatial detail (Genovart et al. 2018). This design also allows us to compare our results with those of studies on similar shearwater species breeding elsewhere. Next, we extracted fishing effort (if any) only for the GPS positions where Cory's shearwaters engaged in intensive foraging behaviour (i.e. each GPS position was associated with the corresponding daily fishing effort in the 10 × 10 km grid cell). GPS position where Cory's shearwaters were classified as travelling, extensive search and resting were excluded from the overlap analysis. Lastly, we quantified the relative Cory's shearwater- fishery overlap per trip by calculating: (1) percentage of time overlapping with fishing vessels and (2) fishing effort in foraging areas.

***Table 4.1:** Tracking period and number of tracked Cory's shearwaters (Calonectris borealis) (number of foraging trips) during pre-laying and chick-rearing for each year of the study (2012−2016).*

Pre-laying	**2012**	**2013**	**2014**	**2015**	**2016**	**Total**
Tracking period	9 - 28 May	10 - 25 May	5 - 22 May	12 May - 1 June	24 May - 7 June	-
N of total tracked Cory's shearwaters	12	8	9	7	10	46
N of tracked Cory's shearwaters with known sex and boldness (N trips)	6 (25)	4 (21)	1 (2)	5 (25)	8 (22)	24 (95)
N males (N trips)	6 (25)	3 (20)	1 (2)	4 (24)	6 (16)	20 (87)
N females (N trips)	0	1 (1)	0	1 (1)	2 (6)	4 (8)

Chick-rearing	**2012**	**2013**	**2014**	**2015**	**2016**	**Total**
Tracking period	4 - 19 September	8 - 21 September	3 - 15 September	2 - 12 September	31 August - 12 September	-
N of total tracked Cory's shearwaters	9	9	8	18	16	60
N of tracked Cory's shearwaters with known sex and boldness (N trips)	6 (51)	8 (43)	6 (35)	15 (75)	13 (62)	48 (266)
N males (N trips)	5 (41)	6 (36)	5 (29)	8 (43)	6 (30)	30 (179)
N females (N trips)	1 (10)	2 (7)	1 (6)	7 (32)	7 (32)	18 (87)

4.2.5. Effect of boldness, sex and breeding stage on overlap with fisheries

To investigate the effect of boldness, breeding stage and sex on the overlap with fisheries, we modelled the percentage of time overlapping with fishing vessels and fishing effort in foraging areas as response variables in linear mixed models (LMMs). Response variables were inspected for normality and homogeneity before each statistical test and transformed when necessary. The fishing effort in foraging areas was standardised (observation – mean / standard deviation), while the percentage of time overlapping with fishing vessels was arcsine-transformed to meet parametric assumptions. We did not test for an interaction between sex and breeding stage due to an unbalanced sex ratio, especially during the pre-laying period (Table 4.1). Trip identity nested within individual ID and study years (2012-2016) were fitted as random effects to account for multiple trips per individual and the effects of environmental variation and irregular sampling. LMMs were also used to test for differences in trip metrics (i.e. trip duration, trip length, maximum distance from the colony and percentage of short trips) and behaviour during foraging trips (i.e. time spent in each behavioural state) between individuals of varying boldness, breeding stage and sex. LMMs were computed using the R packages *'lme4'* (Bates et al. 2015) and *'lmerTest'* (Kuznetsova et al. 2017). All statistical analyses were conducted in R v.3.6.2 (R Core Team 2018). All data are presented as mean ± SD (standard deviation). Differences were considered statistically significant when *p*-value ≤ 0.05.

4.3. Results

4.3.1. Foraging trip characteristics

Overall, we recorded 361 foraging trips made by 72 adult Cory's shearwaters of known sex over 5 breeding seasons (Fig. 4.1): 24 Cory's shearwaters were tracked during pre-laying (95 trips) and 48 during chick-rearing (266 trips). We collected tracking data from 22 females and 50 males over both breeding stages combined (Table 4.1). Sex ratio was more skewed towards males during pre-laying (20 males vs. 4 females) than during chick-rearing (30 males *vs* 18 females). Foraging trips differed between breeding stages (Fig. 4.1), with trip duration (mean ± SD: 2.2 ± 3.4 *vs* 1.6 ± 1.1 days; $F_{4,356}$ = 3.82, *p*-value= 0.05), trip length (61.0 ± 135.0 *vs* 31.1 ± 45.0 km; $F_{4,356}$ = 7.71, *p*-value= 0.001), maximum distance from colony (112.7 ± 241.9 *vs* 58.2 ± 71.5 km; $F_{4,356}$ = 10.69, *p*-value= 0.001), percentage of time spent in intensive search (31.0 ± 15.8 *vs* 22.5 ± 8.8 %; $F_{4,\ 356}$ = 18.88, *p*-value= 0.001) and percentage of time spent resting (29.6 ± 11.2 *vs* 23.2 ± 10.9%; $F_{4,356}$ = 12.72, *p*-value= 0.001) all higher during pre-laying than chick-rearing. Although Cory's shearwaters made significantly higher foraging effort during the pre-laying period, individuals made mainly short trips in both breeding stages (pre-laying: 78.9% short trips *vs* chick-rearing: 64.3%) (Fig. 4.2). Trip metrics and behaviour during foraging trips were not influenced by sex (all models: *p*-value > 0.07) or by boldness (all models: *p*-value > 0.15).

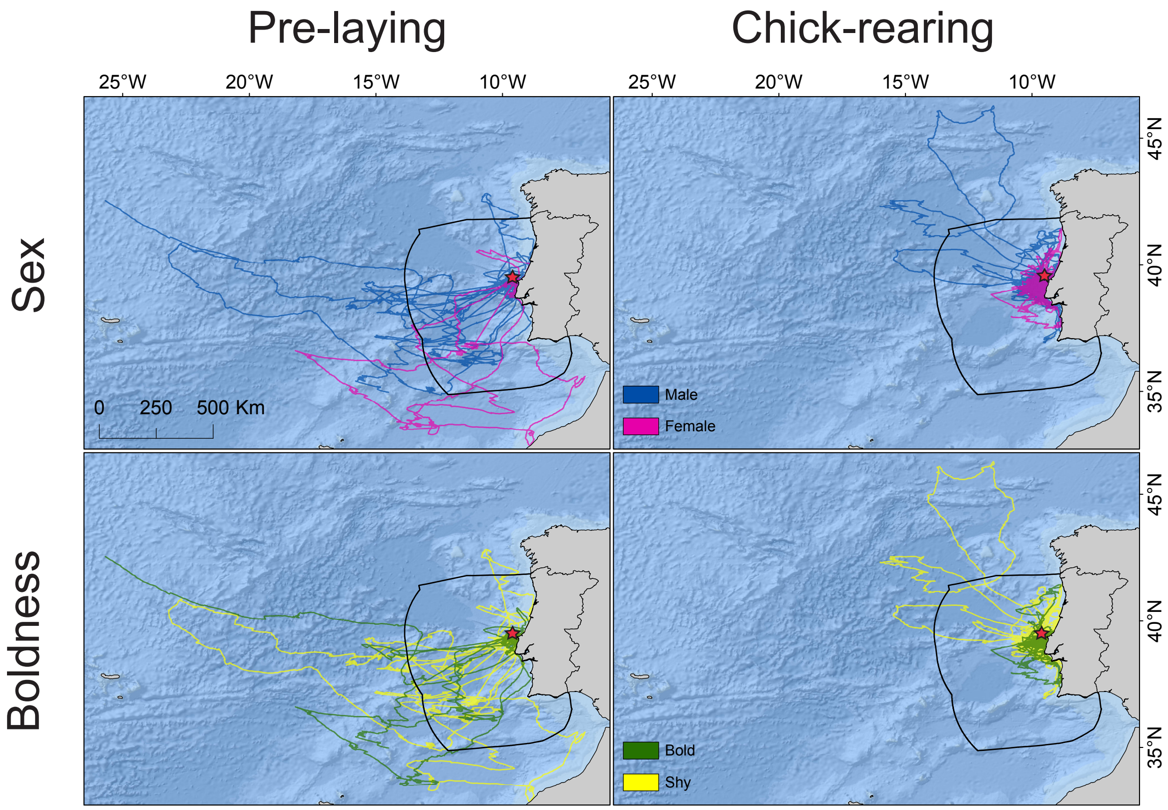


Figure 4.1: *Foraging range for Cory's shearwaters (Calonectris borealis) breeding at Berlenga Island, Portugal (red star) in relation to breeding stage (pre-laying vs chick-rearing), sex (males vs females) and boldness (bold vs shy) over 5 consecutive breeding seasons (2012-2016), overlaid on bathymetry of the region (where darker blue indicates increasing depth). Black solid line represents the Portuguese Exclusive Economic Zone (EEZ).*

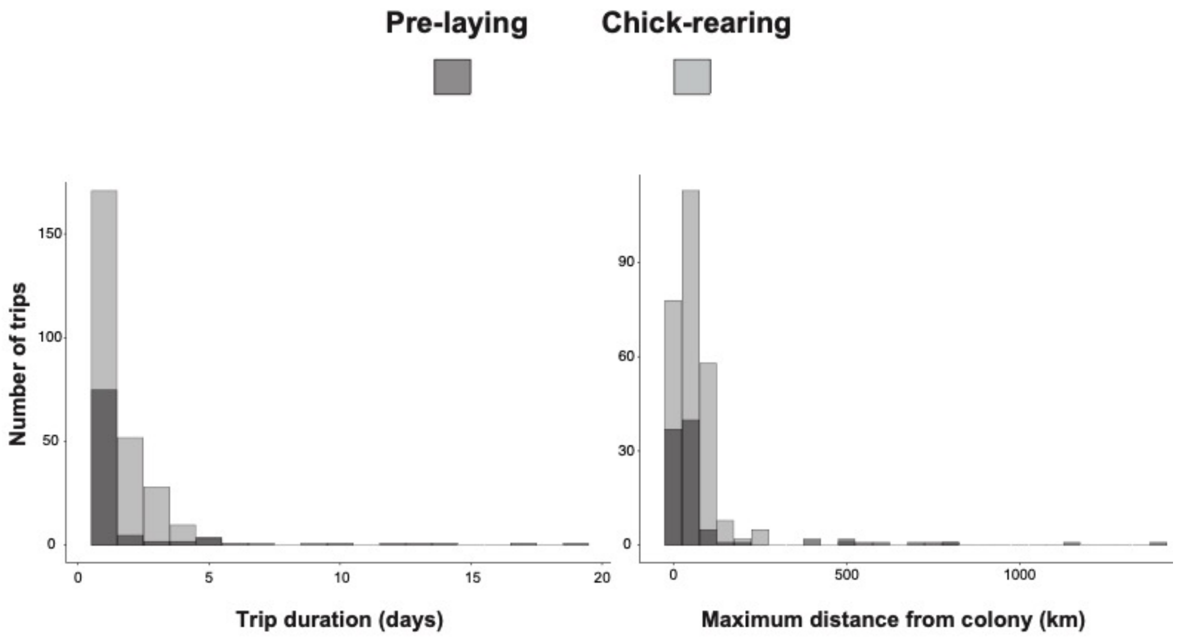


Figure 4.2: *Frequency of occurrence (number of trips) by trip duration (days) and maximum distance from the colony (km) during pre-laying and chick-rearing periods. For both breeding stages, short trips were defined as ≤1 day and ≤100 km and long trips as >1 day and >100 km.*

4.3.2. Drivers of variation in overlap with fisheries: effect of boldness, breeding stage and sex

We found that foraging Cory's shearwaters overlapped with fisheries at least once in 318 of the 361 trips (88.1 %): 256 trips (70.9 %) with fixed gear, 285 trips (78.9 %) with purse seiners and 236 trips (65.4 %) with trawlers. Overall, more trips where Cory's shearwaters and fisheries overlapped occurred during chick-rearing (78.3 %) than during pre-laying (21.7 %) (Fig. 4.3). Moreover, all the trips where overlap occurred were within the Portuguese Exclusive Economic Zone (EEZ); 93.1% of trips were within a radius of 100 km of the colony and 84.3% of trips were within a radius of 50 km (Fig. 4.3). Although fishing vessels were present on most foraging trips, Cory's shearwaters only spent on average 13.3% of their foraging time in the same area as fishing vessels within the Portuguese EEZ. The percentage of time overlapping with fishing vessels was relatively similar for all gear types: 17.9% of their time was spent in the same area as fixed gear, 14.1% as purse seine vessels and 7.3% as trawlers. Similarly, the fishing effort in foraging areas was also relatively similar for all gear types: fixed gear spent 0.70 hours in Cory's shearwater foraging areas, purse seine vessels spent 0.65 hours and trawlers spent 0.76 hours. Percentage of time Cory's shearwaters spent foraging in the same areas as fixed gear and purse seine vessels differed between breeding stages, with relatively higher overlap occurring during pre-laying (27.2% and 22.5%, respectively) than during chick-rearing (16.0% and 11.5%, respectively) (Table 4.2). This represents a variation in the overlap of approximately 11% for both fishing gears. Neither the percentage of time overlapping with fishing vessels nor the fishing effort in foraging areas were influenced by boldness, sex or the interaction of these factors with gear type (Table 4.2)

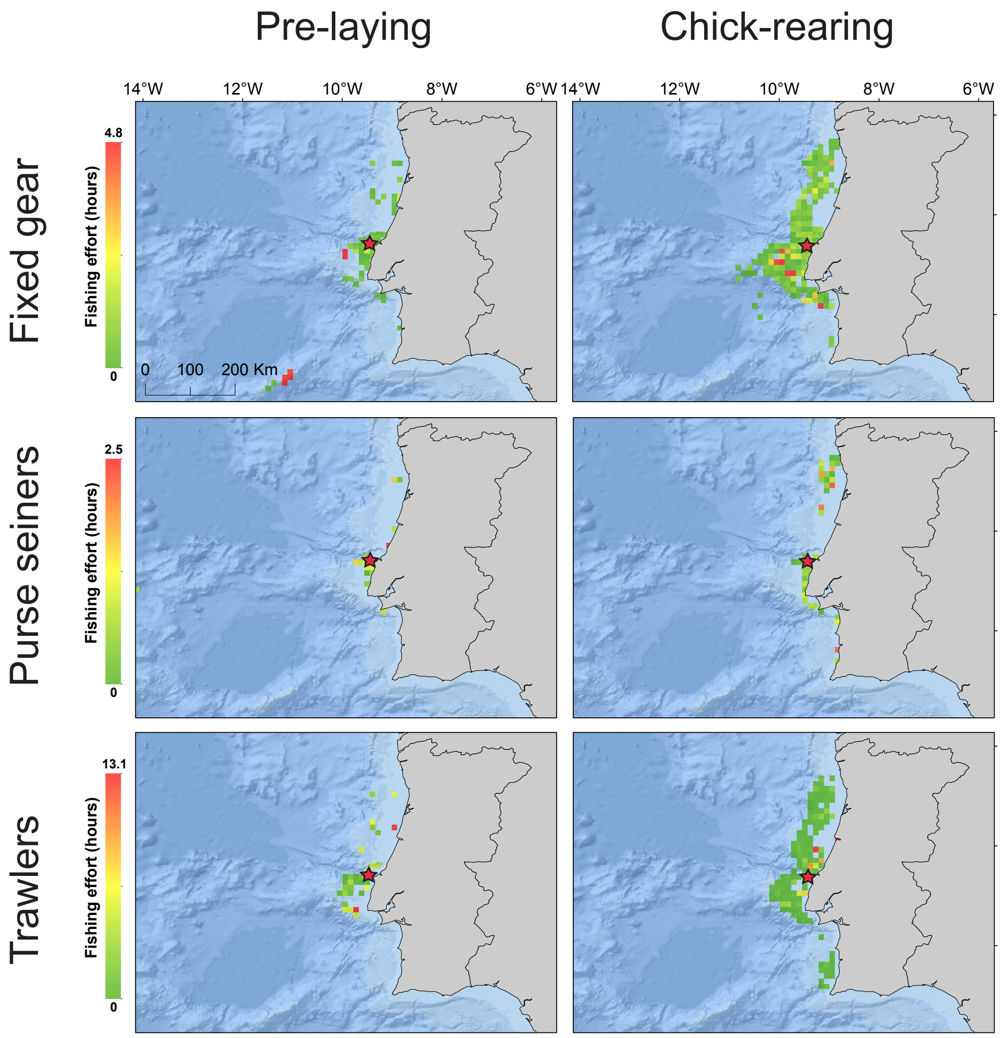


Figure 4.3: *Extent of overlap between foraging Cory's shearwaters breeding at Berlenga Island (red star) and industrial fishing vessels along the Portuguese coast during the pre-laying and chick-rearing periods. Values are calculated as the average number of fishing hours fixed gear vessels, purse seiners and trawlers spent in the same area as foraging shearwaters at a resolution of 10 × 10 km grid cells. Fishing effort is overlaid on bathymetry of the region (where darker blue indicates increasing depth. Fixed gear includes pots and traps, set gillnets and set longlines.*

Table 4.2: *Results of linear mixed models (LMMs) testing the effects of boldness (bold vs shy), breeding stage (pre-laying [PL] vs chick-rearing [CR]) and sex (male vs female) on the percentage of time shearwaters spent foraging in the same area as fisheries and the average number of hours fixed gear, purse seiners and trawlers spent fishing in Cory's shearwater foraging areas. Fixed gear included pots and traps, set gillnets and set longlines. Each model included trip identity nested within individual ID and study years (2012–2016) as a random term. Differences were considered statistically significant when p-value ≤ 0.05 (in **bold**).*

	Percentage of time overlapping with fishing vessels				Fishing effort in foraging areas			
Fishing gear	**Fixed effects**	**LMM**	***p*-value**	**Effect**	**Fixed effects**	**LMM**	***p*-value**	**Effect**
Fixed gear	Boldness	$F_{4,251}$= 0.11	0.74		Boldness	$F_{4,251}$= 0.35	0.56	
	Breeding stage	$F_{4,251}$= 11.70	**< 0.001**	PL > CR	Breeding stage	$F_{4,251}$= 1.43	0.23	
	Sex	$F_{4,251}$= 4.07	0.06		Sex	$F_{4,251}$= 1.37	0.25	
	Boldness x Sex	$F_{4,251}$= 0.01	0.96		Boldness x Sex	$F_{4,251}$= 0.51	0.51	
Purse seiners	Boldness	$F_{4,280}$= 0.02	0.90		Boldness	$F_{4,280}$= 0.01	0.99	
	Breeding stage	$F_{4,280}$= 15.62	**< 0.001**	PL > CR	Breeding stage	$F_{4,280}$= 2.49	0.12	
	Sex	$F_{4,280}$= 2.59	0.11		Sex	$F_{4,280}$= 2.80	0.11	
	Boldness x Sex	$F_{4,280}$= 0.01	0.99		Boldness x Sex	$F_{4,280}$= 0.20	0.65	
Trawlers	Boldness	$F_{4,231}$= 0.91	0.34		Boldness	$F_{4,231}$= 2.86	0.10	
	Breeding stage	$F_{4,231}$= 0.08	0.78		Breeding stage	$F_{4,231}$= 0.16	0.69	
	Sex	$F_{4,231}$= 0.20	0.66		Sex	$F_{4,231}$= 0.01	0.94	
	Boldness x Sex	$F_{4,231}$= 2.20	0.14		Boldness x Sex	$F_{4,231}$= 0.54	0.54	

4.4. Discussion

In this study, we investigated whether foraging Cory’s shearwaters spatially overlapped with fisheries over 5 consecutive breeding seasons and whether overlap varied as a function of boldness, sex and breeding stage. Our findings suggest that despite the high density of fishing vessels within the mainland EEZ of Portugal, Cory’s shearwaters spent little time foraging in the same areas as fisheries during the breeding season. In contrast to our predictions, Cory's shearwaters spent more time foraging in the same areas as fixed gear and purse seine vessels during pre-laying than during chick-rearing. Moreover, we found no evidence of boldness or sex differences in the overlap with fishing vessels. Below we discuss the potential reasons that foraging Cory’s shearwaters show little overlap with fishing vessels within Portuguese national waters and explain the drivers of variation in overlap with fisheries.

