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Nathalie Monteiro Almeida

TROPICAL SEABIRDS AS INDICATORS OF HUMAN STRESSORS AND AS TOOLS FOR MARINE SPATIAL PLANNING IN THE TROPICAL ATLANTIC

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

Dezembro de 2021

Tropical seabirds as indicators of Human stressors and as tools for marine spatial planning in the Tropical Atlantic

Departamento de Ciências da Vida

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b) Others

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[2] 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.

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Abstract

Anthropogenic pressures on the marine environment have long impacted the marine ecosystems and its associated species. All over the world, seabird populations are affected by these pressures, with significant population declines on all taxa. To attenuate these populational declines and ensure associated ecosystem conservation, researchers use tracking devices to identify areas of important seabird conservation, while distinguishing areas of high human pressure where urgent management is needed. Thus, in this thesis I used fishermen perceptions and vessel tracking with species distributions to identify species that are more prone to fishery bycatch, while using seabird multi-species tracking data to designate areas of marine conservation (Key Birds and Biodiversity Areas – KBA) inside the Cabo Verde islands Exclusive Economic Zone (EEZ). Main results of this thesis are: (1) the debate of the current knowledge on the identification of indicator species and biodiversity hotspots which are important for marine spatial planning and design of Marine Protected Areas (MPAs) (Chapter 1); (2) fishermen's' observations indicated Cabo Verde shearwaters as having the highest risk of bycatch in the Cabo Verde fisheries, associated with artisanal handlines, closely followed by brown boobies and red-billed tropicbirds. Additionally, while fish-landing changes occurred due to variables affecting the marine food web, shearwater chick development was also correlated with changes in fish-landings influenced by prey availability in the ocean (Chapter 2); (3) confirming fishermen's reports, overlap and foraging response-changes to fishing vessels' proximity was higher for Cape Verde shearwaters often attending artisanal boats using handlines, while brown boobies attended more industrial vessels and red-billed tropicbirds and red-footed boobies had low response to fisheries' effort and distribution (Chapter 3); (4) Boobies exhibit plasticity in their foraging ecology, adapting to different circumstances of environmental conditions and competitors, while breeding stage and presence of marine physical features play an important role in their foraging decisions. Interesting ecological outcome was related with the spatial, behavioural and trophic segregation of female brown boobies in relation to male brown boobies and male and female red-footed boobies, when the two species co-exist in sympatry (Chapter 4); (5) current MPA network in the archipelago is not sufficient for species conservation, requiring large area expansion. However, key areas identified are very coastal and mainly require national management of seasonal MPA implementation with an emphasis on local community involvement and active management. Added bycatch and vessel collision mitigation measures are recommended to decrease direct fishing pressure impacts on the seabird community of the Cabo Verde archipelago (Chapter 5); and finally (6) this study shows that the use of species distributions to identify breeding, feeding and congregating sites, while overlapping with fishing pressure on the surroundings of their breeding sites is extremely valuable to ensure MPA design, management, and effectiveness for species protection. As such, areas should be large enough to embrace all the important features to ensure conservation, while considering temporal and spatial changes between and within species and ensuring effective and active regulations to minimize the impact of any existing anthropogenic threats. Overall, this thesis confirms interactions of Cape Verde shearwater and other species with fisheries inside de archipelago of Cabo Verde, how coastal species foraging behaviours are influenced by environmental variability in a tropical region and informs marine spatial planning for the nation's EEZ against existing protected areas, highlighting the need to revaluate these areas also taking into consideration both socio-economic and ecological aspects of updating the network of MPAs within the Cabo Verde archipelago.

Keywords: Seabird Ecology, Fishery landings, Seabird-fisheries interactions, Bycatch, Key Bird and Biodiversity Areas, Marine Protected Areas

Resumo

As pressões antropogénicas no ambiente marinho há muito impactam os ecossistemas marinhos e suas espécies associadas. Em todo o mundo, as populações de aves marinhas são afetadas por essas pressões, com declínios populacionais significativos em todos os taxa. Para atenuar esses declínios populacionais e garantir a conservação do ecossistema associado a essas espécies, os pesquisadores usam dispositivos de rastreamento para identificar áreas de importante conservação das aves marinhas, enquanto distinguem áreas de alta pressão humana onde a gestão urgente é necessária. Assim, nesta dissertação utilizei a perceção dos pescadores para designar áreas de conservação marinha (Areas Chave de Aves e Biodiversidade - KBA) dentro da Zona Económica Exclusiva (ZEE) das ilhas de Cabo Verde. Os principais resultados desta tese são: (1) o debate sobre o conhecimento atual sobre a identificação de espécies indicadoras e hotspots de biodiversidade que são importantes para o ordenamento do território marinho e conceção de Áreas Marinhas Protegidas (AMPs) (Capítulo 1); (2) as observações dos pescadores indicaram que as cagarras de Cabo Verde apresentam o maior risco de captura acidental nas pescas cabo-verdianas, associadas às linhas de mão artesanais, seguidas pelo alcatraz-pardo e pelos rabos-de-junco. Além disso, enquanto as mudanças no desembarque de peixes ocorreram devido a variáveis que afetam a cadeia trófica marinha, o desenvolvimento de crias de cagarra também foi correlacionado com mudanças nos desembarques de peixes influenciados pela disponibilidade de presas no oceano (Capítulo 2); (3) confirmando os relatos dos pescadores, a sobreposição e as mudanças de resposta de alimentação à proximidade dos navios de pesca foram maiores para as cagarras do Cabo Verde, principalmente para os barcos artesanais usando linhas de mão, enquanto os alcatrazes-pardos interagiram mais com embarcações industriais e

os rabos de junco e alcatrazes-de-patas-vermelhos tiveram baixa resposta ao esforço de pesca e sua distribuição (Capítulo 3); (4) Alcatrazes pardos exibem plasticidade em sua ecologia de alimentação, adaptando-se a diferentes circunstâncias de condições ambientais e competidores, enquanto o estágio de reprodução e a presença de características físicas marinhas desempenham um papel importante em suas decisões de alimentação. Um resultado ecológico interessante foi relacionado à segregação espacial, comportamental e trófica de alcatrazes pardos fêmeas em relação aos alcatrazes-pardos machos e alcatrazes-de-patas-vermelhas machos e fêmeas, quando as duas espécies coexistem em simpatria (Capítulo 4); (5) a atual rede de AMPs no arquipélago não é suficiente para a conservação das espécies, exigindo grande expansão de área. No entanto, as principais áreas identificadas são muito costeiras e requerem principalmente a gestão nacional através de AMPs sazonais. Recomenda-se a aplicação de medidas de mitigação contra as capturas acessórias (bycatch) e colisões com navios para diminuir os impactos da pressão direta da pesca na comunidade de aves marinhas do arquipélago de Cabo Verde (Capítulo 5); e, finalmente (6) este estudo mostra que o uso de distribuições de espécies para identificar locais de reprodução, alimentação e congregação, e sobreposição com a pressão da pesqueira nos arredores de seus locais de reprodução é extremamente valioso para garantir o projeção, gestão e eficácia da AMP na proteção das espécies . Essas áreas devem ser grandes o suficiente para abranger todas as características importantes para garantir a conservação, ao mesmo tempo considerando as mudanças temporais e espaciais entre as espécies, garantindo regulamentações eficazes e ativas para minimizar o impacto de quaisquer ameaças antropogénicas existentes. No geral, esta tese confirma as interações da cagarra de Cabo Verde e outras espécies com a pesca dentro do arquipélago de Cabo Verde, como os comportamentos de alimentação das espécies

costeiras são influenciados pela variabilidade ambiental em uma região tropical e informa o planejamento espacial marinho para o ZEE nacional relativamente as áreas protegidas existentes , realçando a necessidade de reavaliar estas áreas tendo também em consideração os aspetos socioeconómicos e ecológicos da atualização da rede de AMPs do arquipélago de Cabo Verde.

Palavras-chave: Ecologia de Aves Marinhas; Desembarque de peixes; Interações de Aves Marinhas e Pescas, Bycatch; Áreas Chave de Aves e Biodiversidade; Áreas Marinhas Protegidas.

Chapter I

General Introduction

1.1 - Importance and human stressors of the marine environment

The extreme importance of the world´s oceans is something that we humans, have always known to be true, if not for its massive size covering 71% of the Earth´s surface and holding large quantities of biodiversity, but also for being the main producer of the Earth's oxygen (50%), fixate atmospheric carbon dioxide, as well as regulating the climate (Costanza 1999; Ronconi et al. 2012). Additionally, the oceans have always presented humanity with many opportunities, which various countries and communities depend on to sustain economic growth, from fisheries and aquaculture for food and nutrition, shipping, mineral extraction, energy production, to ecosystem services and activities related to eco-tourism (Ababouch and Carolu 2015). However, there is clear evidence that direct and indirect anthropogenic effects such as overfishing and climate change, affect the equilibrium of marine ecosystems through bottom-up and top-bottom cascading effects on marine food webs. Simple temperature changes in the ocean, causes shifts in the planktonic community, collapsing top-communities, the same way unsustainable fishing activities affect commercially targeted predators, causing changes in biomass and affecting bottom-communities. Top and bottom communities may also be indirectly influenced by environmental changes and fishing pressure respectively, through cascading interactions with directly affected communities, while planktivorous fishes in middle-communities also play a key role in marine food web changes (Daskalov 2002; Lynam et al. 2017). Both ocean temperature changes and fishing were identified as the highest threats to marine ecosystems by Halpern et al. (2007), being the former influenced by land-based activities, as was most of the threats identified, and the latter based on ocean activities. These threats play a lethal role in the equilibrium of marine ecosystems, and yet must be addressed with caution, to assure the recovery of fish biomass and habitats, and still lookout for the needs of people and communities that depend on coastal and marine activities for their own sustenance.

The right to ownership of coastal marine environments can be found in early human civilization laws, claiming that "…The right of fishing in the sea from the shore belongs to all men…" (Weinstein et al. 2007). Furthermore, if you consider that 84% of countries have a coastline with direct access to oceans and seas, it is possible to imagine the amount of pressure these ecosystems have endured over the centuries (Martínez et al. 2007). The current situation shows that the world's oceans are in peril: a) overfishing has dramatically reduced fish stocks causing negative effects to marine megafauna (Williams 1998; Jackson et al. 2001; Tsui et al. 2020) and, b) climate change is warming and acidifying marine ecosystems, inflicting further stress in the oceans wreak havoc on marine life (King et al. 2010; Doney et al. 2012; Huntington et al. 2019; Hastings et al. 2020). Thus, finding suitable sentinel species of the Human impacts on the Oceans is extremely important to then anticipate processes disrupting biodiversity patterns and apply conservation measures to obstruct or mitigate such events.