4.4.1. Overlap of breeding Cory’s shearwaters and fisheries in the mainland EEZ of Portugal

Overlap analysis revealed that although fishing vessels were present in most foraging trips occurring within the mainland EEZ of Portugal, Cory’s shearwaters rarely foraged in the same areas as fisheries, regardless of gear type. Our results contrast with those reported for other species of shearwaters breeding in areas of intense fishing pressure, where competition for food resources is expected to be higher. For instance, breeding Pink-footed shearwaters (*Ardenna creatopus*) were shown to extensively overlap with industrial purse seine fishing fleets targeting small pelagic fish off the West coast of Chile (Carle et al. 2019). Nevertheless, our findings are in line with recent studies finding low spatial overlap or few encounters between a wide range of seabird species and fishing vessels (Sztukowski et al. 2017, Cianchetti-Benedetti et al. 2018, Grémillet et al. 2019, Clark et al. 2020, Bonnet-Lebrun et al. 2020). Cianchetti-Benedetti et al. (2018) found that Scopoli’s shearwaters breeding in the central Mediterranean exhibited limited interaction with fishing vessels during chick-rearing, in contrast to patterns observed in other populations of the same species in the western Mediterranean (Soriano-Redondo et al.

2016). The authors suggested that this limited overlap may indicate that Scopoli's shearwaters prefer to exploit "natural" high-quality prey during the breeding period, when food is plentiful in the area, rather than scavenge for low-quality prey discarded during fishing operations. Similar results were reported for Northern gannets (*Morus bassanus*) in Iceland, with a low overlap with fisheries and preference to forage on "natural" prey (Clark et al. 2020) and Cape gannets (*Morus capensis*), which only foraged in association with industrial fisheries when numbers of pelagic fish were low near the breeding colony (Tew Kai et al. 2013).

Despite the variation in foraging effort across breeding stages, the majority of Cory's shearwaters in our study made mainly short trips, both in duration and length. The prevalence of short trips indicates conditions of high prey availability near the breeding colony, as demonstrated in previous studies (Paiva et al. 2017). The West coast of the Iberian Peninsula is characterised by a strong April-September upwelling (matching Cory's shearwaters' breeding period), which provides optimal conditions for aggregations of large pelagic fish populations (Sousa et al. 2008), including some of the main prey of Cory's shearwaters such as European pilchard (*Sardina pilchardus*), horse mackerel (*Trachurus trachurus*), Atlantic mackerel (*Scomber scombrus*), European anchovy (*Engraulis encrasicolus*) and garfish (*Belone belone*) (Paiva et al. 2010e, Alonso et al. 2012). Thus, we suggest that Cory's shearwaters breeding off the West coast of Portugal are likely to be influenced by the high prey availability near the colony, and can feed on "natural" prey, rather than lower quality prey discarded by fishing vessels. To some extent, this was confirmed by onboard observations from artisanal fishing vessels operating along the West coast of the Iberian Peninsula showing that few Cory's shearwaters were seen attending fishing vessels and the species was rarely recorded as bycatch during the breeding period (Valeiras 2003, Oliveira et al. 2015, Calado et al. 2020).

4.4.2. Drivers of variation in the overlap with fisheries

We found some variation in the overlap between Cory's shearwaters and fisheries across the breeding period. Contrary to our predictions, Cory's shearwaters spent relatively more time foraging in the same area as fixed gear and purse seine vessels during pre-laying than during chick-rearing. While the evidence is circumstantial and supported only by the overlap results, we suggest that individuals are likely to exhibit higher behavioural plasticity in the use of foraging habitats early in the breeding season because they are less constrained by breeding duties (Paiva et al. 2010b, 2013b, Quillfeldt et al. 2019). Thus, birds might follow fishing vessels or use fishing areas during pre-laying, which ultimately enhances bycatch exposure during this period. A comparably higher overlap with longline fisheries during the pre-breeding or incubation period, and likely higher reliance on fishery-related resources, was also observed for Flesh-footed shearwaters (*Puffinus carneipes*) in New Zealand (Thalmann et al. 2009, Reid et al. 2012). The only other study to examine the link between boldness of a seabird population and fisheries distribution found that neither sex nor boldness of Black-browed albatrosses influenced their overlap with longline fisheries operating in the Indian Southern Ocean (Patrick & Weimerskirch 2014). However, the authors suggested that differences in overlap with fisheries may occur only in systems where fishing activity and breeding seabirds co-occur in the colony surroundings, as is the case in our study population (Patrick & Weimerskirch 2014). Similar to Patrick & Weimerskirch (2014), we found no sex or boldness-related effects on the overlap between foraging Cory’s shearwaters during the breeding season and industrial fishing vessels operating within the Portuguese EEZ. We also found no influence of sex or boldness on trip metrics or at-sea foraging behaviour. Previous tracking studies reported no sexual segregation in foraging strategies or evidence for competitive exclusion in Cory’s shearwaters (Magalhães et al. 2008, Navarro & González-Solís 2009, Paiva et al. 2010e), except during periods of unfavourable environmental conditions and likely lower prey availability (Paiva et al. 2017, Krüger et al. 2019). Most of the tracking datasets used in this study were collected in years of good environmental conditions and likely higher prey availability. We suggest that intra-population differences in overlap with fisheries may be stronger during periods of food scarcity. Future studies should look at the influence of varying environmental conditions on the seabird−fishery overlap (Reyes-González et al. 2021).

4.4.3. Methodological considerations

The probability of encounter between seabirds and fisheries is commonly estimated by examining the overlap between the distribution of GPS-tracked birds and that of fisheries at several spatio-temporal scales (Le Bot et al. 2018). However, spatial overlap does not necessarily imply direct interactions with vessels but rather suggests that seabirds and fisheries are targeting the same areas and sharing the same resources (Pichegru et al. 2009, Torres et al. 2013, Collet et al. 2015). Detailed information on seabird−fishery interactions is only possible with onboard observations (Le Bot et al. 2018), which are logistically demanding and mainly used for regular monitoring of marine biodiversity in relatively small and coastal areas. Our methodological approach is not suitable for investigating fine-scale seabird−fishery interactions. Instead, it provides reliable information on general patterns and drivers of spatial overlap between GPS-tracked Cory's shearwaters and satellite-detected fishing effort for a relatively large area, such as the mainland EEZ of Portugal. The results presented here should be interpreted as a proxy for potential exposure to fishing gear or bycatch risk and are of particular importance because little is known about the overlap between industrial fishing fleets and *Calonectris* populations outside the Mediterranean Sea. The amount of time foraging seabirds overlapped with large-scale distribution of fishing effort was previously shown to accurately model the impact of bycatch on population dynamics (Tuck et al. 2001, Votier et al. 2010, Genovart et al. 2018), and to pinpoint high-risk areas with a strong probability of encounter over vast oceanic areas (Clay et al. 2019b). This methodology is commonly used to assess bycatch risk patterns in highly mobile marine predators such as seabirds (Genovart et al. 2018), marine mammals (Cronin et al. 2012, Baylis et al. 2018) and sharks (Queiroz et al. 2016, 2019). A similar methodological approach was used to quantify the spatial overlap between trawling fisheries operating on the Patagonian shelf and South American fur seals (*Arctocephalus australis*) breeding in the Falkland Islands (Baylis et al. 2018). By overlapping the foraging activity of GPS-tracked South American fur seals with daily resolution fishing effort, the authors mapped the areas of greatest overlap over the Argentinean EEZ at a near real time scale.

4.4.4. Conclusions and implications for bycatch

Our study shows that despite the high density of fishing vessels within the mainland EEZ of Portugal, Cory’s shearwaters spent little time foraging in the same areas as fisheries during the breeding period. We suggest that scavenging is likely to be limited in areas of high prey availability and that seabirds may prefer to feed on “natural” prey during the breeding period, particularly during chick-rearing. Thus, the population studied here may have relatively low exposure to industrial fisheries at large spatial scales. However, this Cory's shearwater population seems to forage more in areas used by fixed gear vessels (e.g. longliners and gillnets) and purse seiners during the pre-laying period. The importance of this fact should not be underestimated, because longline fisheries and gillnets represent the most lethal fishing gear, particularly for procellariform species (Anderson et al. 2011, Žydelis et al. 2013). Furthermore, spatial overlap could be underestimated in this study because: (1) radio-based Automatic Identification System (AIS) data used to track vessel movements are mainly limited to large industrial fishing fleets, thus do not account for the distribution of smaller artisanal fishing fleets; and (2) industrial fishing can also switch off their AIS systems (Ford et al. 2018) making these data a conservative picture of their at-sea distribution and effort. Future studies using recently developed radar detectors combined with GPS loggers may empirically detect real interactions with fishing vessels and confirm drivers of variation in overlap with fisheries (Weimerskirch et al. 2018, 2020a).

4.5. Supplementary Information

Table S4.1: *Summary and frequency of behaviours displayed by Cory's Shearwaters (Calonectris borealis) when exposed to a novel object in the nest during the boldness tests.*

Behaviour	Abbreviation	Mean ± SD number of times birds displayed each behaviour	Maximum number of times a bird displayed the behaviour	Number of birds that displayed the behaviour
Pecking	Peck	0.20 ± 0.87	10	21
Vocalization	Voc	0.02 ± 0.14	1	6
Snapping	Snap	0.18 ± 0.69	8	29
Standing	Stand	0.13 ± 0.48	4	22
Swallowing	Swall	1.24 ± 1.33	6	89
Move head	Head	1.20 ± 1.18	6	97
Blinking	Blink	3.17 ± 5.95	46	69
Twitching	Twitch	1.18 ± 2.47	24	75
Open wings	Wing	0.08 ± 0.34	3	16
Turn around	Turn	0.17 ± 0.52	4	33
Shake head	Shake	0.43 ± 0.94	7	49
Move away	Move	0.15 ± 0.38	2	38
Open the bill	Bill	0.06 ± 0.30	3	10
Inspecting the object	Insp	0.11 ± 0.41	4	16
Excavating	Excav	0.01 ± 0.08	1	2
Touching object	Touch	0.04 ± 0.31	3	7
Egg accomodation	Egg	0.02 ± 0.29	5	3

Table S4.2: *Summary of the Non-Metric Multi-Dimensional Scaling (NMDS) outputs for boldness scores.*

Behaviour	MDS1	MDS2	MDS3	MDS4
Pecking	-0.23	0.06	-0.25	0.01
Vocalization	-0.10	-0.11	-0.54	0.27
Snapping	-0.03	-0.01	-0.06	-0.01
Standing	-0.43	0.34	-0.05	0.17
Swallowing	-0.23	-0.20	0.08	-0.08
Move head	0.27	-0.16	0.01	0.01
Blinking	0.16	0.24	-0.11	-0.30
Twitching	0.11	0.33	0.37	-0.01
Open wings	-0.20	0.05	-0.20	0.17
Turn around	-0.12	0.07	-0.18	0.17
Shake head	-0.06	-0.03	0.08	0.09
Move away	-0.02	0.08	-0.02	0.43
Open the bill	-0.17	0.06	-0.35	-0.14
Inspecting the object	-0.22	-0.06	-0.35	-0.09
Excavating	0.09	0.45	-0.47	0.35
Touching object	-0.21	0.17	-0.21	0.27
Egg accomodation	-0.47	-0.21	0.01	0.19

Figure S4.1: *The recording device (LED headlamp, 6.2 x 4.0 x 3.5 cm, ~70 g; Lighting EVER ®) coupled to a Campark Action Camera HD Waterproof Camera (6 x 2,5 x 4 cm, ~77 g; Campark®) that was presented to the shearwaters as a novel object within the nest in the boldness tests in the field. Photo credits: Jorge M. Pereira.*

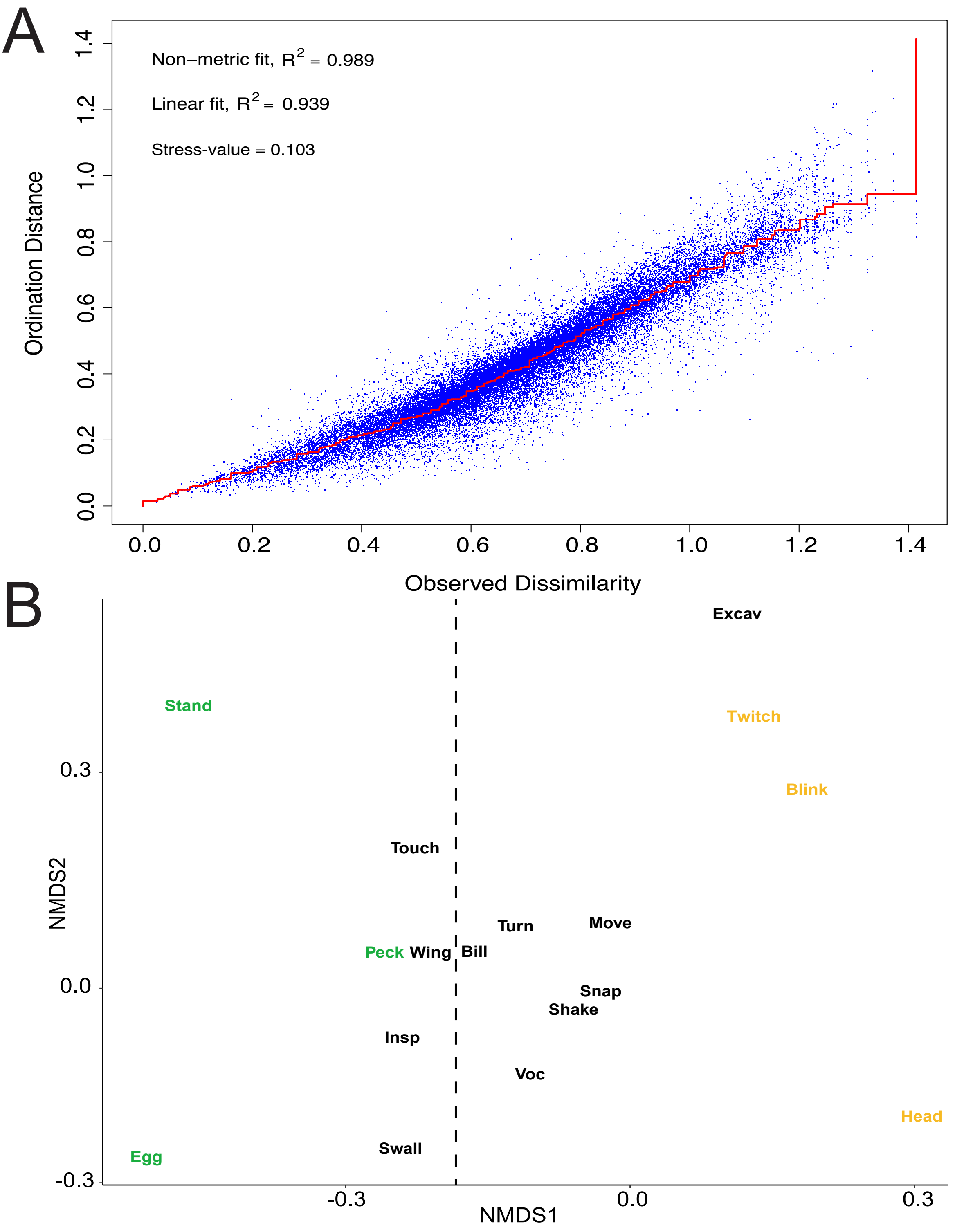


Figure S4.2: *(A) Stress-values represent the extent to which a two-dimensional plot is accurate in summarising the separation of observations, with values lower than 0.2 indicating a good NMDS analysis (Clarke 1993); (B) Two-dimensional Non-Metric Multi-Dimensional Scaling (NMDS) with a stress-value of 0.103, to obtain a graphical distribution of Cory's shearwaters displayed behaviours during the boldness tests. The black dashed line highlights the median boldness scores displayed in the first NMDS axis. Behaviours typically associated with bold (green) and shy individuals (yellow) are highlighted following Krüger et al. (2019).*

Chapter 5

Using a multi-model ensemble forecasting approach to identify key marine protected areas for seabirds in the Portuguese coast

This chapter is published as:

Pereira JM, Krüger L, Oliveira N, Meirinho A, Silva A, Ramos JA, Paiva VH (2018) Using a multi-model ensemble forecasting approach to identify key marine protected areas for seabirds in the Portuguese coast. *Ocean & Coastal Management* 153:98–107.

Abstract

Marine protected areas (MPAs) have been established across all marine environments, though their coherence and effectiveness in protecting umbrella species remains unclear. We used a multi-model ensemble forecasting approach, on 8-years of at-sea censuses of 30 seabird species to identify candidate MPAs in the West coast of Portuguese, prioritising important areas for their conservation based on their occurrence and distribution. We overlapped the outputs generated by the Ensemble Ecological Niche Models (EENMs) with layers representing important environmental stressors (fishing intensity, ship density and oil pollution risk), and calculated loss in conservation value using them as cost layers. Three key marine areas were identified along the Portuguese coast: (1) for breeders, there was a key marine area encompassing the Tagus and Sado estuaries and Berlengas archipelago; (2) for non-breeders and migratory species two important areas were identified in the northern and southern coast. The key marine area identified in the northern coast is characterised by high productivity and biodiversity and can be affected by oil pollution from the refineries and the intensive ship traffic in this area. Also, the area identified in the southern coast of Portugal for migratory seabirds overlaps extensively with areas of high fishing activity. Our results show that the important bird and biodiversity areas (IBAs) established along the Portuguese coast protect more than a third of the areas that we prioritised for breeding species and the official MPAs near 65% of the same areas. In contrast, current IBAs and national legislation protect less than 4% of the coastal areas that we prioritise for non-breeding species in this study. Our study, combining multi-species distribution with environmental constraints induced by human activities, allowed us to assess the coherence of the Portuguese marine planning and identify candidate areas to join the Portuguese network of marine protected areas. Our results, employing data from annual at-sea surveys together with the human stressors known to affect the Portuguese coast, proved to be an extremely useful strategy to identify spatial conservation areas along the Portuguese coast as well as to access the adequacy and consistency of those areas. Despite the constraints of this demanding approach, we are confident that our study provides a reliable strategy to inform marine conservation efforts and management planning in similar coastal environments elsewhere, characterised by strong coastal upwelling movements.

Keywords: European seabirds at-sea census, Ensemble ecological niche models, Environmental stressors, Marine protected areas, Zonation software.

5.1. Introduction

Marine protected areas (MPAs) are recognised as key tools to provide a network-framework for integrated area-based biodiversity MPAs (Lovejoy 2006). MPAs were firstly established in coastal areas but are now being established across all marine environments. The suitable design and management of MPAs rely mostly on the quality of the ecological information used to identify key marine areas (Abecasis et al. 2014, Fulton et al. 2015). These data will help decision-makers allocate the initial position and boundaries of priority areas for conservation based on the species' habitat fidelity and will also provide important information for the management of already established MPAs (Maxwell et al. 2014, 2015). Marine predators, such as seabirds, may be used as biological indicators to identify and prioritise areas for marine conservation because they are wide-ranging, long-lived marine predators and their distribution often overlap with that of other marine predators and with important anthropogenic stressors, such as fisheries (Maxwell & Morgan 2013, Lescroël et al. 2016)

Coastal ecosystems are heavily impacted by human activities, which can be difficult to take into account during MPA identification and design (Maxwell & Morgan 2013). To truly protect the biodiversity of marine ecosystems, MPA implementation must take into account the relation between the distribution of marine organisms, oceanographic processes and the impact of environmental stressors (e.g. ocean acidification, oil pollution, vessels traffic density, fisheries density, etc.) on marine biodiversity (Halpern et al. 2008, Fulton et al. 2015). Besides climate change effects, fisheries are considered the environmental stressor with a major impact on marine biodiversity, responsible for modifying worldwide ecosystems and for reducing populations of marine top predators (Rolland et al. 2010, Brown et al. 2015). Because fisheries' distribution often overlaps with biodiversity hotspots (Queiroz et al. 2016), and bycatch is one of the main causes for seabirds' high mortality levels (Croxall et al. 2012), already established protected areas may not be enough for the conservation of all seabird species (Krüger et al. 2017). Therefore, it is important to assess which species are truly protected by the currently established MPAs (Lascelles et al. 2012, Ramirez et al. 2017).

Multi-species approaches based on the overall species' occurrence and diversity are usually desirable and have been used to identify biodiversity hotspots across large spatial scales (Nur et al. 2011, Raymond et al. 2015, Briscoe et al. 2016, Maslo et al. 2016). Several studies used shipboard surveys, following the European Seabirds at Sea (ESAS) procedures (Tasker et al. 1984, Camphuysen & Garthe 2004) to identify seabird hotspots and use that information to develop potential MPAs scenarios in offshore waters (Nur et al. 2011, Arcos et al. 2012). Several important marine areas were prioritised and identified based on the occurrence and distribution of seabird species and proposed to integrate the current worldwide network of MPAs (Lascelles et al. 2016). The marine important bird and biodiversity areas (IBAs) represent one of the most recent wide-ranging European efforts to identify key marine areas and the first step for MPA establishment (Lascelles et al. 2012). However, the effectiveness of coastal MPAs for the conservation of highly mobile marine predators and targeted species is not usually assessed by combining oceanographic data with environmental stressors.

Most seabird species are closely distributed within a range of dynamic oceanographic processes which enhance oceanic productivity and prey availability, and so require more complex analyses such as dynamic modelling approaches (Louzao et al. 2011b) or a combination of multiple modelling techniques (Araújo & New 2007, Oppel et al. 2012, Zhang et al. 2015, Scales et al. 2016). However, most studies used a single-algorithm approach, such as the widely used Maximum Entropy (MaxEnt) modelling technique, despite their frequent over-fitting on habitat suitability predictions which limit their predictive ability and performance (Torres et al. 2015). An alternative to reduce potential bias and increase the robustness in predictions is to adopt a multi-model ensemble forecast by combining the best predictive outputs of each modelling technique into one unique weighted average surface (Araújo & New 2007, Thuiller et al. 2009). Ensemble Ecological Niche Modelling (EENM) has been used successfully for identifying at-sea areas for marine predators, including sea turtles (Pikesley et al. 2013) and seabirds (Oppel et al. 2012, Legrand et al. 2016, Scales et al. 2016, Fox et al. 2017).

In this study, we predicted the spatial distribution of 30 seabird species sighted through at-sea shipboard surveys (ESAS methodology) over the Portuguese coast. We predicted the spatial distribution of seabird species using a multi-model ensemble forecasting approach within the BIOMOD2 platform (Thuiller et al. 2009). The distribution of seabird species was analysed in relation to their phenology (breeders and non-breeders), and within a complementarity-based spatial prioritisation method using the Zonation software to identify key marine areas with widely varying conservation returns and costs (e.g. fishing density, oil pollution risk and ship traffic) to the marine environment (Moilanen et al. 2005, Leathwick et al. 2008). Finally, we examined the spatial overlap between the already established MPAs recognised by international and national organizations and our proposed key marine areas. Our study goes a step further when compared with a previous study (Oppel et al. 2012) because it combines the distribution of several umbrella species using a multi-model ensemble forecasting approach and prioritises their habitat use throughout the West coast of Portugal. We intended to assess the coherence of the existing network of MPAs over this region and to identify new candidate areas that would enrich such a network and further contribute towards marine conservation.

5.2. Methods

5.2.1. Seabird sightings data

Shipboard surveys were conducted along the Portuguese coast during spring (March to May) from 2004 to 2012. The study area was limited by the continental shelf out to the 200 m depth contour, plus the Gulf of Cádiz between 36° N and 42° N, and 6° W and 10° W (Fig. 5.1). We used a standard European methodology, the European Seabirds At Sea Surveys ESAS; (Tasker et al. 1984, Camphuysen & Garthe 2004): observations were collected in units of linear transects, described as a continuous 180° forward scan with concurrent 300 m wide strip transect, in a 5 min. period and the occurrences were expressed in densities - birds per kilometre (bird/km^2) (Meirinho et al. 2014). All seabirds in contact with water, within a 300 m strip transect band, were accounted as observations.

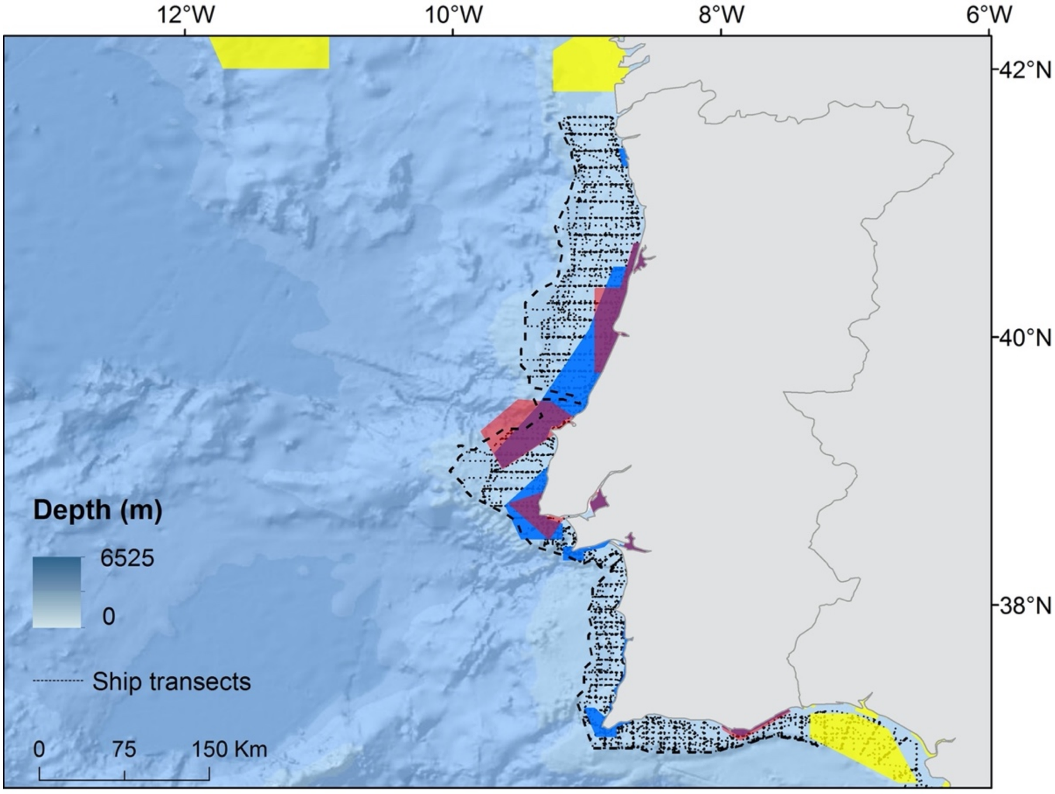


Figure 5.1: *Map showing the overall effort during the 8-years of the surveying period (2004-2012) along the Portuguese coast. At-sea shipboard surveys (represented by small black dots) were used in this study for the Ensemble Ecological Niche Modelling of individual species within the Exclusive Economic Zone (EEZ) of Portugal. The 200 m isobath is also shown (black dashed line) and is overlaid on bathymetry of the region. Portuguese Marine Protected Areas (MPAS; blue), Portuguese marine important bird areas (IBAs; red) and Spanish MPAs (MPAs; yellow).*

5.2.2. Oceanographic predictors

A range of static and small-scale remote sense environmental predictors were used to characterise the marine environment, and to predict the habitat suitability for each seabird species. Bathymetric data, taken as water depth, was extracted from the NOAA Global Relief (https://www.ngdc.noaa.gov/mgg/global/global.html) for a grid of 0.01° (approximately 1 km). Dynamic predictors were extracted as monthly composites in ASCII files from different websites of satellite imagery: Sea surface temperature (SST), Chlorophyll-*a* concentration (CHL) and Sea surface height (SSH). Both SST and CHL concentration were used in a spatial resolution of 0.04° (approximately 4 km) from Aqua MODIS and extracted from NASA Ocean Color browser (http://oceancolor.gsfc.nasa.gov/cms/). To analyse the consistency of oceanic productive areas, a time series of CHL concentration data was extracted for a long-term period (2002 - 2012). Cells with a CHL concentration > 1 mg m^{-3} were assigned a value of 1 and lower values assigned zeros (Haug et al. 2015). SSH was also extracted for a grid of 0.04° from the AVISO satellite images (http://www.aviso.altimetry.fr/en/my-aviso.html). SST, CHL and SSH anomalies (SSTA, CHLA and SSHA, respectively) for each month were computed by calculating the difference between the mean peak of the variable for a given month and the observed average for a month over a 10 year (2002-2012). Then, all dynamic predictors were imported to the GIS environment (ArcGIS 10.2) and assembled in a single raster by extracting the median peak of each three-monthly composite seasonal raster (i.e. Spring, Summer, Autumn and Winter) to integrate as independent variables into the modelling process. All environmental predictors were assembled to a 0.04° cell size grid. GIS software was also used to compute gradients of the static and dynamic predictors. Gradients in depth, SST and CHL concentration were determined by estimating rates of change by moving a window function (3 × 3 grid cells; function = [(max. value − min. value) × 100] / (max. value). The gradient in depth was used as a proxy of oceanic deep surface slope. Frontal regimes appear more contrasted in CHL and SST gradients, as zones of strong chlorophyll-*a* concentrations and quick changes in water masses temperature. Using CHL and SST gradients, instead of their standalone values allowed to identify and calculate the oceanic frontal regimes. Distance to land was computed in the R environment, in order to calculate the minimum direct distance to the coastline. Further details on environmental variables used in the Ensemble Ecological Niche Models are shown in Table S5.1 and Fig. S5.1.

5.2.3. Ensemble Ecological Niche Modelling (EENM)

Previous studies reported that a multi-model ensemble forecasting framework is desirable for predicting seabird habitat distribution when compared with the use of single-algorithm models (Oppel et al. 2012, Scales et al. 2016). In the ensemble forecasting approach, modelling outputs result in a unique forecast ensemble surface contributing to overcome some of the limitations of correlative/statistical modelling techniques and thus improving the robustness and the accuracy of the projections (Araújo & New 2007).

The assessment of the correlation is a strategy implemented to reduce the skewing effect on results derived from spatial autocorrelation of variables (Barry & Elith 2006). To minimise autocorrelation problems, a sensitivity analysis was conducted before the modelling process to select less correlated variables (Torres et al. 2015). Strongly correlated predictors (|≥.70|) were identified and removed from the calibration process, based on a multivariate correlation, by estimating all pair-wise Spearman rank correlation coefficients to avoid autocorrelation problems (Graham 2003, F. Dormann et al. 2007, Halvorsen et al. 2016) (Graham 2003; Dormann et al. 2007; Halvorsen et al. 2016). This analysis allowed us to remove and select different variable predictors to calibrate the models, avoiding spatially biased models caused by autocorrelation problems.

We applied the ensemble forecasting approach with the previously selected variables using only species that occurred along the Portuguese coast. The assessment of species distribution is supported on niche-based modelling techniques of a correlative nature, using the BIOMOD2 R package implemented in R 3.3.2 software (R Core Team 2019). This modelling procedure allows to run different modelling techniques as bioclimatic envelopes, regression, classification methods and machine learning methods: (1) Artificial Neural Networks (ANN); (2) Classification Tree Analysis (CTA); (3) Flexible Discriminant Analysis (FDA); (4) Generalised Additive Models (GAM); (5) Generalised Boosting Models (GBM); (6) Generalised Linear Models (GLM); (7) Multiple Adaptive Regression Splines (MARS); (8) Maximum Entropy Models (MaxEnt); (9) Breiman and Cutlers Random Forest for classification and regression (RF); and (10) Surface Range Envelops (SRE) (Thuiller et al. 2009). Then, the weighted combination of results from the different modelling techniques were assembled in a single consensus model, using only useful models in terms of capacity to discriminate suitable from unsuitable conditions (AUC ≥ 0.70) (See Supplementary Information 1 for details on the BIOMOD2 settings).

The accuracy of the modelling outputs was assessed using the Area Under the Curve of the Receiver Operating Characteristics (AUC of ROC) and True Skill Statistic (TSS). The AUC is: (1) a threshold-independent statistical measure accepted as suitable for assessing the performance of the models, because it assesses the models' ability to discriminate suitable from unsuitable conditions (Liu et al. 2005, 2013, Pearson et al. 2006, Lobo et al. 2008); and (2) estimates the likelihood that a randomly selected presence point is located in a raster cell with a higher probability score for species occurrence than a randomly generated point (Araújo et al. 2005, Elith et al. 2006). AUC ranges between 0.5 and 1, where value 1 indicates perfect discrimination ability and 0.5 indicates a low discriminatory capacity of the model. Output models are usually considered as having an excellent discriminatory ability when AUC ≥0.90, good for 0.80 < AUC < 0.90, acceptable for 0.70 < AUC < 0.80, bad for 0.60 < AUC < 0.70 and invalid for 0.50 < AUC<0.60 (Engler et al. 2004, Araújo et al. 2005).

5.2.4. Habitat prioritisation

The outputs from Ensemble Ecological Niche Modelling were used to calculate area conservation value and thus identify priority areas for conservation according to each approach using the Zonation software v. 3.1.1 (Moilanen et al. 2005, Lehtomäki & Moilanen 2013). Zonation is considered one of the best software to produce a complementarity-based prioritisation across the landscape based on the distribution of biodiversity features and constraint data such as costs and habitat connectivity (Kukkala et al. 2016). It is one of the best software to optimise the selection of conservation targets when prioritising habitat connectivity is desired (Delavenne et al. 2012). Zonation is a software that calculates values on raster grid cells, according to the occurrence of species or features, based on a set of pre-established rules related to habitat response (Moilanen & Wintle 2007). Zonation ranks cells by iteratively removing the least valuable remaining cell until the complete landscape has been prioritised (Moilanen et al. 2005). The final output is scaled according to the EENMs probability of occurrence and ranging from 0 (least important areas) to 1 (most important areas). Each species was weighted by its International Union Conservation of Nature (IUCN) status as follows: least concern (LC) = 1; near threatened (NT) = 2; vulnerable (VU) = 3; endangered (EN) = 4 and critically endangered (CR) = 5. Boundary penalty curves (Moilanen & Wintle 2007), were empirically constructed based on IUCN conservation status of the species, body size and home range size (Leathwick et al. 2008). Three categories were used: (1) low sensitivity; (2) mid sensitivity; and (3) high sensitivity, based on an exponential relation between the proportion of unoccupied area around a grid cell and the proportion of reduction in conservation value (See Fig. S5.2 in the Supplementary Information). The importance area records were calculated for each phenology (See Table S5.2 in the Supplementary Information). We were very conservative in prioritising marine key areas because our objective was to guarantee the retention of high-quality areas; thus for each phenological state, we selected the areas that were within 10% (90% of conservation value) of the distribution threshold (areas of 5% and 1% threshold) (Moilanen et al. 2005, Oppel et al. 2012, Dias et al. 2017, Krüger et al. 2017). The degree of spatial overlap was inspected between the locations of the 1% priority areas for each scenario, the official MPAs (http://www.mpatlas.org) and the established IBAs (http://maps.birdlife.org/marineIBAs/default.html).

5.2.5. Effects of the human activities on the conservation value of targeted areas

We used cost layers based on the distribution of the three most important human activities known to affect the Portuguese coast to quantify the changes in conservation value within target areas: fishing density (only > 15 m vessels), oil pollution risk, and ship traffic (See Fig. S5.3 in the Supplementary Information). Methods for calculating cost layers are fully described in Supplementary Information 2. Zonation reduces the value of a grid cell in accordance with the value of the cost layer. In this sense, we calculated the conservation value using each cost layer independently. After that, we extracted the grid values within marine IBAS, MPAs and the key areas identified by the Zonation model with null cost constraints (1% key areas- KEYs). Conservation value calculated with cost layers was subtracted from the original conservation value with null cost (Krüger et al. 2017) to calculate the change in conservation value. Negative values (indicates a decrease in conservation value) were set to 1 and positive values (indicates an increase in conservation value) were set to 0. Then a binomial GLM was applied to test the effects of the human activities (fishing density, oil risk and ship traffic) on the probability that a given area has its conservation value decreased, considering differences between phenology groups (breeders and non-breeders) and among target area types (IBAs, MPAs and KEYs).

5.3. Results

5.3.1. Ensemble Ecological Niche Model

Most of the overall EENMs presented good or very good predictive performance in discriminating suitable from unsuitable conditions, ranging from (AUC= 0.74; TSS= 0.47) to (AUC= 0.97; TSS= 0.91) and averaged 0.88 ± 0.08 AUC (Table 5.1). From the ten modelling techniques used, there were five that performed better: GBM, GLM, MARS, MaxEnt and RF, respectively (See Table S5.3 in the Supplementary Information). The most significant variables with the highest proportion of importance in all EENMs were DCOAST and CHLG (Table 5.1). BATG was the third more important predictor. SSTG, CHLA and SSTA were the least important predictors.

Two major patterns of seabird species distribution were evident over the Portuguese coast: (1) species strongly associated with coastal waters; and (2) species occurring in coastal and pelagic waters (Table 5.3). The less accurate models were associated with species whose distribution was predicted beyond the continental shelf and slope to pelagic waters such as the Arctic jaeger (*Stercorarius parasiticus*), Arctic tern (*Sterna paradisaea*), Band-rumped storm-petrel (*Hydrobates castro*), Bulwer's petrel (*Bulweria bulwerii*), Manx shearwater (*Puffinus puffinus*) and Red phalarope (*Phalaropus fulicarius*) (See Fig. S5.4 in the Supplementary Information). The most accurate models were restricted to species strongly associated with coastal waters. From March to May breeding species in the Portuguese coast (Audouin's gull (*Larus audouinii*), Cory's shearwater (*Calonectris borealis*), European shag (*Gulosus aristotelis*) and Yellow-legged gull (*Larus michahellis)*) shared coastal waters with non-breeders such as Balearic shearwater (*Puffinus mauretanicus*), Common guillemot (*Uria aalge*), Common scoter *(Melanitta nigra*), European storm-petrel (*Hydrobates pelagicus*), Great black-backed gull (*Larus marinus*), Great skua (*Catharacta skua*), Lesser black-backed gull (*Larus fuscus*), Mediterranean gull (*Larus melanocephalus*), Northern gannet (*Morus bassanus*), Razorbill (*Alca torda*) and Sandwich tern (*Thalasseus sandvicensis*) (See Fig. S5.4 in the Supplementary Information).