1.2. Marine Protected Areas (MPAs) effect on marine biodiversity

To alleviate the stress resultant from Human activities (e.g., fisheries, climate change) on the marine environment, governments are designing Marine Protected Areas (MPAs). According to the IUCN 2008 Guidelines (Day et al. 2019), "A protected area is a clearly defined geographical space, recognized, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values". The "movement" for MPA network establishment has been driven by the Convention on Biological Biodiversity (CBD) since 2010, to improve the status of biodiversity by safeguarding ecosystems, species and genetic diversity (Strategic Goal C). This goal, intended that "By 2020… 10 per cent of coastal and marine areas, especially areas of particular importance for biodiversity and ecosystem services, are conserved through effectively and equitably managed, ecologically representative and well connected systems of protected areas and other effective area-based conservation measures, and integrated into the wider landscapes and seascapes" (Aichi target 11) (https://www.cbd.int/). These networks are extremely important for sustainable development from an ecological, social, and economic point of view, by ensuring marine ecosystem functions, managing conflicts concerning the use of natural resources and efficiently using them in a sustainable way. Their role in decreasing habitat degradation, loss of endangered species and restoring fish stocks is one of their many advantages (WCPA/IUCN 2007).

The growth leap in MPA coverage since the year 2000 (0.7%) has been unprecedented, from 2 million km^2 to nearly 28 million km^2 (>7%) today (UNEP-WCMC and IUCN 2021), looming the 10% goal of the Aichi target 11. However, the greatest coverage of MPAs remains within countries' Exclusive Economic Zones (EEZs) (~18% of 39% total EEZ coverage) in contrast to the ones within Areas Beyond National Jurisdiction (ABNJ) or "High seas" (1% of 61% total ABNJ coverage) (UNEP-WCMC and IUCN 2021). Although this is being adopted by many countries, according to the Marine Protection Altas (https://mpatlas.org/), only a small percentage (2.7%) of all oceans are effectively protected and the majority does not receive proper management actions.

Nevertheless, a new recommendation goal has been proposed to achieve 30% protection and conservation of the global ocean by 2030, with more than 70 countries, supporting this new goal appointed by the CBD (https://marine-conservation.org).

But protecting the ocean is not an easy task to achieve. Although it may seem homogeneous at first glance, this immense water mass is all but static, constantly changing in time and space (Ballance 2007), requiring certain plasticity from organisms that live and/or depend on it. In such a highly changing environment, the lack of physical barriers that prevent species from exiting protective sanctuaries, may be a challenge for MPA design, considering that most marine animals are highly mobile, travelling long distances between areas used year-round (González-Solís et al. 2007; Block et al. 2011; Guzman et al. 2018; Hromádková et al. 2020). Thus, MPAs must be designed keeping in mind the needs and habitat preferences of each target species, as well as the Human use of the marine environment (Catchpole and Gray 2010; Maxwell et al. 2015).

Most MPAs are designed to improve fisheries management (e.g.(Stevenson and Tissot 2013), but recent examples include the use of marine top-predators in the process of MPA design and marine conservation and planning (e.g.(Handley et al. 2020). The choice between using single species or multiple-species has been for long, a matter of discussion to identify MPAs at various scales (Ronconi et al. 2012), but regardless of the chosen approach, most studies rely on the identification of marine animals “hotspots (Lascelles et al. 2012). Nevertheless, the effectiveness of MPAs and conservation tools is still under scrutiny, with many undergoing discussions about the best approaches for identifying and managing them. Choosing between static and dynamic MPAs, has also been some of the discussions on MPA effectiveness, with studies showing seasonal variation in species distributions (Krüger et al. 2017; Thiebot et al. 2019) and suggesting that dynamic seasonal

MPAs may similarly and effectively protect species, while causing less impacts on sustenance anthropogenic activities (Krüger et al. 2017).

Although in the scientific world, there are many papers published on marine animal tracking for assessing species distributions, it is evident that current marine management and policy in many areas make little use of such data when implementing marine spatial planning. There is possibly a barrier between science and policy, either because the two worlds do not speak the same language or information does not reach legislators and policymakers as easily as science is spread around their own community (Hays et al. 2019; Sequeira et al. 2019). Communication obstacles can be as simple as a definition divergence, e.g., when both the scientific community and policymakers have a slightly different definition for the term 'Migratory Movement'. This divergence can and have led to the exclusion of species, that by scientific and biological standards, should be considered migratory (Dunn et al. 2019).

Still, tracking marine animals is probably the most effective way to assess marine fauna distributions, and by overlapping threats with distribution maps, it is possible to identify areas deserving further protection (Hays et al. 2016, 2019). However, it can also be problematic if the information does not reach policymakers or does not reach them in a format that can be translated into policy. This is particularly imperative because marine species are highly migratory, travelling around the world's oceans and crossing geopolitical boundaries such as countries EEZs, as well as depending on international cooperation's while travelling along ABNJs (Block et al. 2011; Harrison et al. 2018; Dunn et al. 2019; Hays et al. 2019; Sequeira et al. 2019). An example of this issue is the leatherback turtle (*Dermochelys coriacea*) in the Pacific ocean, which was recorded travelling across 32 countries and high seas (Harrison et al. 2018).

Nevertheless, there are still good examples around the world, where the use of marine animal tracking effectively informed marine management and conservation, through the creation of conservational policies. From seabirds, marine mammals, sea turtles, to fish taxa, tracked individuals or multiple taxa around target areas have been used by stakeholders to improve conservation management in many areas around the world (e.g. Augé et al. 2018; Requena et al. 2020). The quality of data provided by species tracking, has (1) improved and developed bycatch mitigation measures and reduced non-target species mortality, (2) established or expanded MPAs, (3) banned target-specific fisheries, permanently or seasonally, if stocks depletion affected populations and/or their predators, (4) placed fishing restrictions outside EEZs, (5) aided the establishment of marine spatial plans, (6) redesigned marine reserves, (7) defined sustainable use zones, (8) recognized the need to preserve certain species, (9) managed fisheries to protect threatened species, (10) provided ways to assess stocks and identified sustainable harvest levels, (11) minimized impacts of human-built infrastructures along waterways, and created boat corridors to lessen boat strikes, among others (Hays et al. 2019).

For Pelagic Marine Protected Areas (PMPAs), management is particularly difficult because they can sometimes comprise EEZs, where decisions and law enforcement towards marine resources are detained by coastal states within 200 nautical miles (nm), and ABNJ, where waters must be internationally managed, requiring multiple collaboration between states, and thus making it a harder task (Game et al. 2009). Although since 2010, many PMPAs have been established, only 10.8% were considered adequately protected in 2019 compared to a low 2.7% in 2010, and most of them were concentrated in the Southern Oceans (Brooks et al. 2020).

The issue with protecting marine migratory species, is that protecting their entire ranges is not feasible. As threats are not the same everywhere, species can be more or less protected depending on where they are. Travelling along continental basins (Block et al. 2011), across oceans (Guzman et al. 2018), performing pole to pole (Egevang et al. 2010; Hromádková et al. 2020) or circumpolar (Weimerskirch et al. 2015) migrations, marine fauna gives an empirical overview of how much the idea of total protection is virtually impossible to accomplish. Instead, identifying critical areas for each species, such as breeding and foraging grounds, migration routes, or important migration stop-overs can be enough to designate MPAs and prevent or decrease mortality probability (Louzao et al. 2006; Shillinger et al. 2008; Ashe et al. 2010; Dawson et al. 2017).

To evaluate whether protected areas are being managed effectively, it is important first to understand if management resources are adequate, if management applications have indeed reduced threats on marine ecosystems, and if established goals have been or are being achieved when compared to an area with no protection whatsoever (Maxwell et al. 2020). When it comes to effective management, many studies reveal that marine protected areas have poor personal and budget capacity to efficiently achieve their goals, and also low enforcement capacity to implement regulations (Gill et al. 2017). Stakeholder engagement was also identified as a factor capable of triggering success when present and failure if absent (Giakoumi et al. 2018).

As to reducing threats, studies have shown that human pressures tend to slow, as opposed to fully halt, inside MPAs. Zupan *et al.* (2018) reports on different effectiveness between fully protected MPAs compared to partially protected, with human extractive impacts completely eliminated at the former and a significant increase in artisanal and recreational fisheries inside partially-protected areas when compared to areas not protected at all. As 94% of all MPAs allow fishing to occur (Costello and Ballantine 2015), the creation of 'partial MPAs' should be treated cautiously, as the level of regulation may be the solution for protection effectiveness as well as the presence of a fully protected area nearby (Zupan et al. 2018b; Claudet et al. 2020). A study with reef sharks inside a large MPA showed significant protection for individuals that stayed inside the area with proper enforcement (White et al. 2017).

When talking about achieving goals, MPAs exhibited an increase in species richness, density and biomass inside sanctuaries, recovery of commercially targeted species (Gill et al. 2017), while showing that communities located near protected areas, using their resources for ecotourism, express lower degree in poverty (Naidoo et al. 2019).

Additionally, Zhao *et al.*, (2020) showed that to achieve 30% protection of the global ocean, protection must be prioritized on continental coasts, island arcs, oceanic islands, the southwest Indian Ridge, the northern Mid-Atlantic Ridge, the Coral Triangle, Caribbean Sea and the Arctic Archipelago, more than half of them located inside EEZs but only 10% located inside MPAs, and less than 1% of them in fishing restricted MPAs.

Moreover, to provide better management to these biodiversity sanctuaries, the continuous development of new technologies has delivered innovative solutions, some of them available for real-time use (Maxwell et al. 2015).

1.2.1. Dynamic management of marine ecosystems

Tracking studies to address species distributions and aid on MPA design, can also give information on the species habitat preference, triggering ocean managements that are called dynamic. One example is the use of daily information on locations with specific temperatures preferred by sea turtles to evade the high risk of bycatch (Hays et al. 2019). A similar pattern was observed in the North Atlantic, with different species of sharks preferring frontal zone areas, where the overlap with Portuguese and Spanish fisheries was very high (80%) (Queiroz et al. 2016).

This use of real-time oceanographic data with existing tracking information is extremely important and can be used as a mitigation measure for bycatch and to avoid over-exploitation of marine resources. Some of these tools exist today, e.g., TurtleWatch (Howell et al. 2015) and WhaleWatch (Hazen et al. 2017), and are available for fisheries along the Pacific Ocean to predict areas where certain species are more likely to occur and thus avoid them as best as possible.

But even with all these innovations, bridging the gap of knowledge between science and policymaking is extremely important and that is exactly where efforts have been directed to lately. Dunn *et al.*, (2019) work summarized most of the issues affecting information exchange for management and policies focused on marine conservation. International Conventions, United Nations Organizations, Regional Seas Organizations, Global Fisheries, International Commissions have all been working towards the inclusion of the connectivity concept to expand into ABNJ, through workshops, spatial management measure modifications, implementation of MPA networks, etc. Site-selection (e.g., IBAs, KBAs), network design (networks of MPAs) and policy recommendations were identified as the three criteria to fit the purpose of including migratory connectivity in policies. A new system, to connect researchers' data outputs to describe migratory connectivity more effectively to policymakers and management organizations, was created and launched in 2019 at the Second UN Intergovernmental Conference, called Migratory Connectivity in the Ocean (MiCO - https://mico.eco/system). From published papers to Policy Fora, MiCO provides knowledge access in usable formats, synthesizing data referring to migratory routes and areas of marine migratory species and closing the gap between data providers and users that will create management tools, recommendations, and policies.

In conclusion, all the efforts towards a future that insures the best conceivable amount of protection to the oceans are still undergoing, with many challenges still to be conquered along the way. Perhaps the biggest challenge is achieving ecosystem conservation while keeping in mind the needs of people associated with coastal and marine ecosystems, in other words, an equilibrium between marine conservation and ocean-based anthropogenic activities (e.g., fisheries).