Table 5.1: *Ensemble Ecological Niche Models performance measured as the Area Under the Receiver Operating Characteristic (ROC) Curve (AUC) and True Skill Statistic (TSS), both calculated over 10-fold cross-validation (Means ± SD). The proportion of predictors importance across all models (mean off all model sets per algorithm), calculated as the percentage of change in AUC and ranging from 0 to 1. Predictors: gradient of bathymetry (BATG), gradient of chlorophyll-a concentration (CHLG), chlorophyll-a concentration anomaly (CHLA), sea surface temperature (SST), gradient in sea surface temperature (SSTG), sea surface temperature anomaly (SSTA) and distance to the coastline (DCOAST). Predictors with major contribution in* ***bold****.*

Species	AUC	TSS	BATG	CHLG	CHLA	SST	SSTG	SSTA	DCOAST
Strongly associated with coastal waters									
Alca torda	0.96 ± 0.05	0.89 ± 0.08	0.15	**0.48**	0.02	0.07	0.05	0.04	**0.44**
Catharacta skua	0.96 ± 0.04	0.86 ± 0.06	0.09	**0.45**	0.01	0.04	0.03	0.01	**0.49**
Fratercula arctica	0.88 ± 0.10	0.74 ± 0.17	0.19	**0.24**	0.04	0.12	0.10	0.07	**0.68**
Larus audouinii	0.94 ± 0.07	0.87 ± 0.13	0.23	**0.53**	0.07	0.48	0.07	0.06	**0.56**
Larus fuscus	0.94 ± 0.05	0.83 ± 0.07	0.08	**0.27**	0.02	0.05	0.03	0.02	**0.60**
Larus marinus	0.95 ± 0.04	0.85 ± 0.06	0.11	**0.25**	0.01	0.04	0.03	0.01	**0.57**
Larus melanocephalus	0.94 ± 0.04	0.84 ± 0.07	**0.13**	0.12	0.04	0.07	0.04	0.05	**0.85**
Larus michahellis	0.96 ± 0.04	0.87 ± 0.06	0.11	**0.34**	0.01	0.03	0.03	0.01	**0.51**
Melanitta nigra	0.95 ± 0.06	0.85 ± 0.11	**0.33**	0.27	0.03	0.11	0.08	0.07	**0.61**
Morus bassanus	0.97 ± 0.03	0.91 ± 0.06	0.05	**0.40**	0.01	0.04	0.02	0.01	**0.42**
Gulosus aristotelis	0.95 ± 0.07	0.89 ± 0.14	**0.41**	0.38	0.03	0.36	0.30	0.11	**0.64**
Phalacrocorax carbo	0.74 ± 0.18	0.50 ± 0.36	0.39	**0.45**	0.18	0.18	0.25	0.19	**0.69**
Puffinus mauretanicus	0.96 ± 0.04	0.88 ± 0.07	0.10	**0.39**	0.03	0.06	0.03	0.02	**0.50**
Sternula albifrons	0.83 ± 0.14	0.67 ± 0.27	**0.25**	**0.25**	0.09	0.16	0.26	0.13	**0.70**
Thalasseus sandvicensis	0.94 ± 0.05	0.83 ± 0.07	0.10	**0.35**	0.02	0.05	0.05	0.03	**0.56**
Uria aalge	0.96 ± 0.05	0.89 ± 0.09	0.15	**0.38**	0.11	0.24	0.08	0.09	**0.37**
Associated with coastal and pelagic waters									
Ardenna gravis	0.85 ± 0.07	0.68 ± 0.14	0.08	**0.68**	0.09	0.11	0.08	0.03	**0.16**
Ardenna grisea	0.91 ± 0.05	0.79 ± 0.09	0.10	**0.53**	0.04	0.07	0.10	0.04	**0.40**
Bulweria bulwerii	0.75 ± 0.09	0.48 ± 0.15	0.15	0.16	0.09	**0.44**	0.11	0.18	**0.42**
Calonectris borealis	0.90 ± 0.08	0.72 ± 0.12	0.08	**0.19**	0.01	0.10	0.03	0.01	**0.47**
Hydrobates castro	0.75 ± 0.13	0.48 ± 0.17	**0.51**	0.25	0.06	**0.30**	0.10	0.04	0.29
Hydrobates pelagicus	0.93 ± 0.04	0.82 ± 0.06	**0.26**	**0.54**	0.09	0.08	0.07	0.01	0.25
Oceanites oceanicus	0.87 ± 0.10	0.69 ± 0.18	0.14	**0.38**	0.11	0.20	0.07	0.06	**0.52**
Phalaropus fulicarius	0.75 ± 0.11	0.50 ± 0.19	0.33	0.23	0.09	**0.47**	0.08	0.09	**0.48**
Puffinus puffinus	0.77 ± 0.10	0.47 ± 0.17	0.11	**0.42**	0.07	**0.40**	0.09	0.09	0.35
Rissa tridactyla	0.86 ± 0.08	0.64 ± 0.13	0.15	**0.53**	0.09	0.24	0.08	0.03	**0.31**
Stercorarius parasiticus	0.79 ± 0.12	0.56 ± 0.21	0.15	**0.52**	0.10	0.20	0.11	0.10	**0.43**
Stercorarius pomarinus	0.84 ± 0.13	0.65 ± 0.16	0.13	**0.53**	0.04	0.08	0.14	0.04	**0.35**
Sterna hirundo	0.88 ± 0.06	0.70 ± 0.10	0.18	**0.42**	0.02	0.10	0.16	0.04	**0.36**
Sterna paradisaea	0.76 ± 0.16	0.53 ± 0.30	**0.46**	0.27	0.08	0.23	0.13	0.12	**0.50**

5.3.2. Location of important areas for seabird species

The areas of highest conservation records included breeders and non-breeders all over the Portuguese coast, from the northern to the southern coast (Fig. 5.2). For breeders, the areas of highest records were off the West central coast of Portugal (Fig. 5.2A), whereas for non-breeders were off the northern and southern coast of Portugal (Fig. 5.2B).

Three important areas were identified and located in the northern, central and southern coast of Portugal (Fig. 5.3). The key marine areas based on the breeder species were concentrated in the same area, in central Portugal between the Sado estuary and the North of Berlengas archipelago (Fig. 5.2). The key marine areas identified for non-breeders and migratory species overlapped almost entirely in the northern coast with the current Litoral Norte MPA (Litoral Norte natural park) and a small fraction in the southern coast, overlapping with the Ria Formosa MPA and IBA (proposed to protect Little terns) (Fig. 5.3). On the other hand, the location of the key marine areas identified for breeding species differed entirely from the areas identified for non-breeders and migratory species (Fig. 5.2). The key marine areas identified for breeding species overlapped in central Portugal with part of the current boundaries of Berlengas MPA (Berlengas special protection area- SPA) and Berlengas IBA (both proposed to protect Cory's shearwaters, Band-rumped Storm-petrels, Balearic shearwaters and Northern gannets), Aveiro-Nazaré MPA, Cabo Raso IBA and Cabo Raso MPA (both proposed to protect Balearic shearwaters and Mediterranean gulls) and also Arrábida MPA (Natural reserve and Arrábida Marine Park) (Fig. 5.3).

The overlap between our proposed key marine areas identified for non-breeding species with the current IBAs and official MPAs was always lower than 4% (3.4% and 3.1%, respectively). However, contrary to non-breeding species, the overlap between the key marine areas identified for breeders with the BirdLife IBAs and the official MPA was considerably higher (37.3% and 63.6%, respectively).

5.3.3. Effects of the human activities on the conservation value of targeted areas

When we added human activities as cost layers the change in conservation value ranged from a decrease of 6.99% to an increase of 6.10%. Extreme values belonged to the non-breeders, while changes for breeders remained within 4% of change (See Fig. S5.5 in the Supplementary Information). The probability of decreasing conservation value by adding costs of human activities did not vary between species phenology, but there were differences among types of costs and types of target areas (Table 5.4). That trend was maintained when factors interacted with the conservation value (Table 5.4). Despite no significant differences between phenology groups, the probability of decreasing conservation value was higher for breeders when the conservation values were at a maximum for most of the cost types and target areas (Fig. 5.4). The trend of decreased probability with increased conservation value also was common in most target areas under most cost types, with the exception of our proposed key marine areas (KEYs) under the influence of fisheries and oil pollution risk (Fig. 5.4). The probability of decreasing conservation value by the effect of fisheries increased for higher conservation value with no cost for breeders. This trend was repeated for both breeders and non-breeders under the influence of oil pollution risk.

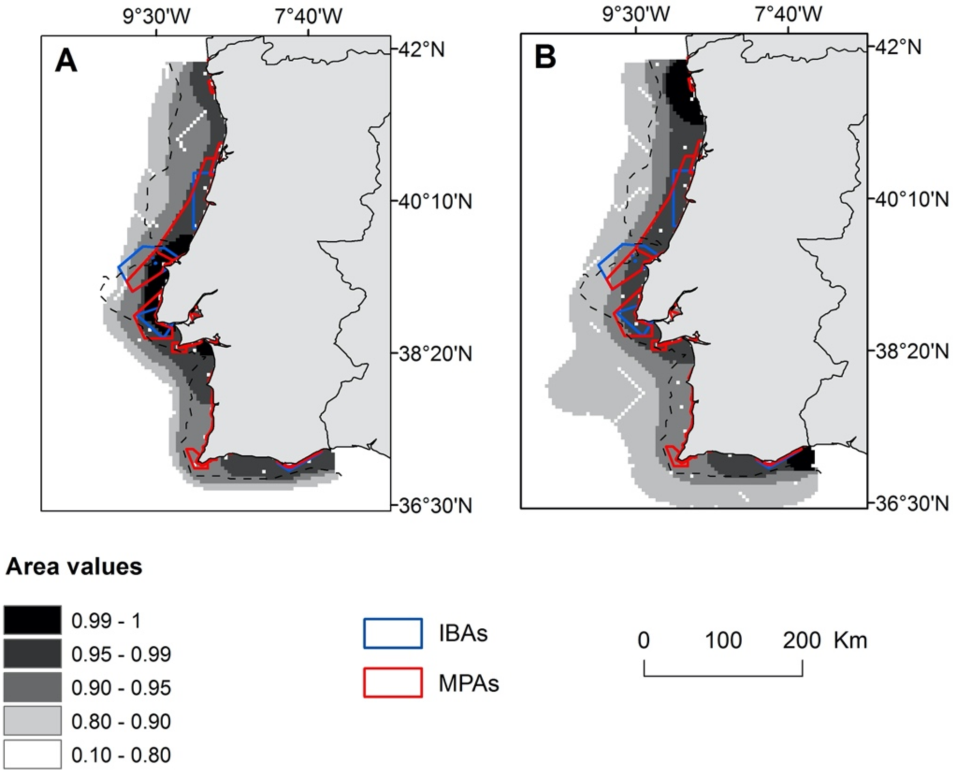


Figure 5.2: *Proportion of conservation value (Zonation scenarios) based on the probability of occurrence of species given their weight and response to fragmentation for: (A) Breeders and (B) non-breeders. Also shown the official marine protected areas (MPAs, red lines) and marine important bird areas (IBAs; blue lines). The 200 m isobath is also shown (black dashed line).*

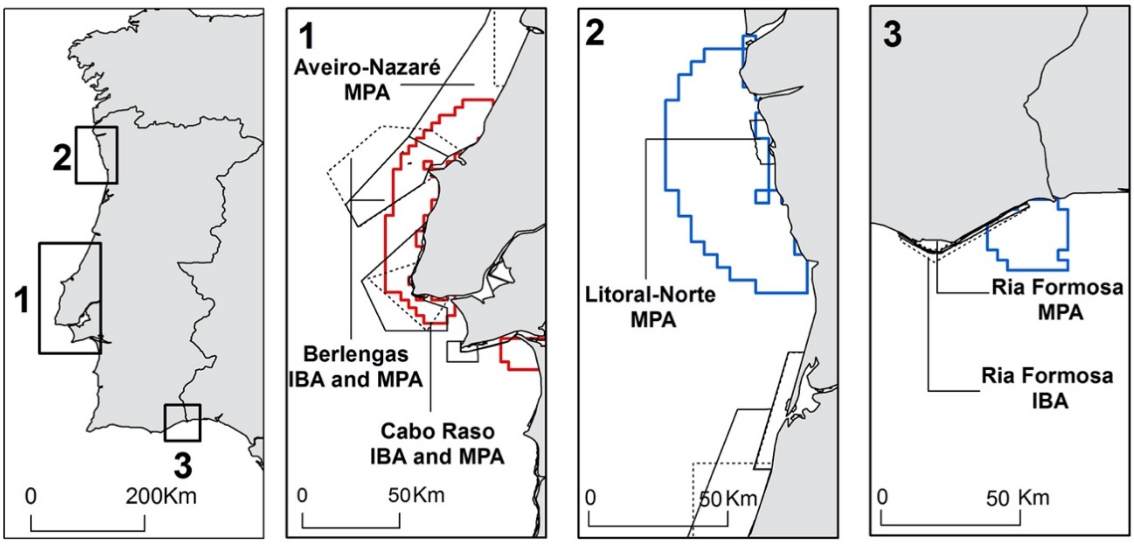


Figure 5.3: *Key marine areas for 99% importance records (1% threshold) overlapped with the official Marine Protected Areas (MPAs, fill lines) and marine important bird areas (IBA; dashed lines). for (1) Breeders (red); (2) and (3) non-breeders (blue).*

Table 5.2: *Results of a binomial generalised linear model (GLM) evaluating the relation between the probability of decreasing conservation value and the conservation value with no cost considering differences among targeted areas under the effect of different human activities (Costs). Differences were considered as statistically significant when p-value ≤ 0.05.*

Model structure	**β ± SE**	***z*-value**	***p*-value**
Conservation Value with No Cost (CV)	-15.1 ± 3.0	-5.057	**<0.001**
Phenology (Non-Breeders)	-1.1 ± 2.6	-0.413	0.68
Cost (Oil Risk)	-2.3 ± 3.0	-0.774	0.44
Cost (Ship Traffic)	16.4 ± 3.2	5.095	**<0.001**
Target Area (KEYs)	-6.3 ± 3.2	-1.924	**0.05**
Target Area (MPAs)	13.1 ± 3.8	3.413	**0.001**
CV*Phenology (Non-Breeders)	-0.2 ± 2.7	-0.006	0.99
CV*Cost (Oil Risk)	1.5 ± 3.1	0.482	0.63
CV*Cost (Ship Traffic)	-17.3 ± 3.3	-5.240	**<0.001**
CV*Target Area (KEYs)	7.3 ± 3.3	2.176	**0.03**
CV*Target Area (MPAs)	-13.0 ± 4.0	-3.252	**0.001**

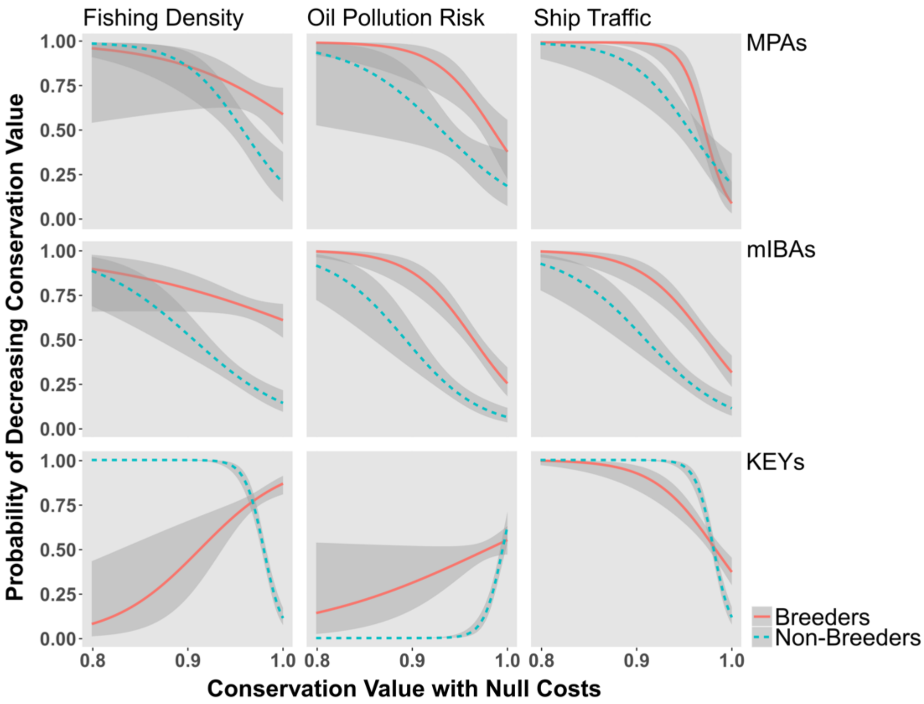


Figure 5.4: *Estimated probability of decreasing conservation value as a function of the conservation value with no costs compared among Target Areas (marine important bird areas - mIBAs, proposed key areas - KEYs and marine protected areas - MPAs) and Human activities (Costs). Lines are binomial trends and its standard error (shaded area).*

5.4. Discussion

We used Ensemble Ecological Niche Models, together with habitat prioritisation scenarios to analyse 8-years of at-sea census data regarding 30 seabird species occurring along the Portuguese coast, to address the suitability of Portuguese marine planning in protecting umbrella species such as seabirds. Two main key areas were identified as congregating: (1) breeding species in West central Portugal, such as Band-rumped storm-petrel, Cory's shearwater, European shags and Yellow-legged gulls; and (2) non-breeding and migratory species in the northern coast of Portugal, including seabird species of conservation concern such as the Atlantic puffin *(Fratercula arctica*), Balearic shearwater, Common guillemot and Sooty shearwater (*Ardenna grisea*). Both areas are likely to be very important for other marine taxa given the strong overlap in the seabird distribution (our study) and cetaceans (Santos et al. 2012). They also matched with a high occurrence of environmental stressors such as oil pollution risk and fishing density. Most of the key marine areas identified for breeding species were broadly within marine IBAs and protected by national legislation, whereas key marine areas identified for non-breeding species did not overlap with either IBAs or MPAs. Nevertheless, although seabirds' distribution tends to overlap with fishing density (only > 15 m vessels) and oil pollution risk, the ranges of change in conservation value we found were particularly low, meaning that most of the official and proposed MPAs are not affected by those stressors.

5.4.1. Models adequacy: testing the boundaries of proposed MPAs and species contribution

The overall models' performance, obtained by comparing the AUC records, suggested that most of the models obtained through a multi-model ensemble forecasting approach were adequate in identifying MPAs and to test the degree of protection offered by their boundaries. Multi-species distribution modelling is reported as a suitable approach to identify important areas for marine predators and biodiversity hotspots (Arcos et al. 2012, Lascelles et al. 2012). In previous studies on the Southwest Atlantic (Krüger et al. 2017), South Atlantic (Dias et al. 2017) and Southern Ocean (Raymond et al. 2015), the combination of several marine predators was considered a good approach to identify important regions where marine predators overlap and which key environmental characteristics they explore. In almost all EENMs, seabirds' distribution was best predicted by the chlorophyll-*a* concentration gradient and distance to coastline: seabirds occur more often in shallow shelf and coastal waters particularly in the continental shelf break, where the strong upwelling enhances primary productivity and resource availability (Oliveira et al. 2009, Lopes et al. 2014).

The key marine area identified for breeding species in West central Portugal broadly overlaps with the most used areas by breeding and resident seabird species in mainland Portugal (Meirinho et al. 2014). Such an area guarantees connectivity, through an ecological corridor, for migratory species between the main areas at the northern and the southern coast of Portugal (Oppel et al. 2012). This contributed to the identification of several mIBAs (e.g. Berlengas and Cabo Raso) and coastal MPAs, including Berlengas MPA, Arrábida Marine Park, Aveiro-Nazaré MPA and Cabo Raso MPA. Cory's shearwaters, European shags and Yellow-legged gulls had a major role in designing the central key marine area because their distribution during the breeding period is usually restricted to the surroundings of their breeding colonies located in the Berlengas archipelago (Paiva et al. 2010d, Meirinho et al. 2014, Ceia et al. 2014a). Little terns were of little use for the identification of the central key marine area, mainly due to the long distance from the nearest breeding colonies, located at Ria de Aveiro, Tagus and Sado estuaries (Meirinho et al. 2014). Audouin's gull was also of little use for the identification of this central key area because their distribution is mostly restricted to the breeding colonies located in Ria Formosa.

We identified the most important areas for non-breeding and migratory species in the northern coast of Portugal between Ria de Aveiro and North coast of Galicia, Spain (i.e. northwestern coast of the Iberian Peninsula), and in the southern coast of Portugal, as also previously identified by (Oppel et al. 2012). The key marine area identified in northern Portugal matched with an area of high biodiversity and high productivity (Lopes et al. 2014, Picado et al. 2014), encompassing several estuaries such as Douro, Minho, Ave, Lima and Cávado. These waters are used by several species during the non-breeding period as a migratory corridor however, they were not previously recognised as important for mobile marine predators or identified as a Portuguese IBA (Oppel et al. 2012). Marine mammals also rely on this area during part of the year, including Short-beaked common dolphin (*Delphinus delphis*), Striped dolphin (*Stenella coeruleoalba*), Risso's dolphin (*Grampus griseus*, short-finned pilot whale (*Globicephala macrorhynchus*), Mink whale (*Balaenopter acutorostrata*), Fin whale (*Balaenoptera physalus*) and Harbour porpoise (*Phocoena phocoena*) (Santos et al. 2012, Hammond et al. 2013, Correia et al. 2015). The attractiveness of these waters for mobile marine top predators is a consequence of the intense summer upwelling that extends mostly from Figueira da Foz to Ria de Aveiro (Zwolinski et al. 2010, Lopes et al. 2014). The key marine area identified in the northern coast is particularly important for Alcid species, such as Atlantic puffin (Guilford et al. 2011), Razorbill (Espín et al. 2012) and Common guillemot (Munilla et al. 2007) during the non-breeding period, with a conservation status of vulnerable and near threatened. Common guillemots used to breed in the Berlengas archipelago but currently is virtually extinct as a breeder (Oliveira et al. 2015). According to (Munilla et al. 2007) and (Oliveira et al. 2015), two major reasons should have contributed for the decline of the southernmost population of the species: (1) fisheries bycatch (entanglement in gillnets and potentially illegal nets) and; (2) low availability of pelagic prey fish, driven by climate change (i.e. ocean warming). We therefore recommend initiating efforts for the creation of a candidate MPA between the IBA of Ria de Aveiro and the MPA of Entorno marino de las rías Baixas. This would promote effective protection and conservation of Alcidae species and threatened migratory species such as the Balearic shearwater, of which the majority of the populations spend the non-breeding period in this region (Guilford et al. 2012, Araújo et al. 2017, Pérez-Roda et al. 2017). The additional area identified in the southern coast of Portugal for non-breeders and migratory species seems relevant as a transition area between the highly productive waters off the Gulf of Cádiz and the estuarine environments of the Ria Formosa, which are very important for the conservation of Balearic shearwaters (Oppel et al. 2012, Pérez-Roda et al. 2017). Migratory birds such as the Balearic shearwater, European storm-petrel, Mediterranean gull, Common tern (*Sterna hirundo*) and Sandwich tern (*Thalasseus sandvicensis*) often make use of the southern coast of Portugal as a migratory pathway, coming from the Mediterranean Iberian coast to their respective non-breeding domains (Arcos et al. 2012).

The Spanish MPA Entorno marino de las Rías Baixas and the Gulf of Cádiz MPA lie North and East, respectively, of the area beyond the at-sea shipboard surveys that cover the study area. Our key marine areas for non-breeders and migratory species seem to anticipate the Spanish MPAs located in the northwestern (Entorno marino de las Rías Baixas MPA) and southern (Gulf of Cádiz) coast of the Iberian Peninsula, validating our results and indicating a reliable prediction of our scenarios to areas that extended beyond the Portuguese waters. Recent tracking information shows that both Spanish MPAs are also highly used by the critically endangered Balearic shearwater, which further validates our proposed key marine areas (Oppel et al. 2012, Guilford et al. 2012, Pérez-Roda et al. 2017).

5.4.2. Anthropogenic constraints and conservation implications

Our analyses based on seabird sightings from at-sea surveys showed that the current mIBAs and MPAs protect less than 4% of the areas that we prioritise for non-breeding species. However, the overlap between the already established mIBAs and the official MPAs with the coastal areas prioritised for breeders was substantially greater than the areas prioritised for non-breeding species meaning that mIBAS encompassed a little more than 35% and the national legislation near 65% of the key marine areas that we identified for breeding species. Our results are in line with those of (Krüger et al. 2017) and (Dias et al. 2017), which showed that the year-round distribution of pelagic seabirds overlapped little with both mIBAs and pelagic MPAs currently legislated for the Southwest and South Atlantic oceans. Despite the small overlap between both IBAs and MPAs and the key marine areas prioritised for non-breeding species (Ramirez et al. 2017), seabirds seemed to provide useful information for marine spatial planning (Thaxter et al. 2012, Lascelles et al. 2012, Ronconi et al. 2012).

Most MPAs are designed to reduce the impact of fishing on endangered/ protected, species (Stevenson & Tissot 2013, Schmiing et al. 2014) and few studies have accounted for other environmental stressors in the design of MPAs, such as oil pollution or commercial ship traffic. Studies comparing changes in conservation value due to the distribution of human stressors have shown ranges of change between 5% and 60% (Leathwick et al. 2008, Krüger et al. 2017). In this respect, the changes in conservation value we found were relatively low, suggesting that most of the official and proposed areas are under little or no substantial impact from human-based stressors. However, the influence of fishing density and oil pollution risk over the value of conservation in the areas we detected using the seabirds distribution provides evidence that the seabird community target areas that match the distribution of those stressors (Karpouzi et al. 2007, Hatch et al. 2008, Krüger et al. 2017). The detection and proposition of new key areas must take into consideration the restriction or management of such activities.

5.4.3. Study limitations and future guidelines

By using multi-species distribution models, we were able to identify key marine areas that were not recognised in previous marine spatial efforts for the Portuguese coast at both national and international levels. Predicting species habitat suitability using presence-only data from at-sea shipboard surveys may not be an ideal approach and the challenges found in this methodology have already been reported by other studies (Ballard et al. 2012, Fox et al. 2017). These challenges may be reflected in several spatio-temporal aspects: (1) seabird sightings within a line transect distance sampling could bring uncertainty to our analysis despite the significant seabird sightings in marine environments during the at-sea shipboard surveys (Camphuysen & Garthe 2004); (2) studies should benefit from the wealth of data from at-sea shipboard surveys that must be gathered over several years and collected year-round and thus covering the areas used by wintering and migratory species (Ballard et al. 2012); and (3) several environmental predictors should be temporally dynamic and hold distinct spatial patterns over long periods during the same time as the at-sea shipboard surveys (Fox et al. 2017). Due to limitations of the sampling method, and the possibility of biasing the survey coverage thus leading to poor modelling outcomes, we were not confident enough to include absence or abundance data (but see discussions about the relation of occurrence, density and relative abundance in Oliver et al. (2012) and Bradley (2016).

Our models presented a poor predictive ability for pelagic species that do not occur often in neritic waters. However, our study benefited from the wealth of data that have been collected over 8-years of at-sea surveys along the Portuguese coast, providing an important annual consistency and robustness to identify key marine areas. Despite being time consuming and logistically demanding, at-sea surveys are used worldwide, sometimes together with oceanographic surveys, to provide regular monitoring of marine biodiversity in coastal areas and redesign of coastal MPAs elsewhere. While in most cases the establishment of MPAs is aimed at improving the management of fishing activities (Schmiing et al. 2014), many MPAs have been implemented opportunistically without prior knowledge of how they may contribute to biodiversity conservation and which factors may threaten species and ecosystems. Despite the cumulative threats that climate change poses to marine species, human activities and other anthropogenic impacts are some of the main causes of habitat degradation (Crain et al. 2008, Maxwell & Morgan 2013, Halpern et al. 2015b). Other at-sea human activities, such as offshore wind farms, may work as a more localised but equally important threat to seabirds (Dierschke et al. 2016, Garthe et al. 2017). In this context, our study demonstrated that at-sea surveys together with human stressors potentially affecting coastal environments, are extremely useful to inform marine conservation efforts and management planning through time. At-sea surveys are also particularly important in coastal areas regarding similar oceanographic conditions characterised by the strong coastal upwelling (e.g. Canary Current ecosystem) or in countries where the marine policy is still in development.

To identify pelagic marine protected areas and improve the conservation potential of these areas we should track highly mobile marine predators throughout the year with high definition GPS tracking devices (Krüger et al. 2017). Future studies should not only focus on identifying potential conservation areas but also on assessing the habitat fidelity and inter-annual movements of mobile marine species over several years, as well as which environmental constraints are threatening their habitats, to inform decision-makers about the coherence of already established MPAs (static *vs*. seasonal MPAs), maximising their conservation potential (Ludynia et al. 2012b, Maxwell et al. 2015, Doherty et al. 2017).

5.5. Supplementary Information

Supplementary Information 1: BIOMOD2 calibration settings: Strategies to overcome uncertainty on habitat modelling

The relative importance of environmental predictors was determined using the built-in method integrated into BIOMOD2, which fits a Pearson correlation between fitted values and predictions, where each variable was randomly permutated (Scales et al. 2016). When both predictors were highly correlated the variable was considered of minor importance. To improve the robustness and to maximise the accuracy of the predictive models, different methodological strategies were set: (1) logistic output format (resulting in a probabilistic scale ranging between 0 and 1 for each grid cell, where higher scores indicate more similar environmental conditions); (2) duplicated occurrences were removed; (3) pseudo-absences were generated 10 000 randomly on 20 iterations; and (4) each model was set with 10-fold cross-validation, with data divided on 70% of the observed locations randomly assigned for the training area calibration and 30% of the data for validation of the same training area (Araújo & Guisan 2006, Elith et al. 2006).

Supplementary Information 2: Methods for calculating cost layers

We used cost layers in order to evaluate the effects of human activities in the change of conservation value within targeted areas. Fishing density was extracted from Blue Hub data storage (https://bluehub.jrc.ec.europa.eu/webgis_fish/) which stores high-resolution data on fishing intensity off European Union waters. This data represents the density of vessels above 15 m length and was calculated from 150 million positions recorded in Europe from September 2014 to September 2015. Details on the calculation of the density are available in (Natale et al. 2015) and (Vespe et al. 2016). Oil risk was calculated based on the occurrence of ports, oil rigs and zones of risk of oil spills (Halpern et al. 2008, 2015b) the position of oil refineries in Portugal. The risk was calculated based on the distance from those points with the distance from refineries having double the weight on the calculation of risk. Ship traffic was also based on the data from (Halpern et al. 2008, 2015b), which is composed of more than one million of Vessel Monitoring System positions from 3374 commercial ships Oil pollution and commercial ship traffic data were extracted from (Halpern et al. 2015a).

Table S5.1: *Description of the environmental predictors used for the modelling calibration process, data source and associated oceanographic processes. Dynamic variables were extracted as monthly mean composites. All the predictors were assembled as the same cell.*

Explanatory variables	Satellite	Spatial resolution	Oceanographic processes
Dynamic			
Sea Surface Temperature (SST, °C)	Aqua MODIS	0.04°	Water masses distribution
Sea Surface Temperature anomaly (SSTA, °C)	Aqua MODIS	0.04°	Water masses distribution
Sea Surface Temperature gradient (SSTG, %)	Aqua MODIS	0.04°	Oceanic fronts
Sea Surface Height anomaly (SSHA, m)	AVISO	0.04°	Presence of eddies
Chlorophyll-*a* concentration (CHL, mg m^{-3})	Aqua MODIS	0.04°	Ocean productivity domains
Chlorophyll-*a* anomaly (CHLA, mg m^{-3})	Aqua MODIS	0.04°	Ocean productivity domains
Chlorophyll-*a* gradient (CHLG, %)	Aqua MODIS	0.04°	Oceanic fronts
Chlorophyll-*a* peak (CHL, mg m^{-3})	Aqua MODIS	0.04°	Ocean productivity persistence
Static			
Bathymetry (BAT, m)	ETOPO 1	0.01°	Ocean depth
Bathymetry gradient (BATG, %)	ETOPO 1	0.01°	Oceanic deep surface slope
Distance to land (DCOAST, Km)	Computed in R environment	0.04°	Maximum distance to coastline

Table S5.2: *Seabird species information included in this study. Species phenology in mainland Portugal, IUCN conservation status and global population trend were also shown for 2018. IUCN conservation status: LC- least concern; VU- vulnerable; NT- near threatened; CR- critically endangered.*

Species	Common name	Phenology in mainland Portugal	IUCN status (2018)	IUCN global trend (2018)
Alca torda	Razorbill	Migrator	NT	Increasing
Ardenna gravis	Great shearwater	Migrator	LC	Stable
Ardenna grisea	Sooty shearwater	Migrator	NT	Decreasing
Bulweria bulwerii	Bulwer's petrel	Migrator	LC	Stable
Calonectris borealis	Cory's shearwater	Summer breeder	LC	Decreasing
Catharacta skua	Great skua	Migrator	LC	Decreasing
Fratercula arctica	Atlantic puffin	Migrator	VU	Decreasing
Hydrobates castro	Band-rumped storm-petrel	Winter breeder	LC	Decreasing
Hydrobates pelagicus	European storm-petrel	Migrator	LC	Decreasing
Larus audouinii	Audouin's gull	Summer breeder	LC	Stable
Larus fuscus	Lesser black-backed gull	Migrator	LC	Increasing
Larus marinus	Great black-backed gull	Migrator	LC	Increasing
Larus melanocephalus	Mediterranean gull	Migrator	LC	Stable
Larus michahellis	Yellow-legged gull	Summer breeder	LC	Increasing
Melanitta nigra	Common scoter	Migrator	LC	Decreasing
Morus bassanus	Northern gannet	Migrator	LC	Increasing
Oceanites oceanicus	Wilson's storm petrel	Migrator	LC	Stable
Gulosus aristotelis	European shag	Summer breeder	LC	Decreasing
Phalacrocorax carbo	Great cormorant	Migrator	LC	Increasing
Phalaropus fulicarius	Red phalarope	Migrator	LC	Decreasing
Puffinus mauretanicus	Balearic shearwater	Migrator	CR	Decreasing
Puffinus puffinus	Manx shearwater	Migrator	LC	Decreasing
Rissa tridactyla	Black-legged gull	Migrator	LC	Decreasing
Stercorarius parasiticus	Arctic jaeger	Migrator	LC	Stable
Stercorarius pomarinus	Pomarine jaeger	Migrator	LC	Stable
Sterna hirundo	Common tern	Migrator	LC	Decreasing
Sterna paradisaea	Arctic tern	Migrator	LC	Decreasing
Sternula albifrons	Little tern	Summer breeder	LC	Decreasing
Thalasseus sandvicensis	Sandwich tern	Migrator	LC	Stable
Uria aalge	Common guillemot	Migrator	LC	Increasing

Table S5.3: *Means ± SD of the modelling technique accuracy measured as the Area Under the ROC Curve (AUC), and True Skill Statistic (TSS) for each seabird species: Artificial Neural Networks (ANN), Classification Tree Analysis (CTA), Flexible Discriminant Analysis (FDA), Generalised Additive Models (GAM), Generalised Boosting Models (GBM), Generalized Linear Models (GLM), Multiple Adaptive Regression Splines (MARS), Maximum Entropy Models (MAXENT), Breiman and Cutlers Random Forest for classification and regression (RF) and Surface Range Envelops (SRE).*

	ANN		**CTA**		**FDA**		**GAM**		**GBM**	
Species	**AUC**	**TSS**	**AUC**	**TSS**	**AUC**	**TSS**	**AUC**	**TSS**	**AUC**	**TSS**
Alca torda	0.98 ± 0.00	0.93 ± 0.01	0.96 ± 0.01	0.92 ± 0.02	0.97 ± 0.01	0.89 ± 0.02	0.98 ± 0.00	0.92 ± 0.02	0.99 ± 0.00	0.93 ± 0.02
Ardenna gravis	0.87 ± 0.03	0.71 ± 0.07	0.86 ± 0.03	0.72 ± 0.05	0.88 ± 0.03	0.73 ± 0.05	0.85 ± 0.04	0.68 ± 0.06	0.90 ± 0.02	0.76 ± 0.05
Ardenna grisea	0.92 ± 0.03	0.82 ± 0.05	0.90 ± 0.03	0.80 ± 0.05	0.94 ± 0.02	0.83 ± 0.04	0.91 ± 0.03	0.78 ± 0.06	0.94 ± 0.02	0.83 ± 0.04
Bulweria bulwerii	0.75 ± 0.11	0.49 ± 0.18	0.68 ± 0.05	0.36 ± 0.08	0.79 ± 0.07	0.51 ± 0.12	0.71 ± 0.11	0.43 ± 0.24	0.82 ± 0.04	0.58 ± 0.08
Calonectris borealis	0.92 ± 0.01	0.75 ± 0.02	0.89 ± 0.02	0.75 ± 0.02	0.92 ± 0.01	0.75 ± 0.02	0.94 ± 0.01	0.77 ± 0.01	0.92 ± 0.01	0.75 ± 0.01
Catharacta skua	0.97 ± 0.00	0.88 ± 0.01	0.95 ± 0.01	0.88 ± 0.01	0.97 ± 0.00	0.87 ± 0.01	0.97 ± 0.00	0.88 ± 0.01	0.97 ± 0.00	0.89 ± 0.01
Fratercula arctica	0.73 ± 0.23	0.87 ± 0.11	0.71 ± 0.25	0.87 ± 0.12	0.91 ± 0.07	0.79 ± 0.14	0.87 ± 0.10	0.71 ± 0.18	0.86 ± 0.17	0.72 ± 0.24
Hydrobates castro	0.74 ± 0.05	0.46 ± 0.08	0.77 ± 0.06	0.52 ± 0.10	0.18 ± 0.06	0.01 ± 0.01	0.72 ± 0.05	0.45 ± 0.07	0.85 ± 0.03	0.63 ± 0.05
Hydrobates pelagicus	0.93 ± 0.01	0.83 ± 0.02	0.91 ± 0.01	0.82 ± 0.03	0.94 ± 0.01	0.82 ± 0.02	0.94 ± 0.01	0.80 ± 0.03	0.96 ± 0.01	0.85 ± 0.01
Larus audouinii	0.95 ± 0.05	0.89 ± 0.07	0.93 ± 0.05	0.86 ± 0.10	0.98 ± 0.01	0.92 ± 0.04	0.87 ± 0.07	0.74 ± 0.14	0.99 ± 0.00	0.94 ± 0.03
Larus fuscus	0.96 ± 0.01	0.86 ± 0.02	0.92 ± 0.01	0.84 ± 0.02	0.96 ± 0.00	0.85 ± 0.02	0.96 ± 0.01	0.86 ± 0.02	0.97 ± 0.01	0.87 ± 0.02
Larus marinus	0.97 ± 0.00	0.88 ± 0.01	0.94 ± 0.01	0.87 ± 0.01	0.96 ± 0.00	0.87 ± 0.01	0.97 ± 0.00	0.88 ± 0.01	0.97 ± 0.00	0.88 ± 0.01
Larus melanocephalus	0.93 ± 0.02	0.84 ± 0.04	0.93 ± 0.01	0.86 ± 0.03	0.95 ± 0.01	0.86 ± 0.02	0.95 ± 0.02	0.85 ± 0.05	0.96 ± 0.01	0.86 ± 0.03
Larus michahellis	0.97 ± 0.00	0.89 ± 0.01	0.95 ± 0.01	0.89 ± 0.02	0.97 ± 0.00	0.89 ± 0.01	0.97 ± 0.00	0.90 ± 0.01	0.98 ± 0.00	0.90 ± 0.01
Melanitta nigra	0.96 ± 0.05	0.89 ± 0.05	0.93 ± 0.04	0.87 ± 0.06	0.97 ± 0.01	0.88 ± 0.03	0.94 ± 0.02	0.86 ± 0.03	0.98 ± 0.01	0.90 ± 0.02
Morus bassanus	0.98 ± 0.00	0.93 ± 0.01	0.98 ± 0.00	0.93 ± 0.01	0.98 ± 0.00	0.92 ± 0.01	0.98 ± 0.00	0.93 ± 0.01	0.99 ± 0.00	0.93 ± 0.01
Oceanites oceanicus	0.89 ± 0.03	0.75 ± 0.04	0.85 ± 0.04	0.71 ± 0.05	0.89 ± 0.03	0.72 ± 0.06	0.84 ± 0.01	0.64 ± 0.17	0.93 ± 0.02	0.77 ± 0.05
Gulosus aristotelis	0.98 ± 0.03	0.96 ± 0.05	0.98 ± 0.03	0.93 ± 0.07	0.96 ± 0.05	0.94 ± 0.06	0.89 ± 0.06	0.77 ± 0.13	1.00 ± 0.00	0.98 ± 0.01
Phalacrocorax carbo	0.80 ± 0.12	0.63 ± 0.22	0.87 ± 0.10	0.98 ± 0.07	0.89 ± 0.18	0.78 ± 0.21	0.90 ± 0.08	0.77 ± 0.14	0.83 ± 0.12	0.13 ± 0.20