1.3. Fisheries

Throughout the long history of mankind´s existence, ever have we extracted resources from the oceans to sustain our own needs, often unaware or ignorant of the potential negative effects of this practice over the marine ecosystems, when practised in excess. As the human population continues to grow, fishing pressures on the oceans to deliver sufficient fish to sustain 39 million people employed in the fisheries sector and feed a population of roughly 8 billion, with an annual consumption rate of fish (3.1%) significantly outpacing the population growth rate (1.6%) (FAO 2020), makes this one of the most concerning issues for the marine environment. Contrastingly, a study performed in 2010 showed that malnutrition of almost 20 million people around the world could have been avoided in the year 2000 if overfishing losses had been prevented (Srinivasan et al. 2010). At the same time, fish landings in very poor countries (specially Africa) contrasted greatly from the actual catches extracted (17% higher than landings) from their waters (Srinivasan et al. 2010). This shows that besides being unsustainable, overfishing generates more loss than actual gains for the human population. In 1999 almost 50% of the world fish stocks were considered fully fished and nearly 30% were over-fished (García and Leiva Moreno 2003), while today fish stocks within biologically sustainable levels have decreased ~24% since 1990 (FAO 2020).

The Food and Agriculture Organization's (FAO) reports on fishery catches, depend mainly on voluntary submissions of member countries, and although it has suggested catches of 86 million tons with a small decline since 1996, Pauly and Zeller (2016)'s Catch Reconstruction' project identified 130 million tonnes in catches, with a subsequent decrease afterwards. Here we come to understand, that besides being a major issue for marine ecosystems and biodiversity, there isn´t a clear knowledge of the actual amount of fish harvested from the oceans, since the quantities of fish landings accounted for, are essentially related to reported fisheries. In areas where policy and law enforcement are hard to apply (e.g. ABNJ), illegal, unregulated and unreported fisheries (IUU) is still a major problem. Estimated in 2009 at 11-26 million tonnes per year, the level of illegal fishing has a significant correlation with countries governance, with developing countries being the most at risk. For instance, catches estimation in west Africa were 40% higher than catches reported (Agnew et al. 2009).

Areas explored by fisheries are usually hotspots of marine top-predators, gathering a vast a array of megafauna, competing for the same fish prey resources (Davoren 2007). Competition often leads to mortality and as clearly stated by the WWF, "Whenever there is fishing, there is bycatch" (https://wwf.panda.org). According to the definition proposed by Davies et al. (2009) "bycatch is a catch that is either unused or unmanaged", bycatch would represent 40.4% of marine catches around the world. Studies on taxon-specific hotspots of global bycatch intensities were also identified in the Southwest Atlantic and the Mediterranean for seaturtles, Eastern Pacific for marine mammals and Southwest Atlantic for seabirds (Lewison et al. 2014). Gillnets represented the fishing gear that presented the biggest risk of bycatch in all regions, while longlines and trawls caught more marine megafauna in the Eastern Pacific Ocean (Lewison et al. 2014). Many other studies have sought out to find patterns in bycatch around the world across different fishing gears, concerning a vast array of marine top predators such as sharks and rays (Oliver et al. 2015), seaturtles (Wallace et al. 2010), marine mammals (cetaceans, pinnipeds, sirenians and otter species) (Read et al. 2006; Reeves et al. 2013) and seabirds (Anderson et al. 2011; Zydelis et al. 2013; Cortés et al. 2017).

Fisheries interactions with marine megafauna do not only resume to accidental catches, as many species depend on discarded fish untargeted by vessels (Depestele et al. 2018). According to an 800 paper review (Alverson et al. 1994), an average of 27.0 million tonnes of fish is discarded every year back to the sea, especially in the Northwest Pacific, with a higher proportion of discards related to shrimp trawl fisheries. In 2005, an update on these values was performed, showing a decrease in annual discards to <10 million tonnes per year (Kelleher 2005; Zeller et al. 2017), while trawl fisheries still appear in the front line of bycatch risk (Kelleher 2005). As expected, discard rates for small scale fisheries are lower compared to industrial fisheries (Kelleher 2005; Zeller et al. 2017), with fleets in the Northwest Pacific and Western central Pacific being responsible for the higher rate of discarded fish (Zeller et al. 2017).

In the past, to perform studies related with species and fisheries interactions, researchers relied basically on on-board observations, and had no way of tracking fishing vessels. Today, innovative real-time technologies have been created to fill this gap and aid researchers and policy makers in decisions concerning marine ecosystem conservation. The Automatic Identification System (AIS), for example, was designed to avoid collision between vessels and serves the purpose of identifying vessels and intentions, something that was not possible in the past (Robards et al. 2016). But this provided important information on vessel traffic in the marine environment, which has been widely used to assess areas of fishery impacts (Wong et al. 2018; Burger et al. 2019; Rowlands et al. 2019). However, AISs can be switched off by vessel owners, especially when it comes to international waters where illegal fisheries are more likely to take place (Weimerskirch et al. 2020). Other technologies, like the Vessel Monitoring System (VMS) is also used to monitor vessel movements and locations, generally inside EEZs, aiding also on many conservation studies (Watson et al. 2018; Weimerskirch et al. 2018; Rowlands et al. 2019).

Another important lack of information that may influence fish stocks are small artisanal fishery vessels which are not required to use either AIS or VMS tracking systems, instead they may choose to do it voluntarily by using AIS Class B transceivers, less expensive and less capable compared to mandatory Class A AIS for bigger vessels (Robards et al. 2016). In smaller, under-developed or developing countries, the use of these devices on artisanal vessels is probably null or at least very low. Nevertheless, recent innovative technologies have been used for monitoring fishing and species, through the use of GPS devices to track artisanal fisheries (Natsir et al. 2019; Cardiec et al. 2020), use of satellite systems to detect and count species from space (Cubaynes et al. 2019), drones for surveillance in coastal areas (Kelaher et al. 2019) and radar vessel detection on tracking devices placed on marine predators (e.g. seabirds) (Weimerskirch et al. 2018, 2020; Grémillet et al. 2019), capable of transmitting information to authorities to detect nondeclared vessels in national and international waters (Weimerskirch et al. 2020), as well as many others.

Knowing all the impacts, and using all the available technologies, 'marine no-take areas' [areas where extractive activities are prohibited, also known as 'marine reserves' (Sala and Giakoumi 2018)] legislatively supported by Marine Protected Areas (MPAs) have been established in some regions of the world as a way to decrease fishery impacts and allow ecosystems to recover, protect marine biodiversity, prevent bycatch of underwater and aerial predators and function as a source of fish stocks to contiguous regions, where fisheries may still occur (Smallhorn-West et al. 2020). While evidence has proven that marine no-take areas are the most effective type of MPAs, with a much higher biomass of fish assemblages when compared to adjacent unprotected and partially-protected areas (Sala and Giakoumi 2018), their numbers are still very small, as 94% of all MPAs allow fishing and less than 1% is no-take (Costello and Ballantine 2015; Day et al. 2019).

Overall, marine ecosystems are directly affected by fisheries, sometimes collapsing food webs and destroying habitats (Lynam et al. 2017). Therefore, these high numbers of overfished populations and negative impacts on marine ecosystems lead to a clear consciousness that sustainability was a failed management attempt. Socio-political pressure still demands for greater harvests, while the ability to predict the amount of harvest that will cause population collapse is still very much uncertain (Botsford 1997).

1.4. Seabirds as sentinels of human stressors

Seabirds are the most easily studied marine top-predators, which typically explore vast pelagic regions and habitats of the marine environment throughout their lives (Schreiber and Burger 2001), making them the best reliable marine fauna group to better understand anthropogenic pressures and have an overall view over the state of the marine ecosystems. Currently, there are around 350 known seabird species around the world (Croxall et al. 2012; Birdlife International 2018), occupying different niches and habitats, with various arrays of adaptations for flying (e.g. albatrosses (Weimerskirch et al. 2004)), diving (e.g. gannets (Croll et al. 1992; Ropert-Coudert et al. 2004)) and swimming (e.g. penguins (Sato et al. 2007; Fish 2016)). About 28% of these species are globally endangered (Croxall et al. 2012; Birdlife International 2018), facing direct and indirect threats at sea (bycatch, vessel light pollution, overfishing, marine pollution, climate change) and at their nesting grounds (introduced predators, nesting habitat loss and degradation, human poaching, light pollution) (Birdlife International 2018; Dias et al. 2019a). These long-lived organisms spend most of their lives at sea, especially during the non-breeding period. Most of them never touch land as immature individuals, only returning to their nesting grounds when they are ready to mate and reproduce (Schreiber and Burger 2001). However, during this time, they are constrained to their nesting sites due to their central place foraging behaviour (Orians and Pearson 1979), returning regularly to their nests, and taking turns incubating the eggs or feeding the chicks, while collecting enough food supply to store their own energy reserves and maintain body condition (Weimerskirch 1998).

Compared to marine mammals and other less conspicuous marine top predators that spend the majority of the time underwater, seabirds are easily accessible, especially during their reproductive period and when colonies are also easily accessible, providing large and valuable samples collected from external morphometrics to different types of external and internal tissues (Mallory et al. 2010). These provide important information about species' body condition (Robertson et al. 2001), presence of contaminants, diseases and parasites (González-Solís and Abella 1997; Mallory et al. 2006; Gilmour et al. 2019b; Lavers et al.

2019; Philpot et al. 2019), foraging ecology, diet and trophic niche (Käkelä et al. 2007; Ramos et al. 2009; Young et al. 2010a; Phillips et al. 2011; Neves et al. 2012; Zajková et al. 2017; Lerma et al. 2020b). However, to link this information with the state of the marine environment it is important to know their distributions, by identifying the areas and habitats they use. In the past, scientists could only rely on observations at sea or at the colony. Today, the miniaturization of tracking devices has been a major breakthrough in seabird ecology studies. From Very High Frequency (VFH) radio tags (Lewis et al. 2002; Wilson et al. 2009; Loring 2016), compass loggers (Paiva et al. 2009), satellite telemetry (Weimerskirch et al. 2006a) geolocators (GLS) (González-Solís et al. 2007; Ramos et al. 2015; Jaeger et al. 2017; Hedd et al. 2018) and Global Positioning System (GPS) loggers (Steiner et al. 2000; Paiva et al. 2010a, 2015; Ramos et al. 2018), tracking of seabirds became possible during breeding (e.g. Catry *et al.*, 2009; Paiva *et al.*, 2009, 2010, 2015; Ramos *et al.*, 2018) and non-breeding phases (Weimerskirch et al. 2006a; González-Solís et al. 2007, 2009; Catry et al. 2009; Ramos et al. 2015). These devices allow the collection of crucial information about bird foraging behaviour (diving depths, flight altitudes and speed, turning angles, time of prey intake), physiology, migration, population sizes, anthropogenic presence and effects on foraging grounds (presence of fishing boats with radar detection), among others (Burger and Shaffer 2008). These devices range in accuracy, from >100km (GLS) to a few meters (GPS), weight, lifespan from days to years, data recovery and costs, being more or less adequate depending on the specie's biology and study goals (Lascelles et al. 2012).

With all this information available, seabirds gained a reputation as bioindicators of marine resources (Cherel and Weimerskirch 1995), with several studies showing correlations between breeding success and marine prey stocks, mostly pelagic fish

(Springer et al. 1986; Velarde et al. 1994; Frederiksen et al. 2007; Paiva et al. 2013a). Many seabird studies reported also important information about ecosystems, indicating regional habitat differences (Iverson et al. 2007), health of the marine environment with the detection of chemical contamination, overfishing, plastic pollution, etc (Cherel and Weimerskirch 1995; Mallory et al. 2010; Gilmour et al. 2019a; Philpot et al. 2019; Gatt et al. 2020). At the same time, areas regularly exploited by these top predators represent critical 'hotspots' of biodiversity and productivity, making seabirds "umbrella species" by encompassing a huge diversity of marine species which would benefit from seabird conservation measures. Central place foraging makes seabirds also sentinels of local to regional environmental processes and human stressors acting at that same spatio-temporal scale. Moreover, changes in the adults' body condition (Paiva et al. 2013b), chick-growth (Quillfeldt et al. 2007) or breeding success (Paiva et al. 2013a) have been used as measurable traits of human-related impacts on the marine environment, such as fisheries along their foraging home ranges.

Seabirds are also known to forage near fishing gears, translating into a seabird-vessel competition. The southern oceans appear to be where the most competition between fisheries and seabirds occur (Grémillet et al. 2018), with seabird food consumption (e.g., cephalopod, euphasiids and small pelagic fish) decrease for diving petrels, terns and frigatebirds (Grémillet et al. 2018).

Another threat to seabirds is the probability of being bycaught during fishing operations. Either because seabirds target the same prey as vessels (competition), steal baits from hooks, or simply feast on discarded whole fish and offal (scavenging) (Soriano-Redondo et al. 2016), these behaviours have potentially deleterious effects at the individual and population levels (Table 1).

Table 1.1 - Bibliography review on seabird bycatch, across different fisheries and locations around the globe.

Study site	Fishery type	Most caught seabirds	Nº bird per year/hook/trip	Year Dataset	Source
Globally					
Globally	Longline	Albatrosses, petrels and shearwaters	160 000/yr	Articles review	(Anderson et al. 2011)
Globally	Gill-net	Common guillemot and others	40 000/yr	Articles review	(Zydelis et al. 2013)
North Atlantic Ocean					
Mediterranean	Demersal longline	Scopoli's, Balearic and Mediterranean shearwaters	274-2198/yr	2011-2015	(Cortés et al. 2017)
	Longline	Gulls and shearwaters	-	1985-2014	(Genovart et al. 2017)
Portugal Coast	Setnets and Demersal longline	Northern gannets	-	2010-2012	(Oliveira et al. 2015)
	Longline	Northern gannets and Cory's shearwater	0.24/trip	2016-2018	(Calado et al. 2020)
Norwegian Coast	Gillnet and Manual longline	Northern fulmar and black guillemot	>14 000/yr	2009	(Fangel et al. 2015)
	Gill-net	Northern fulmar, common guillemot	1589-11500/yr	2006-2015	(Bærum et al. 2019)
Northwest Atlantic	Guill-net	Murres	3053-14054/yr	2000-2003	(Davoren 2007)
	Longline	Shearwaters, gulls, gannets, petrels	-	1992-2016	(Zhou et al. 2019)
South Atlantic Ocean					
Southwest Atlantic	Longline	Black browned albatross	0.42/1000 hooks	1998-2004	(Jiménez et al. 2009)
South Africa	Longline	White-chinned petrel, shy type albatrosses	450/yr	2006-2013	(Rollinson et al. 2017)
Indian Ocean					
Southern West Australia	Purse seine	Flesh-footed shearwater	0.59-1.10/trip	2009-2010 and 2017-2018	(Norriss et al. 2020)
Pacific Ocean					
Central North Pacific	Longline	Black-footed albatross	100 000/yr	1994-2000	(Lewison and Crowder 2003)

Posing a higher risk of bycatch, longlines have long been linked with seabird populational declines (Lewison et al. 2004), estimating 160,000 seabirds killed every year around the world, due to longline bycatch, with albatrosses, petrels and shearwaters being the most affected species (Anderson et al. 2011). Zhou et al. (2019) studies in the Western North Atlantic identified the four most important ecological traits that may lead to longline seabird bycatch: (1) local seabird abundances in a longline targeted area, pose a higher risk of bycatch, as probabilities of seabird targeting fishing gears are higher, due to competitive scavenging (Gilman et al. 2016); (2) bigger sized birds appear to be more vulnerable to longline fisheries, since baits are easier to swallow compared to smaller species (Brothers et al. 1999); (3) behaviours such as scavenging or plunge-diving were identified as the most bycatch-prone feeding tactics (Brothers et al. 1999; Calado et al. 2020) and (4) also connected with the timing-period of hook settlement near the surface, and during hauling, when birds are most prone to steel untouched baits on hooks (Huin and Croxall 1996). These periods may be critical if coinciding with the hours where seabirds are mostly active, frequently around sunrise and sunset (Belda and Sánchez 2001; Soriano-Redondo et al. 2016). For this reason, one of the measures proposed in the Mediterranean sea to mitigate bycatch (Belda and Sánchez 2001; Sánchez and Belda 2003; Cortés and González-Solís 2018) was to settle hooks during the night, when petrels and shearwaters are less active and/or have reduced visibility to spot baited hooks, as was observed in other studies (Murray et al. 1993; Melvin et al. 2013).

Discard is probably the most targeted easy-meal birds seek near vessels, followed by bait when discards are not available. This was observed in the Mediterranean, with trawlers acting as buffers for seabird and longline vessel interactions, with almost 0% probability of attendance to longlines when >20 trawlers were present in the area, to 40%

when only one trawler was present (Soriano-Redondo et al. 2016). Discards are undeniably a reliable option when natural prey is scarce, which naturally would happen along areas with high fishing pressure (Maynard et al. 2020), especially for non-breeding individuals (Grémillet et al. 2008). Other seabird species, like the opportunistic scavenger yellow-legged gull (*Larus michahellis*), may actually depend on these fishery unwanted resources, causing the expansion of their populations (Karris et al. 2018), the same way other species may rely on most of their energy intake from discards (Arcos and Oro 2002). As such, fisheries management actions to reduce discards should be treated with caution, since it can also have negative effects on species (Arcos and Oro 2002; Soriano-Redondo et al. 2016). Nonetheless, to some seabird populations, reproduction is bound to fail when the only available food is low-quality fishery discards in contrast with high-quality pelagic fish (Pichegru et al. 2007; Grémillet et al. 2008). Additionally, compared to pelagic fish, discards accumulate much higher rates of mercury and other contaminants (Arcos et al. 2002), negatively affecting species in the long-term. Discards also contain certain fish species, that are not usually available to seabirds, due to depth and nocturnal habits, which could either be an advantage or a potential threat to seabirds when ingested. A study in Brazil found many deceased seabirds with signs of choking from feeding on a particular fish that typically occurs at depths not accessible to most seabirds, and with nocturnal habits, making it even harder for certain species to have access to it (Benemann et al. 2016). Other studies show that the use of discards can be a result of intra-specific competition and not a foraging preference (Cianchetti-Benedetti et al. 2018). Nevertheless, whether seabirds are indeed attracted to fishing vessels has yet to be determined, as overlap may be influenced by many different factors, such as individual strategies and specialization (Votier et al. 2010; Granadeiro et al. 2011; Patrick et al. 2015), sex-specific foraging

(Torres et al. 2013; García-Tarrasón et al. 2015; Reyes-González et al. 2020), vessel type, activity and distance or simply by the common use of area and habitat (Torres et al. 2013; Bodey et al. 2014; Collet et al. 2017).

Either way, using seabirds as our target species, we end up gaining a more general view of the associated marine environment, direct and indirect impacts of human activities, fish stock availability, and other predators feeding in association. Identifying these hotspots of biodiversity is also extremely important for conservation action purposes and MPA establishment.

1.5. The importance of tropical marine areas: the example of Cabo Verde

There is a clear relationship between society wealth and ecological zones around the globe. Temperate regions, with enhanced marine productivity and encompassing most of the world´s developed countries according to the World Bank, have long been used as study areas in contrast with tropical ecozones, in which countries are generally very poor and with lower marine productivity ecosystems (Longhrust and Pauly 1987; Sachs 2001). This fact perhaps explains some of the lack of undergone studies along these regions when compared to higher latitudes (Weimerskirch 2007).

Tropical oceans comprise 50% of the total area of open water on the planet (Longhrust and Pauly 1987), with temperatures of the sea surface ranging along 15°C to 25°C between sub-tropical and tropical waters (Lalli and Parsons 1997b). Compared to higher latitudes, these marine areas are typically oligotrophic (Longhrust and Pauly 1987; Lalli and Parsons 1997a; Weimerskirch 2007), with high sea surface temperatures throughout the year and low chlorophyll-*a* concentrations, preventing nutrients present in denser, cooler and deeper layers of the sea, to reach sunlit areas and made available to phytoplankton, leaving the nutrient-rich water trapped bellow. This consequently causes low abundance and production of phytoplankton, which affects the total biomass of subsequent trophic levels (Ballance and Pitman 1999; Weimerskirch et al. 2004; Behrenfeld et al. 2006). As such, tropical waters, compared to seasonally productive temperate waters, are usually unpredictable in terms of prey fish availability and distribution. In such cases, fish are usually found scattered or patchily distributed across water masses, usually associated with physical structures (e.g. fronts, continental shelves, seamounts) (Hunt and Schneider 1987; Xavier et al. 2004; Yen et al. 2004; Weimerskirch 2007; Paiva et al. 2009, 2017) and marine features (e.g. upwelling, eddies, gyres) (Hunt and Schneider 1987; Kai et al. 2009; Della Penna and Gaube 2020), viewed as spatial proxies of high marine productivity (Lalli and Parsons 1997a; Ballance et al. 2006; Scales et al. 2014). Other studies have also connected prey fish with the presence of underwater predators (e.g. tunas, dolphins, sea turtles), driving them to the surface, through vertical migration (Hebshi et al. 2008).

The Atlantic is a vast ocean located between the American and the European and African Continents. The South Atlantic is influenced by warm waters coming from the Pacific and Indian oceans, travelling northward to the North Atlantic. Colder waters are fed by the North Atlantic Current (NAC) coming from the poles and travelling southward towards the equator, across the South Atlantic into the Indian and Pacific Ocean, causing a permanent exchange of water between oceans. At the centre, the Atlantic is crossed by the Mid-Atlantic Ridge (MAR), with many large seamounts, dividing the western and eastern basin of the Atlantic (Steele et al. 2001). The water circulation of the Atlantic is influenced by the North clockwise warm-water Subtropical Gyre and South counter-clockwise warm-water Subtropical Gyre. The North gyre includes the Gulf Stream (GS) flowing north-east to the NAC, feeding warm waters to the North Atlantic and Europe, into the Canary Current (CC), in the eastern side of the Atlantic, reaching the North Equatorial Current (NEC) and finally meeting the GS in a permanent loop (Lalli and Parsons 1997a; Steele et al. 2001).