Phalaropus fulicarius	0.76 ± 0.08	0.52 ± 0.15	0.72 ± 0.06	0.46 ± 0.14	0.82 ± 0.08	0.59 ± 0.12	0.73 ± 0.09	0.49 ± 0.16	0.84 ± 0.08	0.65 ± 0.14
Puffinus mauretanicus	0.97 ± 0.00	0.90 ± 0.01	0.95 ± 0.01	0.90 ± 0.01	0.97 ± 0.00	0.89 ± 0.01	0.98 ± 0.00	0.90 ± 0.01	0.98 ± 0.00	0.91 ± 0.01
Puffinus puffinus	0.72 ± 0.08	0.41 ± 0.12	0.78 ± 0.04	0.54 ± 0.06	0.81 ± 0.02	0.52 ± 0.05	0.76 ± 0.06	0.44 ± 0.09	0.87 ± 0.03	0.62 ± 0.05
Rissa tridactyla	0.82 ± 0.06	0.61 ± 0.09	0.85 ± 0.05	0.66 ± 0.06	0.84 ± 0.04	0.62 ± 0.05	0.87 ± 0.03	0.62 ± 0.05	0.93 ± 0.02	0.76 ± 0.06
Sterna hirundo	0.83 ± 0.05	0.66 ± 0.01	0.86 ± 0.04	0.72 ± 0.07	0.89 ± 0.02	0.71 ± 0.04	0.89 ± 0.02	0.71 ± 0.04	0.93 ± 0.01	0.78 ± 0.03
Sterna paradisaea	0.69 ± 0.24	0.46 ± 0.34	0.82 ± 0.15	0.64 ± 0.29	0.89 ± 0.16	0.76 ± 0.20	0.55 ± 0.09	0.11 ± 0.18	0.87 ± 0.11	0.64 ± 0.29
Sternula albifrons	0.88 ± 0.07	0.75 ± 0.15	0.87 ± 0.10	0.75 ± 0.20	0.80 ± 0.13	0.68 ± 0.14	0.59 ± 0.11	0.22 ± 0.16	0.84 ± 0.11	0.76 ± 0.16
Stercorarius parasiticus	0.78 ± 0.10	0.62 ± 0.12	0.83 ± 0.04	0.65 ± 0.08	0.85 ± 0.05	0.65 ± 0.08	0.77 ± 0.07	0.50 ± 0.10	0.89 ± 0.03	0.72 ± 0.07
Stercorarius pomarinus	0.82 ± 0.08	0.65 ± 0.10	0.83 ± 0.05	0.67 ± 0.10	0.67 ± 0.36	0.51 ± 0.32	0.82 ± 0.07	0.60 ± 0.12	0.91 ± 0.02	0.74 ± 0.04
Thalasseus sandvicensis	0.95 ± 0.01	0.86 ± 0.02	0.92 ± 0.02	0.84 ± 0.02	0.96 ± 0.01	0.84 ± 0.02	0.96 ± 0.01	0.85 ± 0.01	0.96 ± 0.01	0.87 ± 0.02
Uria aalge	0.99 ± 0.01	0.92 ± 0.02	0.96 ± 0.02	0.93 ± 0.02	0.97 ± 0.02	0.92 ± 0.03	0.97 ± 0.03	0.95 ± 0.03	0.99 ± 0.01	0.94 ± 0.02

	GLM		**MARS**		**MAXENT**		**RF**		**SRE**	
Species	**AUC**	**TSS**	**AUC**	**TSS**	**AUC**	**TSS**	**AUC**	**TSS**	**AUC**	**TSS**
Alca torda	0.99 ± 0.00	0.93 ± 0.01	0.99 ± 0.00	0.93 ± 0.01	0.93 ± 0.04	0.84 ± 0.07	0.99 ± 0.00	0.92 ± 0.01	0.84 ± 0.02	0.68 ± 0.05
Ardenna gravis	0.84 ± 0.09	0.68 ± 0.17	0.88 ± 0.02	0.88 ± 0.05	0.89 ± 0.02	0.76 ± 0.05	0.89 ± 0.03	0.71 ± 0.05	0.67 ± 0.04	0.34 ± 0.07
Ardenna grisea	0.93 ± 0.02	0.83 ± 0.04	0.92 ± 0.06	0.80 ± 0.09	0.95 ± 0.02	0.85 ± 0.04	0.93 ± 0.02	0.79 ± 0.03	0.78 ± 0.03	0.56 ± 0.06
Bulweria bulwerii	0.72 ± 0.06	0.46 ± 0.09	0.69 ± 0.17	0.37 ± 0.13	0.82 ± 0.05	0.60 ± 0.10	0.76 ± 0.06	0.49 ± 0.08	0.74 ± 0.07	0.48 ± 0.14
Calonectris borealis	0.92 ± 0.01	0.75 ± 0.01	0.93 ± 0.01	0.76 ± 0.02	0.92 ± 0.01	0.74 ± 0.02	0.94 ± 0.01	0.78 ± 0.01	0.68 ± 0.02	0.36 ± 0.04
Catharacta skua	0.97 ± 0.00	0.88 ± 0.01	0.97 ± 0.00	0.88 ± 0.01	0.97 ± 0.00	0.88 ± 0.01	0.98 ± 0.01	0.89 ± 0.01	0.85 ± 0.02	0.69 ± 0.04
Fratercula arctica	0.90 ± 0.06	0.76 ± 0.11	0.87 ± 0.09	0.72 ± 0.17	0.90 ± 0.07	0.77 ± 0.10	0.90 ± 0.07	0.78 ± 0.12	0.88 ± 0.08	0.72 ± 0.14
Hydrobates castro	0.73 ± 0.11	0.46 ± 0.11	0.83 ± 0.05	0.61 ± 0.09	0.85 ± 0.04	0.64 ± 0.08	0.82 ± 0.04	0.64 ± 0.10	0.58 ± 0.03	0.16 ± 0.07
Hydrobates pelagicus	0.95 ± 0.01	0.84 ± 0.02	0.95 ± 0.02	0.86 ± 0.03	0.96 ± 0.01	0.84 ± 0.01	0.95 ± 0.02	0.84 ± 0.03	0.83 ± 0.02	0.66 ± 0.05
Larus audouinii	0.97 ± 0.02	0.91 ± 0.05	0.96 ± 0.02	0.93 ± 0.04	0.99 ± 0.00	0.95 ± 0.04	0.98 ± 0.00	0.94 ± 0.03	0.79 ± 0.07	0.59 ± 0.13
Larus fuscus	0.96 ± 0.01	0.86 ± 0.02	0.96 ± 0.01	0.86 ± 0.02	0.94 ± 0.07	0.81 ± 0.13	0.97 ± 0.01	0.87± 0.02	0.83 ± 0.02	0.66 ± 0.05
Larus marinus	0.97 ± 0.00	0.88 ± 0.01	0.97 ± 0.00	0.88 ± 0.01	0.95 ± 0.05	0.82 ± 0.08	0.98 ± 0.00	0.88 ± 0.01	0.85 ± 0.02	0.70 ± 0.03
Larus melanocephalus	0.95 ± 0.01	0.86 ± 0.02	0.95 ± 0.01	0.86 ± 0.03	0.95 ± 0.04	0.85 ± 0.07	0.96 ± 0.01	0.85 ± 0.03	0.84 ± 0.03	0.68 ± 0.07

Larus michahellis	0.97 ± 0.00	0.89 ± 0.01	0.98 ± 0.00	0.90 ± 0.01	0.98 ± 0.00	0.89 ± 0.01	0.98 ± 0.00	0.90 ± 0.01	0.85 ± 0.01	0.70 ± 0.02
Melanitta nigra	0.98 ± 0.00	0.92 ± 0.02	0.96 ± 0.02	0.89 ± 0.04	0.90 ± 0.12	0.75 ± 0.22	0.97 ± 0.02	0.88 ± 0.04	0.83 ± 0.05	0.66 ± 0.10
Morus bassanus	0.97 ± 0.02	0.91 ± 0.03	0.99 ± 0.00	0.93 ± 0.01	0.98 ± 0.00	0.91 ± 0.02	0.99 ± 0.00	0.94 ± 0.01	0.87 ± 0.01	0.74 ± 0.01
Oceanites oceanicus	0.91 ± 0.02	0.76 ± 0.04	0.92 ± 0.04	0.79 ± 0.07	0.93 ± 0.02	0.80 ± 003	0.93 ± 0.03	0.74 ± 0.06	0.61 ± 0.06	0.22 ± 0.10
Gulosus aristotelis	0.97 ± 0.04	0.93 ± 0.09	0.93 ± 0.06	0.87 ± 0.12	1.00 ± 0.00	0.97 ± 0.02	0.98 ± 0.03	0.93 ± 0.06	0.81 ± 0.09	0.62 ± 0.19
Phalacrocorax carbo	0.73 ± 0.14	0.47 ± 0.27	0.64 ± 0.16	0.26 ± 0.33	0.97 ± 0.02	0.94 ± 0.04	0.82 ± 0.11	0.64 ± 0.22	0.53 ± 0.07	0.14 ± 0.06
Phalaropus fulicarius	0.70 ± 0.06	0.48 ± 0.08	0.74 ± 0.05	0.48 ± 0.08	0.84 ± 0.05	0.65 ± 0.11	0.82 ± 0.09	0.65 ± 0.11	0.57 ± 0.08	0.15 ± 0.13
Puffinus mauretanicus	0.97 ± 0.00	0.89 ± 0.01	0.98 ± 0.00	0.90 ± 0.01	0.96 ± 0.05	0.86 ± 0.09	0.98 ± 0.00	0.90 ± 0.01	0.85 ± 0.02	0.70 ± 0.03
Puffinus puffinus	0.81 ± 0.04	0.55 ± 0.03	0.77 ± 0.07	0.49 ± 0.01	0.80 ± 0.11	0.50 ± 0.18	0.83 ± 0.03	0.52 ± 0.04	0.53 ± 0.04	0.07 ± 0.02
Rissa tridactyla	0.88 ± 0.03	0.64 ± 0.06	0.90 ± 0.03	0.71 ± 0.05	0.90 ± 0.03	0.71 ± 0.05	0.93 ± 0.03	0.72 ± 0.72	0.65 ± 0.04	0.30 ± 0.08
Sterna hirundo	0.91 ± 0.02	0.74 ± 0.04	0.92 ± 0.03	0.77 ± 0.05	0.91 ± 0.02	0.75 ± 0.04	0.91 ± 0.02	0.75 ± 0.04	0.74 ± 0.03	0.47 ± 0.07
Sterna paradisaea	0.83 ± 0.12	0.73 ± 0.18	0.78 ± 0.14	0.56 ± 0.28	0.83 ± 0.16	0.74 ± 0.23	0.74 ± 0.08	0.51 ± 0.15	0.67 ± 0.12	0.34 ± 0.24
Sternula albifrons	0.96 ± 0.04	0.90 ± 0.08	0.84 ± 0.09	0.69 ± 0.19	0.69 ± 0.00	0.93 ± 0.01	0.82 ± 0.09	0.66 ± 0.17	0.67 ± 0.11	0.34 ± 0.23
Stercorarius parasiticus	0.88 ± 0.04	0.70 ± 0.19	0.81 ± 0.05	0.61 ± 0.07	0.60 ± 0.16	0.32 ± 0.20	0.85 ± 0.05	0.63 ± 0.09	0.66 ± 0.07	0.33 ± 0.14
Stercorarius pomarinus	0.89 ± 0.04	0.73 ± 0.05	0.88 ± 0.04	0.71 ± 0.05	0.92 ± 0.01	0.74 ± 0.06	0.87 ± 0.03	0.71 ± 0.06	0.71 ± 0.07	0.41 ± 0.13
Thalasseus sandvicensis	0.96 ± 0.01	0.87 ± 0.02	0.96 ± 0.01	0.86 ± 0.02	0.96 ± 0.01	0.86 ± 0.02	0.97 ± 0.01	0.85 ± 0.02	0.81 ± 0.02	0.63 ± 0.04
Uria aalge	0.99 ± 0.00	0.94 ± 0.02	0.99 ± 0.01	0.94 ± 0.02	0.91 ± 0.04	0.81 ± 0.08	0.99 ± 0.01	0.94 ± 0.02	0.84 ± 0.03	0.69 ± 0.06

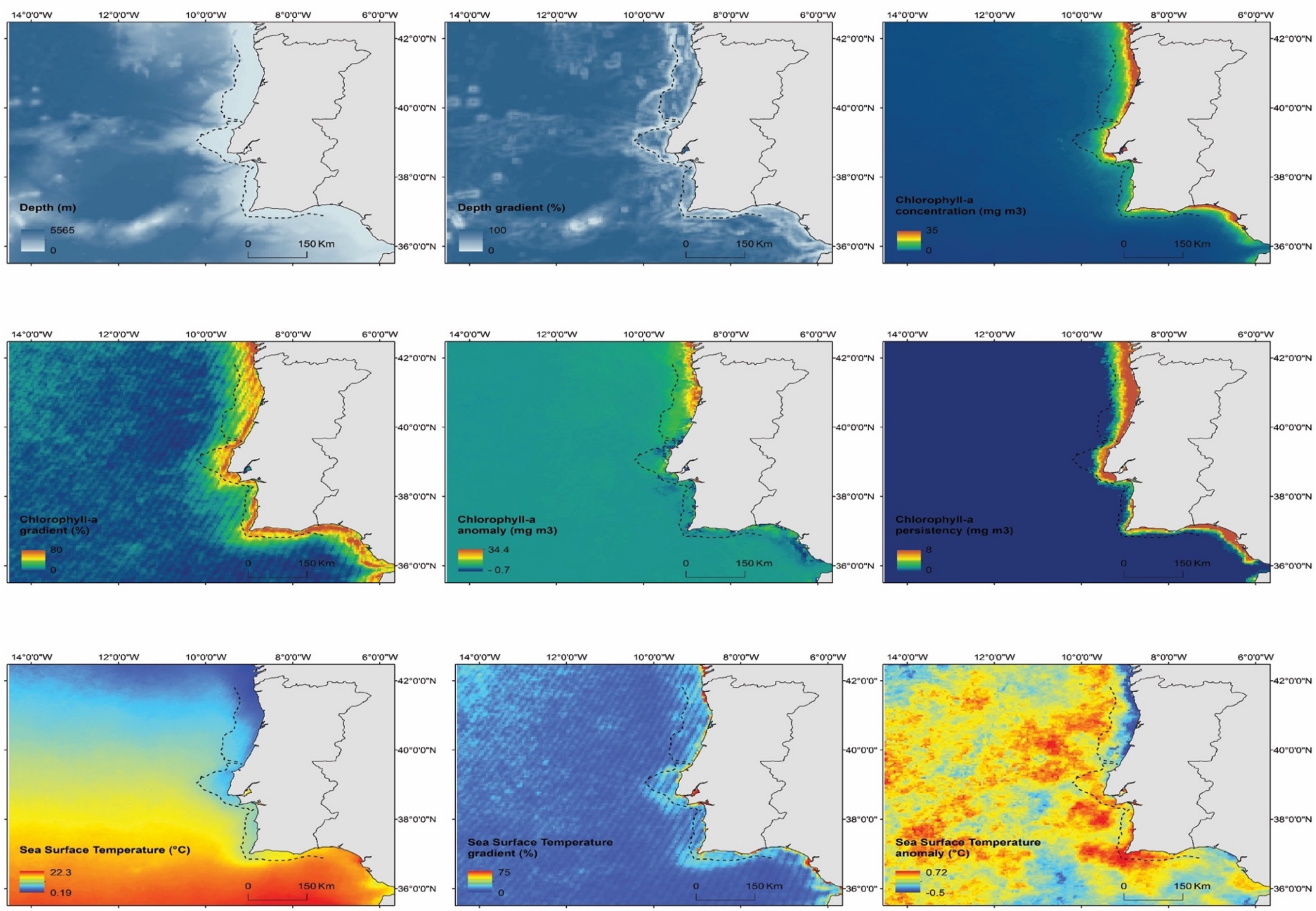


Figure S5.1: *Environmental predictors used for Ensemble Ecological Niche Modelling. The 200 m isobath is also shown (black dotted line).*

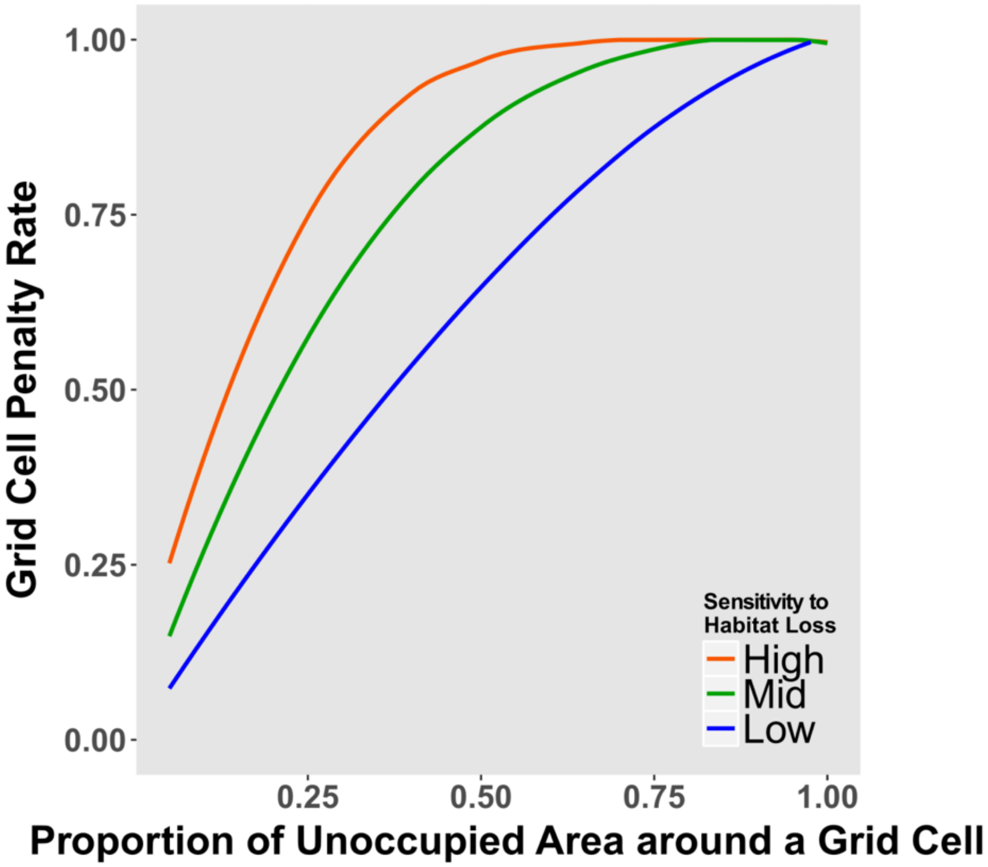


Figure S5.2: *Boundary Quality Penalty curves constructed based on the sensitivity of species to habitat loss around an unoccupied cell. The penalty rate is the proportion of value decreased for a given cell if the proportion of cells around it is unoccupied by the species. The proportion is calculated in the grid size of the species files and varies depending on the known mobility of each species and its IUCN conservation status. The proportion for highly mobile species is calculated using more grid cells than the less mobile ones.*