At the subtropical East Atlantic, the CC is also fed by the Azores Current (AC), delivering cool water from the North Atlantic Centre Waters (NACW) to the West African coast, turning westward and passing along the top northern waters of the Cabo Verde islands before becoming the NEC (Hagen 2001; Fernandes et al. 2004; Mason et al. 2011; Peña-Izquierdo et al. 2012a). South of the islands, the North Equatorial Countercurrent (NECC) flows eastward, affected seasonally by the Intertropical Convergence Zone (ITCZ), and turning north to feed the Mauritanian Current (MC) (Fernandes et al. 2004). The ITCZ along with trade winds blowing from east to west, generate Ekman upwelling during summer, driving an offshore upwelling system, extending from Morocco to the Guinea Gulf, and from the African coast to mid and west Atlantic, depending on the season (Doi et al. 2009; Peña-Izquierdo et al. 2012a; Faye et al. 2015). This system causes the formation of a thermal upwelling dome, called Guinea Dome (GD), fed by cyclonic circulation coming from the NECC and the North Equatorial Under Current (NEUC) during the summer, as a consequence of the ITCZ moving northward, and by the NEC (Doi et al. 2009; Peña-Izquierdo et al. 2012a). During winter the ITCZ moves south weakening the NECC, forcing the GD to move southeast. This will also cause the weakening of the MC from summer to winter (Doi et al. 2009). With the influence of different currents around the islands, receiving waters from the NACW and waters from de subtropical South Atlantic, this area is the rendezvous point of different water masses forming a large-scale productive frontal system, called the Cabo Verde Frontal Zone (CVFZ) (Zenk et al. 1991; Pérez-Rodríguez et al. 2001), stretching from de archipelago to Cape Blanc, where pelagic migratory fish aggregate (Fernandes et al. 2004) (Fig.1).

Upwelling in the adjacent coastal area of West Africa is permanent throughout the year between Cape Blanc and the Canary Islands (Canary Upwelling Current (CUC), 20ºN and 25ºN), influenced by the Trade Winds, with a peak during spring and autumn, constituting one of the four major eastern boundary current (EBC) systems (Barton et al. 1998; Thomas et al. 2001; Peña-Izquierdo et al. 2012). Higher concentrations of chlorophyll-*a* are between 10-20ºN (2.0-5.0 mg m^{-3}), while at higher temperate latitudes (~35ºN), approaching the Iberian Peninsula, chlorophyll-*a* seasonality is weaker, and concentrations are much lower (< 2.0 mg m^{-3}) (Thomas et al. 2001). To the North and South, the upwelling phenomena is seasonal, occurring during winter and spring below 20ºN, extending chlorophyll-*a* from the coast to open ocean through eddies and filaments (Pelegrí et al. 2005; Arístegui et al. 2009), and during summer and early autumn above 25ºN (Lalli and Parsons 1997a; Hagen 2001; Fernandes et al. 2004; Arístegui et al. 2009). The CC transports cold (⩽23°C) waters from these upwelling areas, feeding nutrients for primary production around the islands of Cabo Verde. Additionally, between July and November, St. Helena and Azores anticyclones cause warm water to reach the southern islands (24º-27ºC), a temperature preference of certain pelagic fish like tuna (Benchimol et al. 2009b). The presence and activity of these subsurface predators, on the other hand, attract marine top predators such as seabirds, looking for better feeding grounds and circumstances that attract prey to the surface (Ballance et al. 2001).

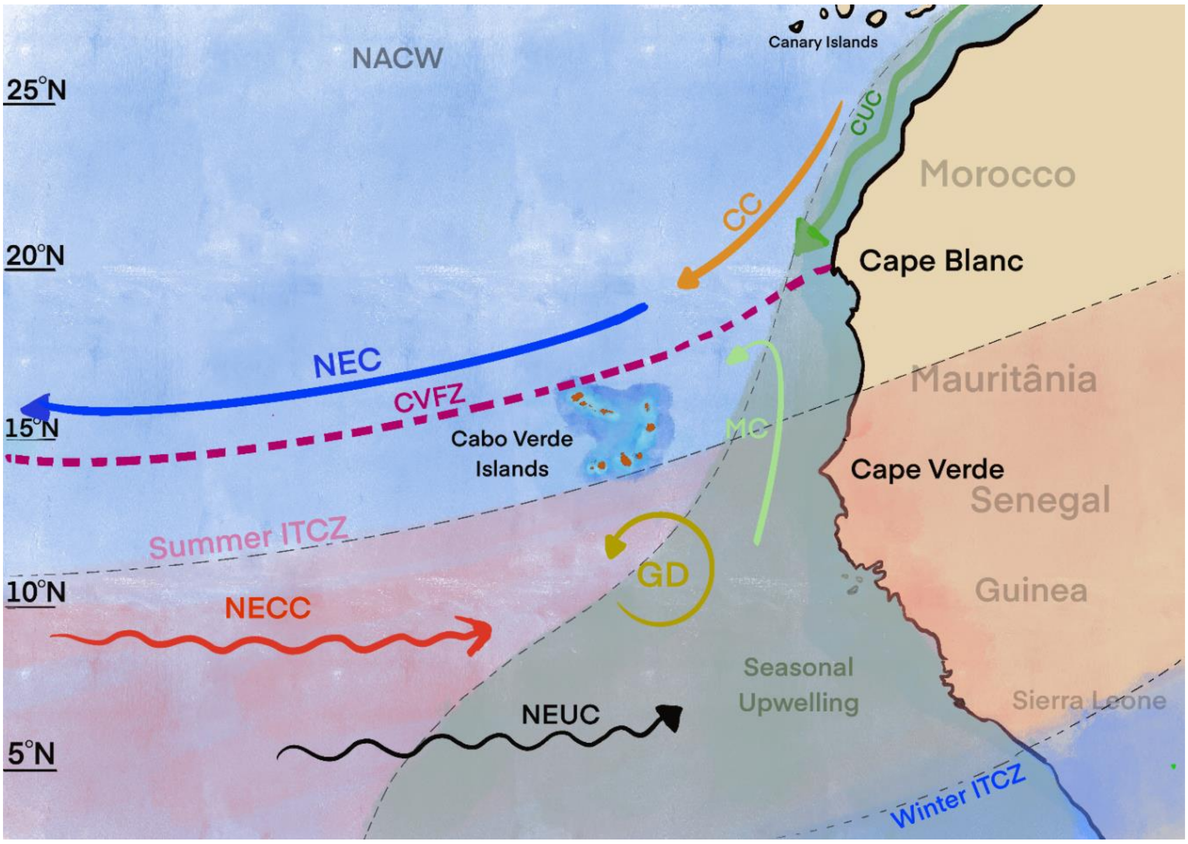


Figure 1.1. Major ocean circulation features around the Cabo Verde islands and West Coast of Africa. NEC – North Equatorial Current; NECC – North Equatorial Counter Current; NEUC – North Equatorial Under Current; CVFZ – Cape Verde Frontal Zone; ITCZ – Intertropical Convergence Zone; GD – Guinea Dome; MC – Mauritanian Current; CC – Canary Current; CUC – Canary Upwelling Current. Map drawn using map information from Fernandes et al. 2004; Izquierdo et al. 2011; Mason et al. 2011.

This area, which includes the Capeverdean archipelago (FAO Zone 34), is also a known hotspot of illegal fishing (https://spyglass.fish/), targeted by non-African and African vessels (Petrossian and Clarke 2020), where the majority of countries are amongst the most vulnerable to climate change (Blasiak et al. 2017). The number of MPAs here is also very low and of small size, located inside countries EEZs, and categorized as less protected/unknown by the Marine Protection Atlas (https://mpatlas.org/countries). In 1996, tropical MPAs were already considered by managers to have low success (Alder 1996), while inadequate or deficient staff capacity was mainly associated with countries of low income in all continents (Gill et al. 2017). Nevertheless, effectively establishing, managing and protecting local MPAs is extremely important to compensate for the lack of protective barriers that prevent species from exiting, and because, as mentioned before, MPAs often work as protective networks by being located in strategic areas corresponding to foraging habitats of local and foreign species, migration routes and/or corridors and wintering areas (Davies et al. 2021b). The Cabo Verde archipelago is a clear example of this, being located near an important area of marine productivity that is the West African Coast (Lloyd 1971; Demarcq and Somoue 2015), and frequently visited by a vast array of migrating and foraging species (Camphuysen and Van Der Meer 2005a; González-Solís et al. 2007; Paiva et al. 2015; Polidoro et al. 2017).

In conclusion, a good legislative framework is important to protect biodiversity. There is a lack of environmental legislative focus, even for most developed countries in Europe, given the important repository of biodiversity protected under the European directives. Such issues have not been examined for developing countries, such as Cabo Verde, with extremely important biodiversity with a relevant role for ecosystems, the economy and human well-being. The Cabo Verde Government has full legislative powers in the field of natural protected areas, and in the control of external borders. Development and enforcement of a legislative framework are important to conserve and restore native populations and important local habitats and should have a strong positive influence on many ecosystem services including cultural services such as eco-tourism.

1.6. Thesis objectives and outline

The main purpose of this thesis is to ultimately identify new Marine Protected Areas (MPAs) and assess the protective power of the existing ones in the Cabo Verde archipelago, an area where biodiversity ecology studies are still very recent, and effective conservation actions rely upon thorough understanding of the overall natural mechanisms in the everchanging marine environment.

On chapter 1 discuss current knowledge on the influence/ impact of Human-related stressors, such as fisheries, on the marine environment and how the implementation of MPAs can aid mitigate the impact of stressors on marine top predators and also guarantee sustainability on the extraction of marine resources.

Chapter 2 focusses on the activity of the capeverdean fishing sector, with some effort on characterizing the domestic fleet operating on the islands, while identifying species that interact with vessels and have the highest potential risk of bycatch. Additionally, we used the Cabo Verde shearwater to verify if changes in fish landings could impact developing chicks.

Chapter 3 used the at-sea distribution of seabird species with higher bycatch on the Cabo Verde fisheries (Chapter 2), to study spatio-temporal seabird-fisheries interactions, by measuring the spatial overlap with fisheires and foraging responses to fisheries activities (fishing effort) using tracked data from domestic small-scale vessels and foreign large-scale vessels tracked via AIS signal.

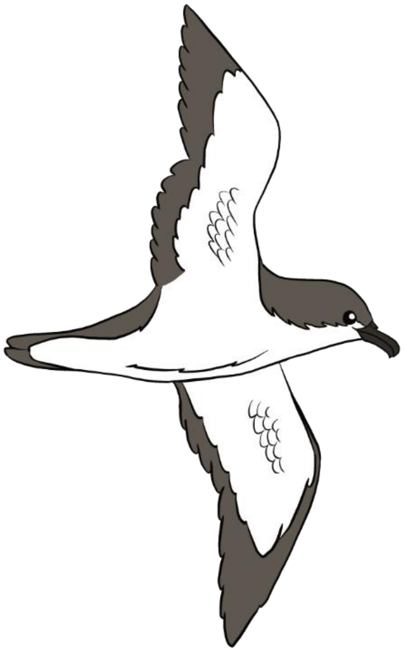
As Cabo Verde fisheries and MPAs are very coastal, chapter 4 went a step further using two species of boobies, one coastal (brown booby) and one comparably more pelagic (red-footed booby), and concentrated on examining their foraging behaviour at much finer scales, to understand how their spatial, behavioural and trophic ecology changes in an oligotrophic environment, verifying intra and inter-specific differences and competition, identifying environmental marine features driving foraging decisions, habitat choices and diet preferences.

Chapter 5 gathers all the available foraging distribution of seabird data collected in this study and over the years, and pools them together with fishing effort to propose new Marine Protected Areas that would effectively embrace an important part of the Cabo Verde seabird population and protect marine species that in association share the same resources and habitats, with an overall effort to include a huge part of the marine ecosystem.

Under chapter 6 I highlight the main outputs emanating from chapters 2 – 5, bias and/ or caveats on those studies and how future work to improve our knowledge on seabirds' foraging ecology, to better support decision-making processes of updating the current network of MPAs of the Cabo Verde archipelago.

Chapter 2

SEABIRD-FISHERIES INTERACTIONS AND THE POTENTIAL OF CAPE VERDE SHEARWATERS AS INDICATOR OF FISHERIES ACTIVITIES



Abstract

Today we are facing a reduction in fish landings due to overfishing, leading to the collapse of marine fish stocks worldwide. According to the Food and Agriculture Organization (FAO) the percentage of fish stocks considered to be still within biologically sustainable levels have decreased with visible negative effects on the health of marine food webs including upper-trophic level predators such as seabirds. In this study, we conducted interviews with fishermen from different island ports and fishing communities in the Cabo Verde archipelago to characterize the activity of domestic fleet and identify seabird interactions with vessels and bycatch. We also explored the influence of climate patterns (i.e., North Atlantic Oscillation – NAO – index), fishery landings (2013-2019), marine primary productivity and abundance of pelagic prey both on the linear growth rate and asymptotic mass of their growing chicks. Our results showed that handlines and purse-seines were the most used fishing gears for artisanal and semi-industrial vessels respectively, targeting mainly sharks, tunas, pelagic and demersal fishes. The Cape Verde shearwater was the most associated species with fisheries and with higher risk of bycatch, particularly for artisanal boats operating handlines, followed by brown boobies and red-billed tropicbirds. Fish landing correlations with environmental predictors (e.g., zooplankton and micronekton biomass, euphotic zone depth) were related to the food web complex, with changes in prey and intermediate species resulting in bottom-up biomass shifts related to the base of the marine food-web and top-to-bottom changes.

Asymptotic mass and linear growth rate of chicks correlated positively with landings of prey species (e.g., small pelagics) and associated predators (e.g., tuna), as well as marine primary productivity variables. These results show that much attention should be paid to the artisanal sector in finding ways to apply bycatch mitigation measures to reduce the risk of bycatch, while changes in fish-landings could be an essential indicator of prey-availability in the ocean which ultimately might affect seabirds' chick development and the overall breeding outcome, with potential demographic repercussion in the mid- to long-term, via lower recruitment into the breeding population.

Keywords: Cape Verde shearwater; Fishermen interviews; artisanal boats; semi-industrial vessels; Fish-landings; Small pelagics; Tuna; Chick development

2.1. Introduction

The practice of harvesting wildlife from water masses by humans, commonly known as fishing, exists since pre-historic times (about 100000 years ago, (Sahrhage and Lundbeck 2012). This activity increased exponentially since the 1950´s, when new technologies made fishing much easier and larger vessels were launched every day, and peaked during the 1980´s. Today we are facing a reduction in fish landings because of overfishing, which lead to the collapse of marine fish stocks worldwide (Pauly et al. 2002). Additionally, vessels catch enormous amounts of unwanted fish and other marine organisms in their fishing gears, which are later discarded back to sea and not always accounted for. However, these discards contribute to the overall proportion of fish caught and affect marine populations in many ways (Zeller et. al 2017). According to FAO (2020), the percentage of fish stocks considered to be still within biologically sustainable levels have decreased 24.2% from 1990 to 2017, which places into perspective the impact of human fisheries to fish stocks today, with visible negative effects on the health of marine food webs (Pauly et al. 1998) including upper-trophic level predators such as seabirds (Grémillet et al. 2016, 2018).

As volant creatures, seabirds have always been known for their navigational attributes, travelling enormous distances to reach wintering and breeding areas along ocean basins and coastal areas (Egevang et al. 2010; Hromádková et al. 2020). Fishermen have always looked for the presence of seabirds to locate fishing banks and fish schools, when other navigational technologies were not available (Montevecchi 2001). Today, areas with major fishing pressures are identified along the Indian, Pacific and central Atlantic oceans (Grémillet et al. 2018), and these areas are also often used by seabirds, leading to potential competition with fisheries (Karpouzi et al. 2007). Grémillet et al. (2018) reported a 19% decrease in the global annual seabird food consumption between 1970-2010 (~40 years), while fishery catches increased by 10%, a reflection of the competition between seabird and fisheries. However, the most recent FAO report (FAO 2020) informs of an even higher increase of > 14% in global fishery captures in only 28 years (1990-2018). Some areas with a declining seabird prey consumption include the majority of the Pacific Ocean, Northern Polar Atlantic, the Central American Caribbean waters and Central East Atlantic, the Mozambique Channel and further south in the West Indian Ocean, coinciding with fisheries increased catches of taxa targeted by seabirds (Grémillet et al. 2018). The southern oceans appear to be where the most competition between fisheries and seabirds occur (Grémillet et al. 2018).

These interactions can have negative and positive impacts, affecting seabirds directly and indirectly. Directly, fisheries may impact seabirds by causing death and injuries as such species are known to forage near fishing gears, and therefore, are often bycaught during fishing operations (Montevecchi 2001). These accidents occur when seabirds target the same prey as vessels (competition), steal baits from hooks, or simply when feeding on discarded whole fish and offal (scavenging) (Soriano-Redondo et al. 2016), with potentially deleterious effects at the individual and population levels. Fisheries can also provide fish discards, a food resource that are often sought by seabird populations that are more opportunistic (Mullers et al. 2009), while the reduction of fish-stocks can indirectly affect seabirds by decreasing the amount of available prey for seabird consumption (Grémillet et al. 2018). Other type of disturbances may occur near vessels affecting seabirds in many ways (e.g., light pollution, oil spills, vessel waist "ghost nets") (Lieske et al. 2019). Longline fishing has been identified as one of most impactful fisheries to seabirds (Lewison et al. 2004), affecting specifically albatrosses, petrels and shearwaters (Anderson et al. 2011).

Certain characteristics may lead to higher seabird bycatch such as the timing of fishing operations (hook settlement near the surface and hauling), and fishing during hours of higher seabird activity (sunrise and sunset) (Belda and Sánchez 2001; Soriano-Redondo et al. 2016; Cortés et al. 2017).

When trying to assess interactions between marine species and fishing vessels, many studies resort to personal interviews with fishermen (Godley et al. 1998; Moore et al. 2010; Oliveira et al. 2015; Lopes et al. 2016; Panagopoulou et al. 2017; Aguilera et al. 2020; Arias-Del-Razo et al. 2020). These have mainly focused on artisanal or small-scale fisheries, using structured interviews directed to interactions, target species, operation characterization, bycatch frequency and species identification using photographs. Many interviews indicate conflicts between fishermen and other natural predators, as they compete for the same resources or engage in scavenging activities. Furthermore, competition between industrial and artisanal fisheries also occur, with small-scale fishermen complaining that fishing conditions have deteriorated over time due to industrial trawler and longline fisheries destructive activities (Panagopoulou et al. 2017).

When choosing an indicator species for the impact of fisheries, it is important that both overlap on their fishing grounds, to reflect changes at the same spatial scale as some types of fisheries may occur at a larger scale, over ocean-basins, while others may operate at a local scale (Montevecchi and Myers 1995). Seabirds have a collective of specific characteristics and traits, which make them adequate to study changes influenced by anthropogenic factors such as fisheries, because they are more accessible during the breeding season when constrained to their colony sites, and their physiology and phenology tend to reflect changes in the marine environment, affecting measures such as breeding success, chick development and foraging effort. For instance, fisheries inducing prey-fish depletion were shown to affect seabird foraging ecology, increasing the foraging ranges of species such as the Peruvian booby (*Sula variegata*) to cope with regional resource decline (Bertrand et al. 2012). Seabird-fishery interaction studies in procellariforms, have revealed high risk of bycatch for shearwaters at the Mediterranean (Cortés et al. 2017) and off Chile (Carle et al. 2019), where vulnerability to fishing gears is high. These fishing practices occur in very closed and coastal environments, with large fishing fleets causing enormous fishing pressure, and seabirds, one way or another, end up interacting with vessels. However, in more open areas, such as the North Atlantic, shearwaters appear to forage mostly not in association with fisheries (Oliveira et al. 2015; Calado et al. 2020; Pereira et al. 2021). This may also be the case in coastal areas with high fishing pressure outside their breeding period (Bugoni et al. 2008b). Besides shearwaters, other species such as gannets have been observed to have high interaction with vessels (Gremillet et al. 2015; Oliveira et al. 2015; Calado et al. 2020), although this may vary according to food availability (Clark et al. 2020).

In the eastern central Atlantic, West African Coast, where the level of illegal fishing is very high (Agnew et al. 2009), assessing the amount of megafauna bycatch is not an easy task, especially in a productive and heavily fished environment as the Canary current upwelling (Laurans et al. 2004; Camphuysen and Van Der Meer 2005b; Worm et al. 2009). This area is commonly used for foraging by seabirds breeding nearby (mainly in the Macaronesia islands) and wintering birds from the northern hemisphere, increasing the risk of bycatch (Wynn and Knefelkamp 2004; Camphuysen and Van Der Meer 2005b; Gremillet et al. 2015; Paiva et al. 2015; Grecian et al. 2016; Monteiro 2019). The Cape Verde shearwater (*Calonectris edwardsii*), breeds in the Cabo Verde islands, foraging around the islands EEZ and with incursions to off West Africa (Paiva et al. 2015). Previous studies have mapped their distributions, reflecting a marked dual foraging strategy during the chick-rearing phase, alternating between short forays within the Cabo Verde waters with longer and distant trips to off West Africa (Paiva et al. 2015). Yet, years with a higher proportion of longer foraging trips to off West Africa have been related with low marine productivity regimes within the archipelago (Paiva et al. 2015; Cerveira et al. 2020), and might be related with a decrease in the abundance of pelagic prey and other marine predators such as tunas. Interviews with Cabo Verde fishermen estimated high levels of Cape Verde shearwater poaching annually (Monteiro 2005) and showed that this is the most vulnerable species to bycatch inside the Cabo Verde EEZ, followed by brown boobies (*Sula leucogaster*) and red-billed tropicbirds (*Phaethon aethereus*) (Monteiro and Correia 2007; Montrond 2020). Therefore, these should be the best species to reflect changes in the marine environment as well changes in fisheries inside Cabo Verde EEZ.