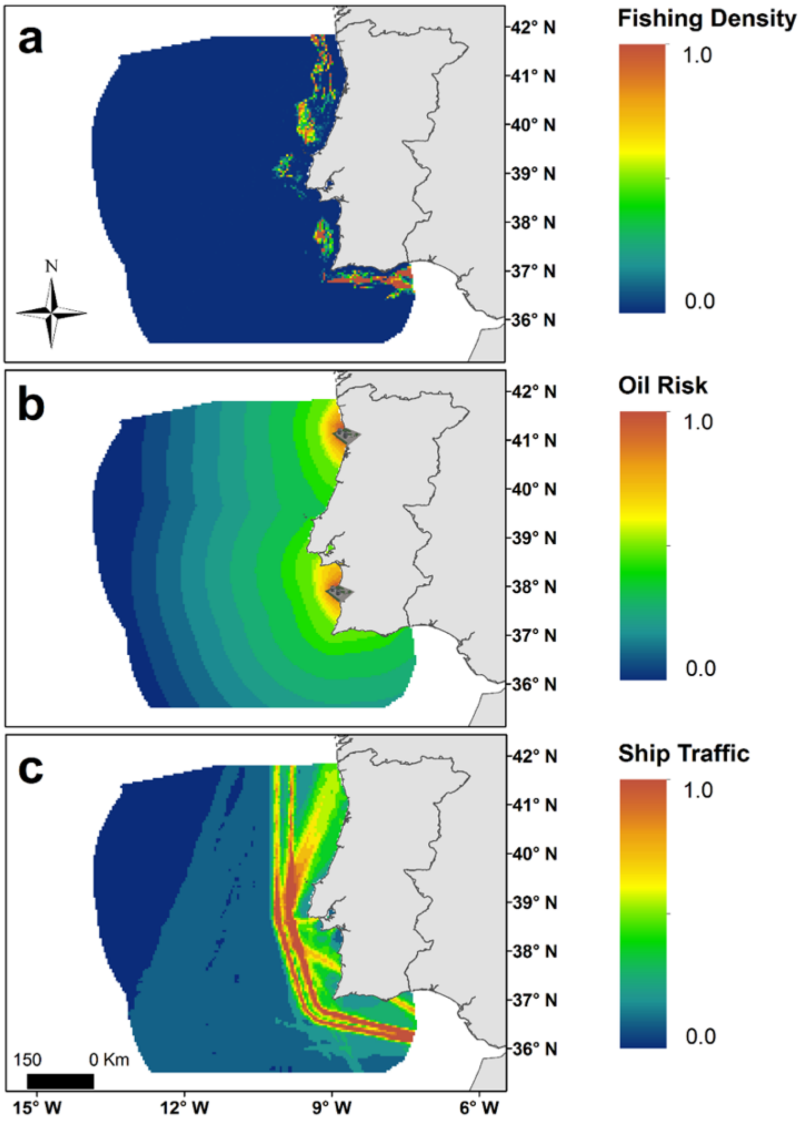


Figure S5.3: *Cost layers rescaled from 0 to 1, based on the maximum value: (a) Fishing Density; (b) Oil Risk; and (c) Ship Traffic.*

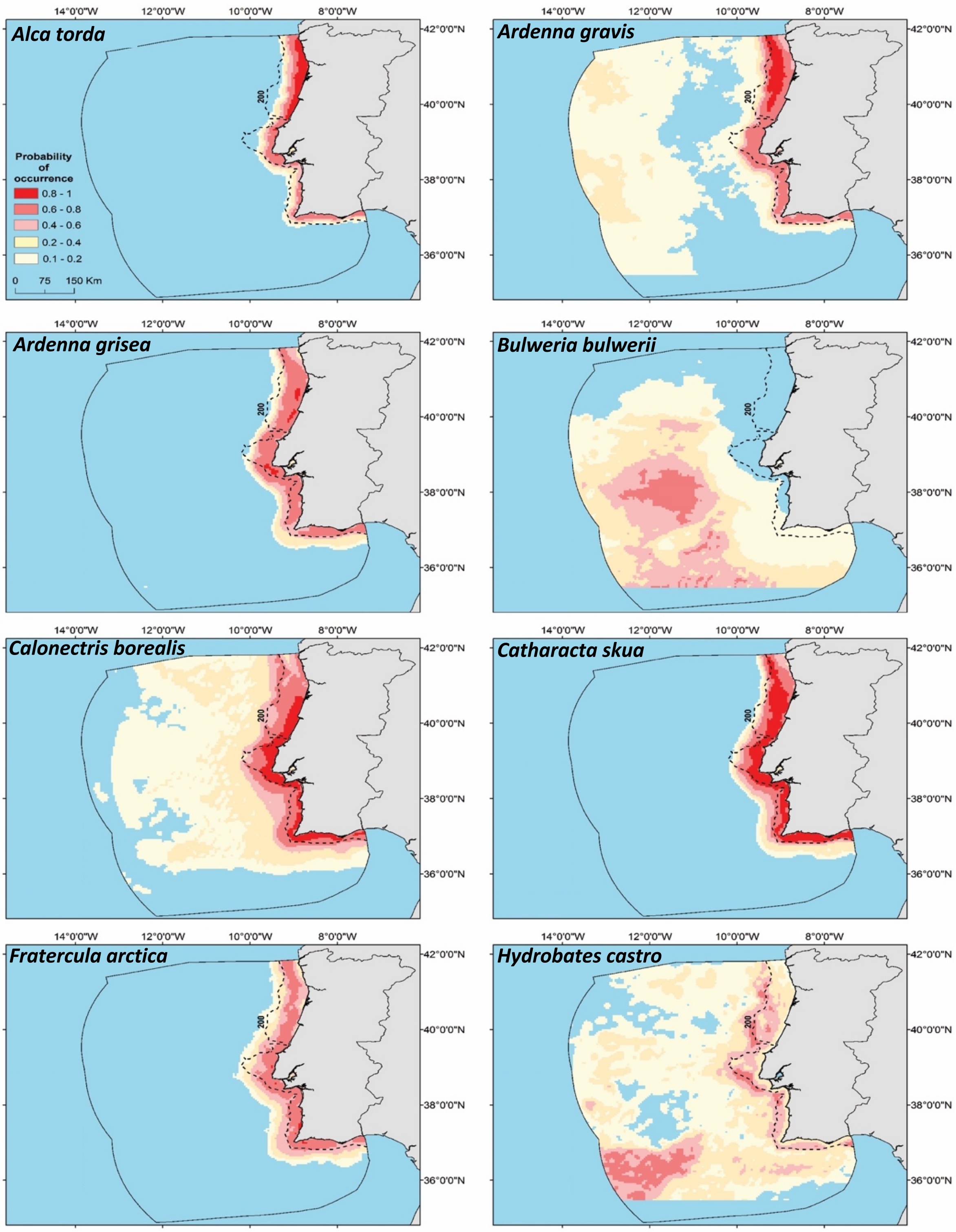


Figure S5.4: *Predicted distribution for all seabird species (integrated in this study) by projecting the Ensemble Ecological Niche Models (EENMs) over the Portuguese Continental Exclusive Economic Zone (EEZ; black fill line). EENMs ranges from low (0) to high (1) records of probability of occurrence on a constant colour ramp between plots. The 200 m isobath is also shown (black dotted line).*

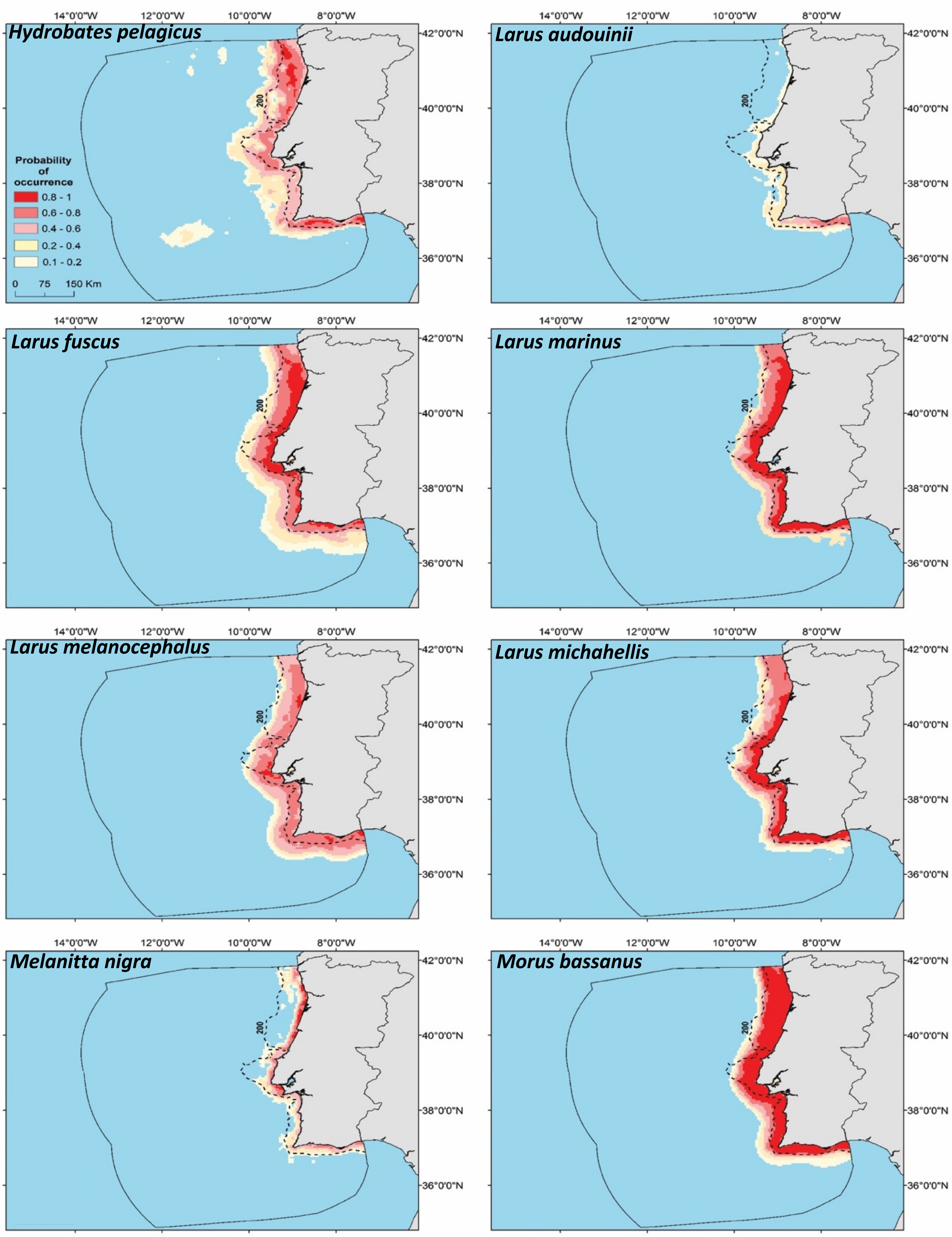
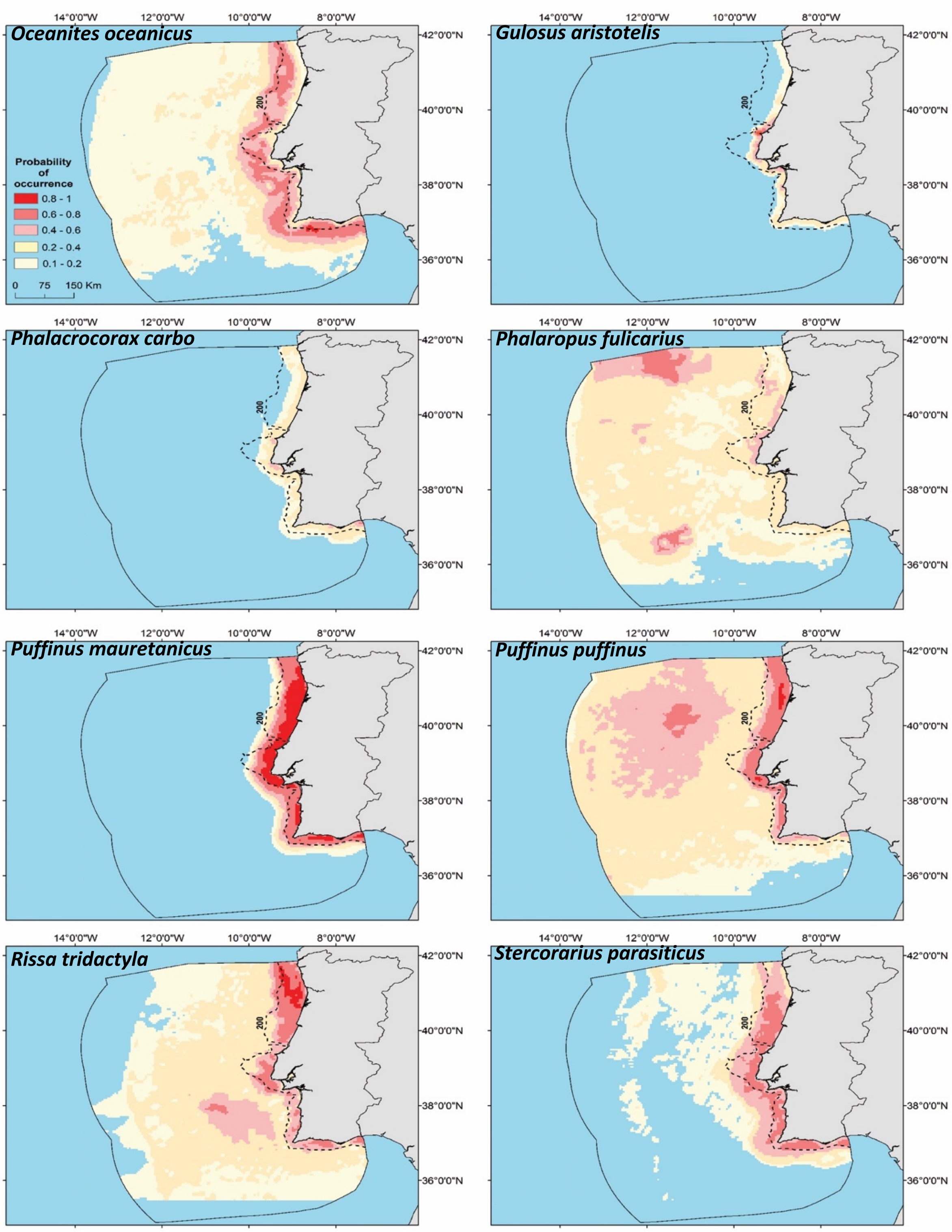


Figure S5.4: *Continuation.*



Oceanites oceanicus

Gulosus aristotelis

Phalacrocorax carbo

Phalaropus fulicarius

Puffinus mauretanicus

Puffinus puffinus

Rissa tridactyla

Stercorarius parasiticus

Figure S5.4: *Continuation.*

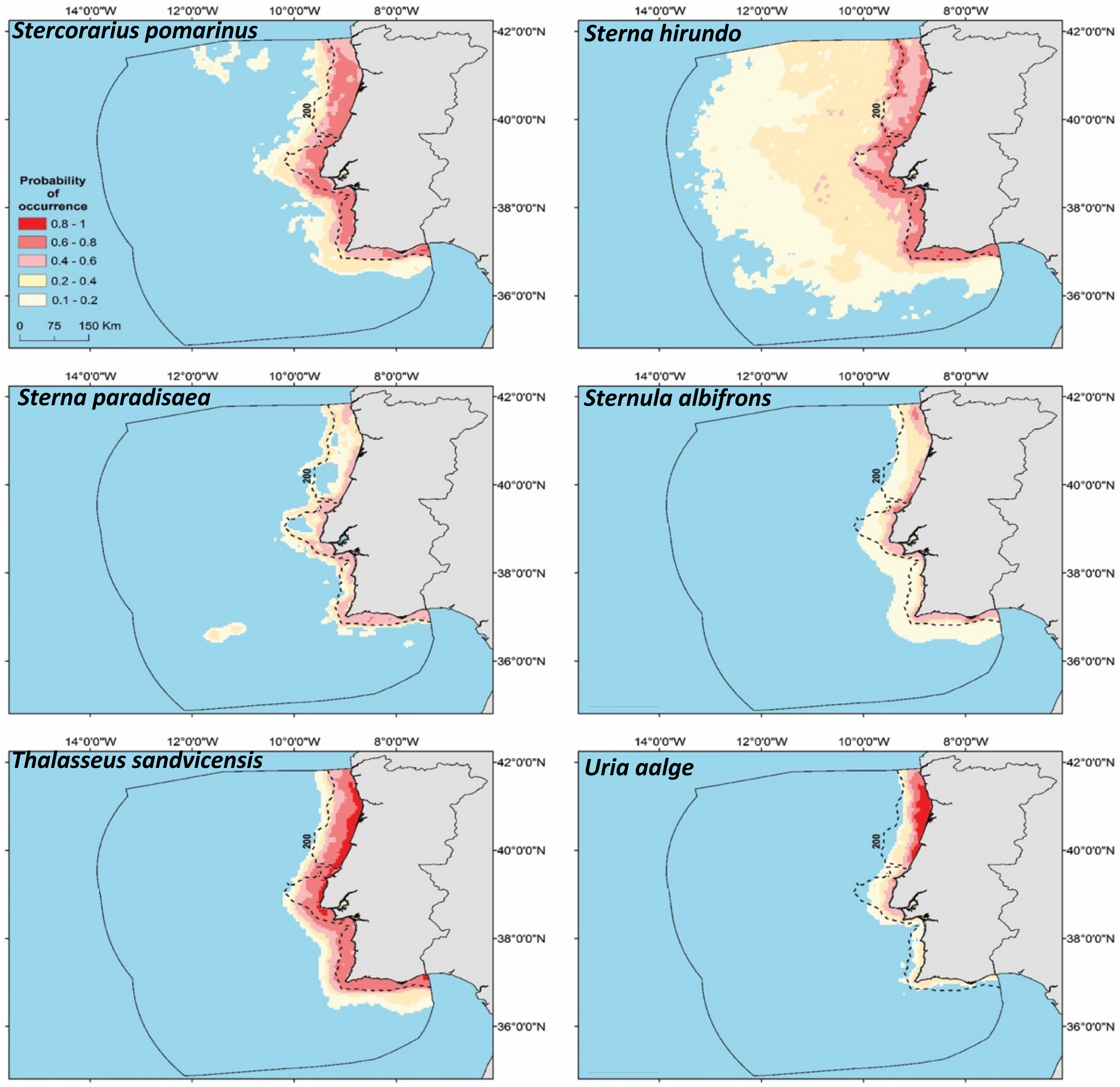


Figure S5.4: *Continuation.*

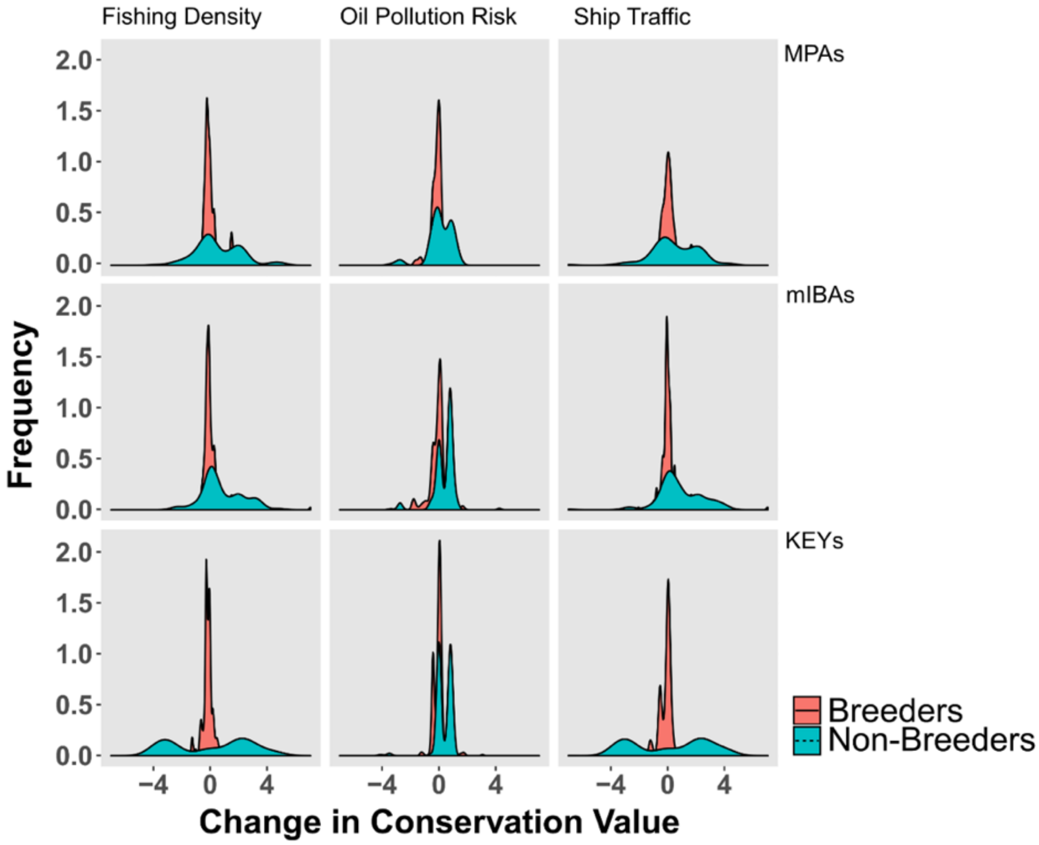


Figure S5.5: *Frequency distribution of the change in conservation value by species phenology (breeders and non-breeders), Target Areas (important bird and biodiversity areas IBAs, our proposed key areas KEYs and marine protected areas MPAs) and Human Activities (Costs).*

Chapter 6

General Discussion

6.1. Overview of the thesis

The results of this thesis allow a better understanding of the mechanisms underpinning the effects of spatio-temporal environmental variability on the at-sea behaviour and foraging decisions of Cory' shearwaters and other seabirds. It also provides a more complete understanding on the spatial overlap between Cory's shearwaters and industrial fisheries within the Portuguese EEZ. Lastly, this work recommends an adaptive framework for the identification of important areas for seabirds which maximise conservation targets, while accounting for anthropogenic pressures in the Portuguese coast.