In this study, I conducted interviews with fishermen from 26 ports and fishing communities in Cabo Verde archipelago to characterize the activity of artisanal and semi-industrial fisheries and identify which seabird species interact more and which are bycaught in higher numbers in fishing gears. Plus, we also compiled fishery landings between 2013 – 2019, made available by the IMAR institute in São Vicente Island, and analysed the influence of marine primary productivity and biomass of zooplankton on landings of tuna, other pelagic predatory fish, and small pelagic prey fish. Finally, also for 2013-2019, we explored the influence of climate patterns (i.e. North Atlantic Oscillation – NAO – index), fishery landings, marine primary productivity and abundance of pelagic prey both within the Cabo Verde archipelago (500 km around Raso Islet) and off West Africa (~300 km from the coastline) on the linear growth rate and asymptotic mass of their growing chicks. Based on previous reported information, we made the following expectations: 1) from all seabird species breeding in the Cabo Verde archipelago, we expect Cape Verde shearwaters and brown boobies to be those interacting more with fisheries and suffering a higher bycatch rate, whilst red-billed tropicbirds should interact less with fisheries; 2) tuna landings should decrease with the decreasing availability of marine productivity at the base of the food-web (nekton concentration) and small pelagic prey, and 3) linear growth rate and asymptotic mass of Cape Verde shearwater chicks should be higher with increasing landings (and availability) of both small pelagic prey and underwater predators, like tuna, because parents are more likely to increase the amount of fish provisioned to their growing chick with higher prey availability and facilitated foraging, respectively.

2.2. Methods

2.2.1. *Fishermen Interviews*

Personal interviews, targeting fishermen from different fishing communities of the Cabo Verde islands, were conducted during 2018 and 2019 (Figure 2.1.). Surveys collected information to characterize local fisheries and estimate potential seabird bycatch, using a questionnaire with 34 questions divided into 3 sections: (1) General data, with information on interviewed fishermen, type and characteristics of the fishing techniques and gear used on the boat; (2) Fishing activity for the type of method used, with details on seasonality, targeted species and baits; and (3) knowledge on interactions between seabirds and fisheries, with details on capture of other marine predators (sea turtles and sharks) (Table S2.1.) . For a better understanding of the questions by local fishermen, interviews were held in Capeverdean creole (local language), and interviewers had previous knowledge

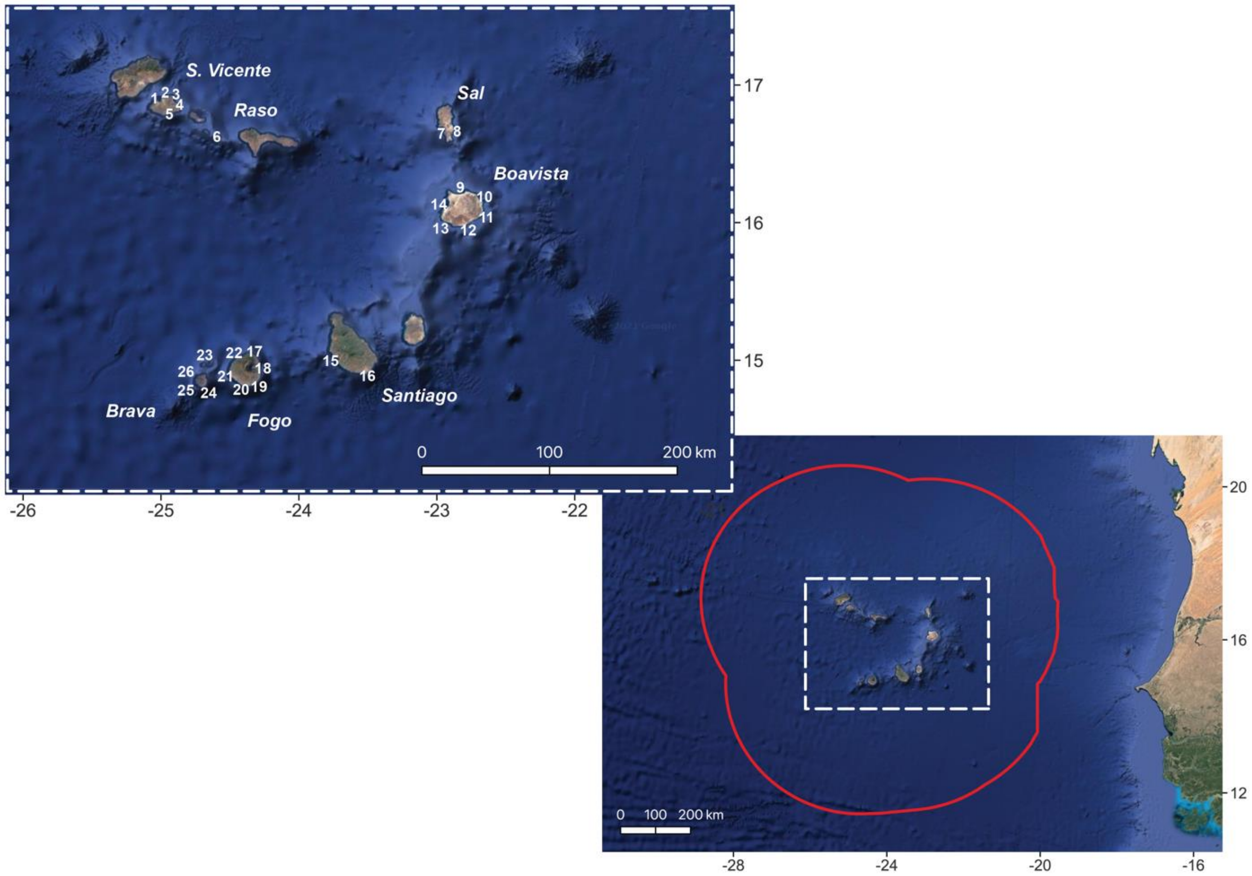


Figure 2.1. Twenty-six fishing ports where fisherman interviews were conducted, over 7 islands of the Cabo Verde archipelago. White dotted line represents the capeverdean territorial land and the red line represents the Cabo Verde Exclusive Economic Zone (see Table 2.2 for further details

on the field (ONG technicians used to work with fishermen, biology students, etc). Because many fishermen use the Marine Protected Area (MPAs) to fish, some interviews took place in such places (e.g., Raso Islet), where they spend the nights in between fishing trips. This was a good strategy to approach fishermen during leisure time and have a less formal conversation. Survey time varied in relation to the number of fishing techniques used on boats, which did not surpass more than two, lasting between 20-30 minutes. To avoid interference and influence of other respondents, interviews were performed individually. Pictures of seabird species and maps were also available to fishermen to better identify species and fishing grounds (Moore et al. 2010; Oliveira et al. 2015; Lopes et al. 2016; Montrond 2020).

Data collection varied across islands and sampling effort did not always correspond to fisheries distributions across islands (Table 2.2), as Santiago would be the island where most boats concentrate (INE 2020). This was more related to the availability of interviewers on each island, logistical constraints, and port locations. Interviews on most islands were performed to represent all fishing communities and focused on accessibility and importance. Although the number of artisanal fisheries interviews (N=209) surpassed greatly the number of semi-industrial vessels (N=25), the sampling size does seem to represent the number of existing artisanal (N=1588 boats) and semi-industrial (N=119 vessels) fishing boats on the archipelago (INE 2020).

Table 2.2. Sampling locations and number of surveys conducted along the Cabo Verde archipelago

Islands	N sampling locations	Sampling Months	Year	Type of fishing	N
São Vicente	6	Nov-Dec	2018	Artisanal	39
				Industrial	22
Raso	1	June, August and October	2018	Artisanal	6
Sal	2	September	2019	Artisanal	4
Boavista	6	Feb, May and December	2018	Artisanal	19
		Feb, April, May	2019	Industrial	3
Santiago	2	April-Jun	2019	Artisanal	24
Fogo	7	Dec	2017	Artisanal	73
		May, Nov, Dec	2018		
		Jan, Feb, Apr 2019	2019		
Brava	3	May	2018	Artisanal	44
		Feb-Mar	2019		

2.2.2. Fish-landings and shearwater chick data

Fish landing data was provided by the IMAR institute in São Vicente, with information on species caught, weight per month/trimester/year, landings on different islands for artisanal and semi-industrial fisheries and for different fishing gears. Because gear was not available for most of our study period (2013-2019), we did not consider this variable. Additionally, we categorized species into three different groups (tuna, pelagic and small pelagic) taking into consideration previous work confirming the predator-prey relationship between seabirds and small pelagic fish (Schreiber and Burger 2001; Engelhard et al. 2014; Rodrigues 2014) and the facilitator role of tuna and other large pelagic fish to foraging seabirds (Au and Pitman 1986; Weimerskirch 2007).

Data on growth parameters of Cape Verde shearwater chicks have been collected since 2013 until 2019 in Raso islet (16°36'40.63"N, 24°35'15.81"W): chick body mass and wing length was measured every 2-4 days to calculate their Linear Growth Rate (g day^{-1}) and Asymptotic Mass (g) (Ramos et al. 2018; Semedo 2020). With progressing chick development, adults will decrease chick-meals so they can achieve optimal flight weight (asymptotic mass) (Rodrigues 2014). As such, changes in fish landings and environmental predictors related to prey availability may affect asymptotic mass and linear growth rate, with the potential to cause development and fledging delay.

2.2.3. Data analysis

Chi-square tests were used to investigate differences among the characteristics of fishing boats from interviewed fisherman. All responses were coded with binary variables

1 and 0 representing "yes" and "no" answers, respectively and we used the sum of all answers to calculate the chi-square test on R.

To provide a better view over the interaction between seabirds and fisheries and seabird bycatch we used zero-Inflated Models with Negative Binomial distribution (ZINB) and accounting for overdispersion (Zeileis et al. 2008) to test the effect of the independent variables: (1) seabird species (2) month of survey (January-December), (3) island (São Vicente, Raso, Sal, Boavista, Santiago, Fogo or Brava), (4) fishing type (artisanal or semi-industrial), (5) fishing gear (gillnet, handline, purse-seine or longline), (6) fishing moment (gear set or gear retrieval) on the probability of seabird bycatch. ZINB models use a reference category against which the remaining data is compared, this was set as the first category on the previous six variables. Base models were validated, checked for collinearity among predictors, overdispersion, residual patterns and observed *vs.* fitted values using *performance* (Lüdecke et al. 2019) and *DHARMa* (Hartig 2019) packages. A set of all possible model combinations were generated using the dredge function within the *MuMIn* package (Bartón 2019), and best model was selected based on the lowest corrected Akaike's information criterion for small sample sizes (AICc). This evaluation included the fisherman ID as a random effect, to control for pseudo-replication issues, because some fishermen were interviewed more than once in different months/ study years. Duplicate interviews represented less than 7% of the overall sample size.

Generalized Additive Mixed Models (GAMMs) were used to test the effect of (1) month, (2) monthly NAO, (3) depth of euphotic zone (m), (4) net primary productivity (mg m^{-2} day^{-1}), (5) biomass of zooplankton (g m^{-2}) and (6) biomass of micronekton in the epipelagic layer (g m^{-2}) on the amounts of (Model 1) tuna, (Model 2) pelagic predators and (Model 3) small pelagic fish (Tons) landed on the Cabo Verde archipelago. GAMMs are commonly used to model multisite-time series data, allowing linear and non-linear relationships between explanatory and response values. We started running models including all the main effects, and the best candidate model was selected based on the second-order corrected Akaike's information criterion (AIC). A difference of less than 2 was interpreted as competing models receiving a similar amount of support from the data (Burnham and Aderson 2002). All analyses were performed with R software ver. 3.5.2 (R Core Team 2018), and significance was set at alpha = 0.05.