More specifically, the main results of this thesis are: (1) seabird tracking is essential for the ecology of marine top predators and towards the prioritisation of conservation goals (Chapter 1); (2) individual-level memory of resource availability and predictability can be an important mechanism explaining spatial foraging segregation within seabird colonies during the breeding period (Chapter 2); (3) Cory's shearwaters from neritic and oceanic populations in the mid-North Atlantic Ocean exhibit contrasting foraging behavioural decisions in response to NAO index (Chapter 3); (4) during the breeding season, Cory's shearwaters rarely forage in the same areas as commercial fishing vessels within the EEZ of mainland Portugal. Yet, Cory's shearwaters are more likely to overlap in the same areas as fixed gear vessels (set longlines, set gillnets, pots and traps) and purse seiners during the pre-laying than during chick-rearing, but less likely to vary among genders and individual boldness (Chapter 4); and (5) the current network of MPAs along the West coast of Portugal is effective for protecting the habitats used by breeding seabirds, but not for those used by non-breeding seabirds (Chapter 5). Main conclusions, limitations, and wider implications of the results of this thesis are discussed in the Chapter 6. Topics that deserve future consideration and research are also discussed below.

6.2. Challenges and future of seabird tracking

Chapter 1 shows how tracking seabird movements have proved invaluable for ecological investigation and for resolving marine conservation issues. Looking forward, it seems likely that developments in hardware and analysis techniques are expected to lead to further discoveries (Hays et al. 2016, Sequeira et al. 2019a). The tendency of devices to become smaller and lighter will allow tracking smaller seabird species, and development of new sensors will provide extra information on behaviour and physiology, as well as environmental conditions (Wilmers et al. 2015, Williams et al. 2020). However, one of the major constraints is battery optimization. Many seabird tracking devices contain lithium batteries, which are ideal for short-term studies but have a relatively short lifespan (usually three or four years for larger batteries), because of a limited number of charging-discharging cycles and vulnerabilities to moisture and salt ingress. Moreover, small batteries may become rapidly depleted if they are unable to locate a satellite, which is particularly problematic for burrow-nesting species, especially during long incubation shifts. GPS-GSM transmitters and other tracking devices equipped with photovoltaic solar-panels are expected to overcome some of the issues related with battery capacity. Soon, scientists will also be able to track birds from space using the international cooperation for animal research using space (ICARUS) initiative. The ICARUS solar-powered transmitters are < 5 g enabling to track a greater number of seabirds, including many poorly-studied smaller species (Wikelski et al. 2007). It is particularly challenging to gather data during the period of seabird immaturity, before first reproduction. So far, studies on movements and at-sea behaviour of early-life stages are more common for medium and large sized seabirds, such as sulids, albatrosses, penguins, petrels and shearwaters (Votier et al. 2017, de Grissac et al. 2017, Orgeret et al. 2019, Louzao et al. 2021), but for smaller species, there is virtually no data (Bicknell et al. 2014).

The widespread use of tracking devices has led to arguing how many and for how long individuals should be tracked to represent the overall behaviour of the population (Sequeira et al. 2019b). Previous studies revealed the importance of sample sizes to make reliable predictions of a population's at-sea distribution (Soanes et al. 2013a, Lascelles et al. 2016). Small sample sizes may not represent the overall colony-level distributions, but rather represent just a small proportion of the population. Larger sample sizes will provide greater confidence in species- or population-level inferences.

Simultaneously, new analytical techniques and visualisation tools will add interpretation of movement data (Fan et al. 2014, Joo et al. 2020). Animal movements often contain noisy, non-linear, spatially and temporally correlated artifacts, requiring a high degree of analytical proficiency to infer behaviours at appropriate spatio-temporal scales (Patterson et al. 2017). To overcome this, scientists have developed several techniques to infer behavioural classifications from movement data. Traditional movement description approaches include first-passage time (FPT), speed/sinuosity thresholds, fractal analysis, residence time and positional entropy (Bennison et al. 2018). More recently, sophisticated techniques such as machine learning and state-space modelling are gaining momentum as powerful tools to infer animal behaviour from movement data (Patterson et al. 2008, Wang 2019, Wijeyakulasuriya et al. 2020). However, these techniques usually need substantial computational capacity, high expertise from the scientist and are also prone to a certain degree of subjectivity. To simplify the behavioural classification of animal movement data, some more user friendly procedures have been recently created (Garriga et al. 2016) and applied to a wide range of seabird species (de Grissac et al. 2017, Jones et al. 2018, De Pascalis et al. 2020).

Answering more complex questions may also require a further level of refinement and instrumentation. Seabird scientists are now able to incorporate several sensors into the tracking devices to measure, for instance tri-dimensional motion, pressure, wet/dry activity and direct quantification of behaviours with the use of miniaturised cameras. Multiple sensor-based tracking can provide a detailed information of where, when and how birds use the surrounding habitat (Patterson et al. 2019), however with a high cost in terms of effort to process and analyse multiple data (Williams et al. 2020). In addition, the development of sophisticated techniques such as artificial intelligence and machine learning are emerging as cutting-edge and powerful tools to process large and complex datasets. The utilisation of ‘training-and-testing’ procedures has proven to be an efficient method for classifying and quantifying behavioural modes over large datasets composed of geographical fixes, accelerometer data and video records with high precision and accuracy (Browning et al. 2018, Yoda 2019, Korpela et al. 2020). However, these methods usually require the use of programming languages and/or processing software whose interfaces are not user friendly for those starting to learn them. With a shallow 'non-machine' learning curve, scientists need to encourage a culture of data sharing and interdisciplinary collaborative work, as a lot of time and effort investment is necessary for scientists to actually become skilled in those methods (López-López 2016).

Seabirds may be effective as ocean sentinels (Hazen et al. 2019), yet there are still many limitations for them as effective monitoring tools. For instance, marine mammals have been used as oceanographic sampling platforms - their large size permitting scientists to equip tags such as conductivity-temperature-depth (CTD) sensors to measure a variety of oceanographic variables in remote areas (Treasure et al. 2017, Nakanowatari et al. 2017, Teilmann et al. 2020). The use of seabirds in this type of remote sensing of the marine environment is still in its infancy, but with huge potential (Harcourt et al. 2019). The use of cameras coupled to GPS devices can give scientists access to environmental conditions on foraging areas, about the fish swarms being targeted by seabirds, interactions with other species and with human activities (Votier et al. 2013, Tremblay et al. 2014, Mattern et al. 2018). In addition, this will allow the identification of previously unknown foraging behaviours, like underwater vocalisations (Thiebault et al. 2019) or the consumption of prey such as jellyfish which is difficult to identify with other methods (Thiebot et al. 2017).

Overall, tracking has fundamentally altered our understanding of the at-sea behaviour of seabirds, providing novel insights for a previously cryptic part of their lives. This has been transformative in terms of conservation and marine spatial planning as it provides evidence that can be used to quantify and, in some cases, mitigate direct threats to seabird populations. It also provides us with the chance to horizon scan and cements seabirds as marine sentinels and flagships for change.

Chapter 1 provides an overview of a very large body of research, and it seems likely that this field will grow in future as tags becoming cheaper and analytical tools are shared more widely. Central to tracking being an effective tool for applied ecology is a detailed understanding of device effects. Collaboration is also crucial - seabirds are global travellers, and it is unrealistic that small research groups will have the resources to be able to operate at the necessary scales to be able to quantify this. While seabird population declines are cause for deep concern, the response of the seabird research community to tracking and its application to conservation is most encouraging.

6.3. Implications for conservation and marine spatial planning

6.3.1. Within-colony differences in the at-sea distribution

Results within Chapter 2 suggest an effect of colony size in the spatial distribution of individuals within populations of colonial seabirds, with implications for the at-sea spatial foraging segregation of closely related shearwaters. However, such differences in behaviour within seabird colonies are likely to vary among locations with varying resource availability. Differences in the at-sea spatial foraging distribution within seabird colonies may have important implications for conservation and marine spatial planning. For example, differences in the at-sea distribution of subsets of a population can determine what proportion of the population is affected by anthropogenic activities or protected by MPAs (Bolton et al. 2019). In one hand, segregation in foraging areas of seabirds from different sub-colonies can result into different levels of collision risk with marine renewable energy installations and other offshore facilities at the population-level. On the other hand, if the foraging areas where birds from different sub-colonies overlap are intensively affected by anthropogenic activities, these threats are likely to impact entire populations, even at longer distances. The conclusions of this chapter highlight the importance of understanding fine-scale spatial segregation and the mechanisms behind the differences in the at-sea foraging behaviour within seabird colonies. Moreover, it highlights for the need to evaluate the at-sea spatial foraging distribution of seabirds in more than one breeding site. This will allow to capture the foraging behaviour variability within a colony, providing meaningful knowledge on marine spatial usage to obtain accurate population assessments and to incorporate into conservation strategies and marine spatial plans.

Similarly to previous research, the data used in Chapter 2 is limited to the chick-rearing period (Hipfner et al. 2007, Bogdanova et al. 2014, Waggitt et al. 2014, Ceia et al. 2015). However, it is unknown whether within-colony differences persist along the entire breeding period and very few other studies addressed this question (Sánchez et al. 2018). Moreover, little information is currently available regarding the occurrence of within-colony differences in the spatial distribution between non-breeding and immature birds from different sub-colonies, as tracking studies are usually carried out on breeding adults only (Bolton et al. 2019). Future research should address those information gaps and look for within-colony differences in foraging behaviour both along the breeding period and among non-breeding or immature birds.

6.3.2. Environmental and climate change

In Chapter 3 it is shown that Cory's shearwaters from different populations across the North Atlantic Ocean differed in foraging behaviour and habitat use, suggesting that individuals may adopt different tactics to cope with the heterogeneity of their habitats or with extreme climate conditions. These results are supported by previous studies suggesting that Cory's shearwaters are able to exhibit great behavioural plasticity when exploiting heterogeneous marine environments (Paiva et al. 2010b, 2013b), and experiencing scenarios of extreme low food conditions (Paiva et al. 2013a).

In some seabird species, behavioural adaptations to environmental changes may be linked with increased foraging costs and reduced breeding success (Kowalczyk et al. 2015). However, we lack a mechanistic understanding of the impacts of those changes on the movement decisions and energetic costs of seabirds. These effects are likely to increase with climate change, as the majority of modelling scenarios predict an increasing frequency, severity and duration of extreme climatic events, such as marine heatwaves, increased storminess and effects of changing wind, in particular at higher latitudes (Young et al. 2011, McInnes et al. 2011, Ummenhofer & Meehl 2017, Sillmann et al. 2017). In this context, it is predicted that species or populations with low levels of behavioural plasticity are likely to be more vulnerable to changes in their environments, as they are less able to exploit different habitats when their main prey becomes scarce (Carpenter-Kling et al. 2020). In contrast, flexible foraging behaviours may play a key role in the ability of a species or a population to adapt to changes in the environment. This hypothesis is partially supported by the results from Chapter 3. When comparing the unfavourable year for the coastal population of Cory's shearwaters in Berlenga Island with an unfavourable year for the oceanic population of Cory's shearwaters in Corvo Island, it is clear that oceanic birds increased foraging effort (i.e. travelled farther from the breeding colony and stayed away longer from the nest) when facing detrimental environmental conditions. However, in the unfavourable year the body condition of adult shearwaters and chick growth rate at

Berlenga Island was way more negative than those from Corvo Island during the unfavourable year for this population. In support to the previous hypothesis, this suggests than when the distribution of resources is unfavourable, oceanic birds increase their foraging effort, but their fitness does not decreased as much as that of coastal birds when facing unfavourable conditions.

In contrast to the population-level foraging plasticity, the ecological implications of spatio-temporal environmental variability at the individual-level are comparatively less studied (Ceia & Ramos 2015). Tracking studies have shown that individual foraging site fidelity occurs in many seabird species and/ or populations (Phillips et al. 2017). However, it is still poorly known whether such individual specialisations persist through the years or vary along the breeding and non-breeding period (Wakefield et al. 2015). Future research should aim to understand whether individual seabirds forage consistently in the same sites across consecutive breeding seasons, and whether variations in individual foraging site fidelity are associated with different foraging costs and breeding output.

6.3.3. Overlap with fisheries and bycatch risk

The results of Chapter 4 suggest that Cory's shearwaters may have relatively low exposure to industrial fisheries when foraging within the EEZ of mainland Portugal during the breeding period. Nevertheless, Cory's shearwaters are more susceptible to forage in the same areas as fishing vessels during the pre-laying period than during the chick-rearing phase. Such low spatial overlap is likely driven by the high prey availability in the colony surroundings and suggests low direct competition for resources. Similar to what has been reported for other seabird populations, Cory's shearwaters may prefer to exploit 'natural' high quality prey during the breeding period, particularly during the chick-rearing when food is plentiful in the area, rather than to scavenge for low quality prey discarded during fishing operations (Tew Kai et al. 2013, Cianchetti-Benedetti et al. 2018, Clark et al. 2020).

The low spatial overlap between Cory's shearwaters and industrial fisheries contrast with those reported for seabird populations breeding in areas of intense fishing pressure and where competition for food resources is higher (Pichegru et al. 2009, Carle et al. 2019). For example, in the western Mediterranean Sea, Scopoli's shearwaters are known to follow fishing vessels (Soriano-Redondo et al. 2016, Reyes-González et al. 2021) and to attend trawlers (Louzao et al. 2011a) and longliners (Laneri et al. 2010). However, in the central Mediterranean the same species is rarely seen attending fishing vessels (Cianchetti-Benedetti et al. 2018). These studies show that overlap with fisheries can vary among seabird populations, which is already documented to occur in other regions and species (Catry et al. 2011, Genovart et al. 2018, Corbeau et al. 2021a b). Future studies should test for differences in seabird-fishery overlap for other Atlantic populations of Cory's shearwaters. Such studies would be important to evaluate the bycatch risk of Cory's shearwaters across the entire North Atlantic Ocean, particularly in the populations close to areas of intense fishing activity such as those near the West African coast (Li et al. 2021).

The results on spatial overlap reported in this thesis could be also underestimated by other reasons. The AIS system used to track vessel movements is mainly limited to large industrial fishing fleets (vessels larger than 15 m), and therefore do not capture the distribution of smaller artisanal fishing fleets. However, it seems unlikely that spatial overlap can be biased towards artisanal fisheries because previous studies already showed that few Cory's shearwaters are seen attending artisanal fishing vessels, and the species is rarely recorded as bycatch during the breeding period along the West coast of the Iberian Peninsula (Valeiras 2003, Oliveira et al. 2015, Calado et al. 2020). Another possible explanation to the low spatial overlap values reported in this thesis could also be related with the intentional disabling of AIS transmitters, usually related with the practice of illicit behaviours such as illegal fishing (Ford et al. 2018). The inability to remotely monitor vessels through their AIS signal, make the data presented in this thesis a conservative picture of the at-sea distribution and effort of industrial fishing fleets. Future studies using recently developed radar detectors combined with GPS loggers may empirically detect real interactions with fishing vessels (Weimerskirch et al. 2018, Grémillet et al. 2019, Corbeau et al. 2019) and have the potential to detect illegal fishing (Weimerskirch et al. 2020a).

6.3.4. Marine Protected Areas

Oceans cover more than 70% of the Earth surface, however they are considered one of the most poorly managed ecosystems on Earth (Irigoien et al. 2004, Maxwell et al.

2014). In 2021 approximately 8% of the world oceans are protected through legal mechanisms and only about 3% of these areas are managed effectively by establishing complementary conservation actions (e.g. no-take marine areas). These numbers are alarmingly low considering that one of the major goals set by the convention on biological diversity's (CBD) is to establish at least 30% of coastal and pelagic areas, including the high seas, as MPAs until 2030. Simultaneously, several studies have been demonstrating that MPAs are an efficient and powerful tool to mitigate the increasing over exploitation of marine resources and degradation of marine habitats, particularly in small-scale and habitat-specific ecosystems (Game et al. 2009, Agardy et al. 2011). However, in most cases the establishment of MPAs is aimed at improving the management of fishing activities (Schmiing et al. 2014). Many MPAs have therefore been implemented opportunistically without prior knowledge of how they may contribute to biodiversity conservation and which factors may threaten species and ecosystems.

By employing a multi-model prioritisation framework to 8-years of at-sea censuses of 30 seabird species, in the Chapter 5 it is recommended an adaptive framework for the identification of candidate MPAs in the Portuguese coast. This methodology pinpoint key marine areas that are not recognised in previous marine spatial efforts for the Portuguese coast at both national and international levels. In this chapter it is shown that the current network of MPAs along the West coast of Portugal is effective for protecting the habitats used by breeding seabirds (i.e. Band-rumped storm-petrel, Cory's shearwater, European shag and Yellow-legged gull), but not for those used by non-breeding seabirds (e.g. Atlantic puffin, Balearic shearwater, Common guillemot and Sooty shearwater). Moreover, these areas matched with a high occurrence of environmental stressors such as oil pollution risk, ship traffic and fishing density, although they were little affected by those stressors.

The suitable design and management of MPAs rely mostly on the quality of the ecological information used to identify key marine areas (Abecasis et al. 2014, Fulton et al. 2015). In the Chapter 5, the key marine areas important for seabirds are identified by predicting species habitat suitability using presence only data from at-sea shipboard surveys. Although this study benefited from a great wealth of information, by gathering 8-years of data on the occurrence of multiple breeding and non-breeding seabird species, the methodology used has some limitations, which may be reflected in several spatio-temporal aspects (Ballard et al. 2012, Fox et al. 2017). For example, at-sea shipboard surveys are time consuming and logistically demanding. As a result of this, at-sea surveys are frequently conducted together with oceanographic surveys, to provide regular monitoring of marine biodiversity in coastal areas and redesign MPAs within EEZs of coastal countries. Despite such constraints, the methodology presented in Chapter 5 provides a reliable strategy to inform marine conservation efforts and management planning in similar coastal environments elsewhere, characterised by strong coastal upwelling movements. In contrast, this methodology exhibits poor predictive ability for pelagic species that do not occur in coastal waters. Monitoring the distribution and activity patterns of seabirds using tracking devices is better suited to identify candidate MPAS in oceanic areas. Understanding shifts in seabird distribution from multiple species using long-term data series including changing environmental and oceanographic conditions is therefore key for implementing dynamic ecosystem-level management in oceanic areas (Le Corre et al. 2012, McGowan et al. 2013, Young et al. 2015, Dias et al. 2018).

Despite decades of research, most studies have focussed on individual species and few studies have addressed the distribution of marine predator assemblages through long time-series. Thus, there is a significant gap in our understanding of the common patterns driving of marine predators' distribution, and therefore no robust knowledge on the ecologically significant areas. Future studies should not only focus on identifying potential conservation areas, but also on assessing the inter-annual movements of multiple marine taxa over several years (Block et al. 2011, Reisinger et al. 2018, Baylis et al. 2019, Hindell et al. 2020). Integrating such source of variation in the identification of potential conservation areas would inform decision-makers about the effectiveness of already established MPAs (i.e. static *vs.* seasonal MPAs), but also maximise their conservation potential (Ludynia et al. 2012b, Maxwell et al. 2015, Krüger et al. 2017).

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