A General Linear Model (GLM) was used to test the effect of landings of (1) tuna, (2) pelagic predatory fish and (3) small pelagic fish, as well as (4) depth of the euphotic zone, (5) net primary productivity, (6) zooplankton biomass and (7) biomass of micronekton in the epipelagic layer on the linear growth rate and asymptotic mass of Cape Verde shearwater chicks from Raso Islet. The depth of the euphotic zone refers to the area from the surface to the depth with sufficient light (1% of its value beneath the surface) to support photosynthesis, reflecting water clarity or turbidity, a quality index of an ecosystem and consequently an important property of primary production (Lee et al. 2007; Soppa et al. 2013; van Ruth et al. 2020). Landings (vars. 1 – 3) and environmental predictors (vars. 4 – 7) were extracted for the months May – October (Cape Verde shearwaters breeding season) between 2013 – 2019, for the area within the Cabo Verde EEZ (see Fig. 2.1). Environmental predictors belong to the SEAPODYM – Spatial Ecosystem and Population Dynamics Model (http://www.seapodym.eu) and were extracted from the Copernicus database (https://myocean.marine.copernicus.eu), at a 0.1° resolution.

2.3. RESULTS

2.3.1. Characterization of fishing events

In terms of artisanal fisheries, handlines were the most used fishing gear (88.5%; $\chi^2_5 = 609.74$, $p < 0.001$), and most boats (87%) had less than 10 m long (Table S2.2). All boats were motorized and 82% of motors had < 30 horsepower (HP) capacity (Table S2.2). On the other hand, purse seine was the most used fishing gear on semi-industrial fisheries (84%; $\chi^2_5 = 66.091$, $p < 0.001$), with most boats (84%) more than 10m long and 40% of them had > 30 HP motors (Fig. S2.1, Table S2.2).

Fishing trips of artisanal boats using handlines were in majority ⩽1 day (55.5%) ($\chi^2_3 = 181.5$, $p < 0.001$), but some of them lasted between 2-5 days or more. Most semi-industrial purse seiners spent longer periods fishing at sea, 2-5 days (36%) or higher (40%) ($\chi_3^2 = 11.96$, $p < 0.01$). Time of operating gears for all types of fisheries were mainly between 6-12h, but this was significant for artisanal fisheries ($\chi^2_4 = 106.21$, $p < 0.001$) (Table S2.3).

The more frequent fish baits used on both artisanal and semi-industrial fisheries were bigeye scad *Selar crumenophthalmus*, mackerel scad *Decapturus macarellus* and crustaceans. Octopus species and blackspot picarel *Spicara melanurus* were also used occasionally on artisanal fisheries. Mackerel scad was the most common bait for artisanal boats, while semi-industrial vessels preferred to use mackerel and bigeye scads (Fig. S2.3).

Target groups included sharks, tunas, pelagic and demersal fishes, molluscs, and crustaceans. Artisanal boats targeted more tuna species (71.8%), bluespotted sea bass *Cephalopholis taeniops* (76.1%) and wahoo *Acanthocybium solandri* (58.9%) followed by Atlantic emperor *Lethrinus atlanticus (*37.3%), Muraenidae (34%), bigeye scad (31.1%) and

Sphyrnidae sharks (33%). Semi-industrial vessels targeted bigeye scad (88%), mackerel scad (84%), tuna species (56%) and wahoo (48%) (Table 2.3).

Table 2.3. Frequency of occurrence of target species on the fishing vessels, by fishing type (artisanal and semi-industrial) in the Cabo Verde archipelago.

Target Group	Target Species	Artisanal (209)	Semi-Industrial (25)
Sharks	Sphyrnidae	33.0	0.0
Tuna	*Acanthocybium solandri*	58.9	48.0
	Thunnus sp	71.8	56.0
	Auxis sp.	8.1	52.0
Pelagic Fish	*Selar crumenophthalmus*	31.1	88.0
	Decapterus macarellus	20.1	84.0
	Spicara melanurus	17.2	24.0
	Caranx crysos	5.3	4.0
	Trachinotus sp.	2.4	4.0
	Trachurus trecae	1.0	4.0
	Belone belone	0.5	0.0
Demersal fish	*Seriola rivoliana*	18.2	4.0
	Xiphias gladius	14.4	0.0
	Caranx lugubris	4.3	0.0
	Elagatis bipinnulata	5.3	0.0
	Diplodus sp.	21.1	4.0
	Sparisoma sp.	10.5	4.0
	Lethrinus atlanticus	37.3	4.0
	Cephalopholis taeniops	76.1	20.0
	Parapristipoma humile	24.9	4.0
	Muraenidae	34.0	8.0
	Lutjanus fulgens	15.8	0.0
	Bodianus sp.	1.9	0.0
	Makaira nigricans	1.0	0.0
	Mycteroperca rubra	2.4	0.0
	Coryphaena hippurus	17.7	12.0
	Sphyraena guachancho	2.4	0.0
	Apsilus fuscus	2.9	0.0
	Virididentex acromegalus	0.5	0.0
	Pseudupeneus prayensis	0.5	4.0
	Sarpa salpa	0.5	0.0
	Bothus podas	0.5	0.0
	Galeoides decadactylus	0.5	0.0
	Priacanthus arenatus	2.9	0.0
	Abudefduf sp.	2.9	0.0

2.3.2. Seabird-fisheries interactions

From all fishermen interviewed, the majority could only identify Cape Verde shearwater (62%), red-billed tropicbird (64%), and brown booby (65%), which were more easily recognizable from a distance due to its specific characteristics and high association with fishing boats (Fig. 2.2A). The majority of fishermen agreed that interactions exist, with 57% of fishermen claiming that the number of seabirds interacting with boats during a specific fishing operation is higher than 25 individuals for both artisanal and semi-industrial fisheries, and acknowledging that there is a negative effect of these interactions attributed mainly to bait loss, and a positive effect when indicating the presence of fish (Fig. 2.3) However, when asked to quantify their economic losses due to seabird negative interactions, less than 5% claimed high costs for both types of fisheries (but were unable to quantify such loss), and 59% of artisanal fishermen and 64% of semi-industrial fishermen claiming it to be non-existent ($\chi^2_3 = 184.36$, $p < 0.001$; $\chi^2_3 = 33.2$, $p < 0.001$).

Concerning their opinion on which type of fisheries more frequently caught seabirds, most fishermen agree that handlines and longlines are the riskiest gear-types for seabirds (Fig. 2.2B). However, when questions started redirecting fishermen towards accidental and intentional catches concerning their own boats, most of them preferred not to answer and seemed a little uneasy or discontent since, as of 2018 (decree law No 1/2018), sea turtle catches are prohibited and punishable by law. Seabird species were also nominated for protection since 2002 (Regulatory decree No 7/2002), like sharks (Resolution No 93/2020), however there are still no punishment measures to insure such protection.

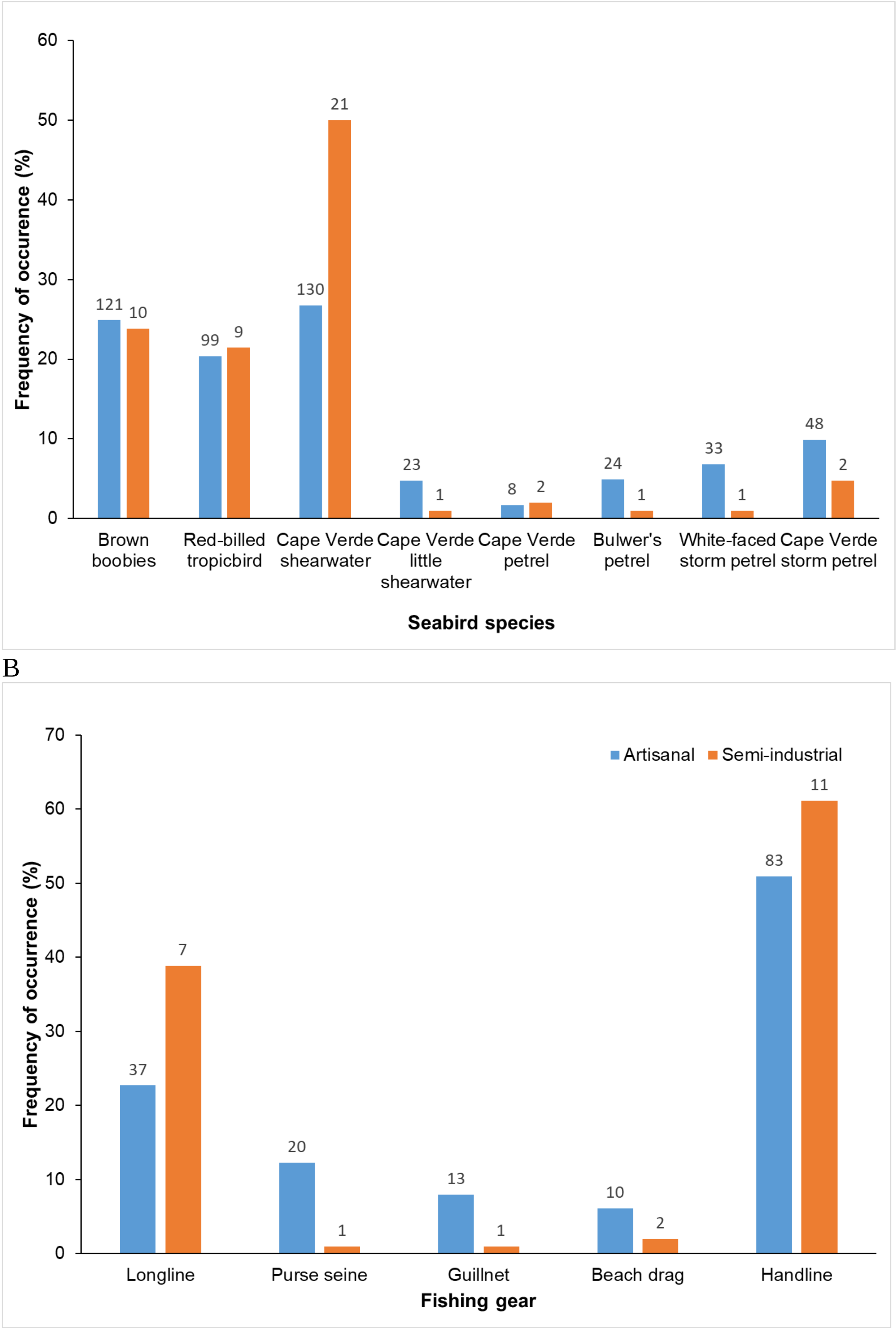


Figure 2.2. Frequency of occurrence of (A) seabird species interacting with fisheries and (B) seabirds by-caught on different fishing gears from artisanal (N = 209 interviews) and semi-industrial (N = 25 interviews) fishing boats operating in the Cabo Verde archipelago. Sample size above each bar.

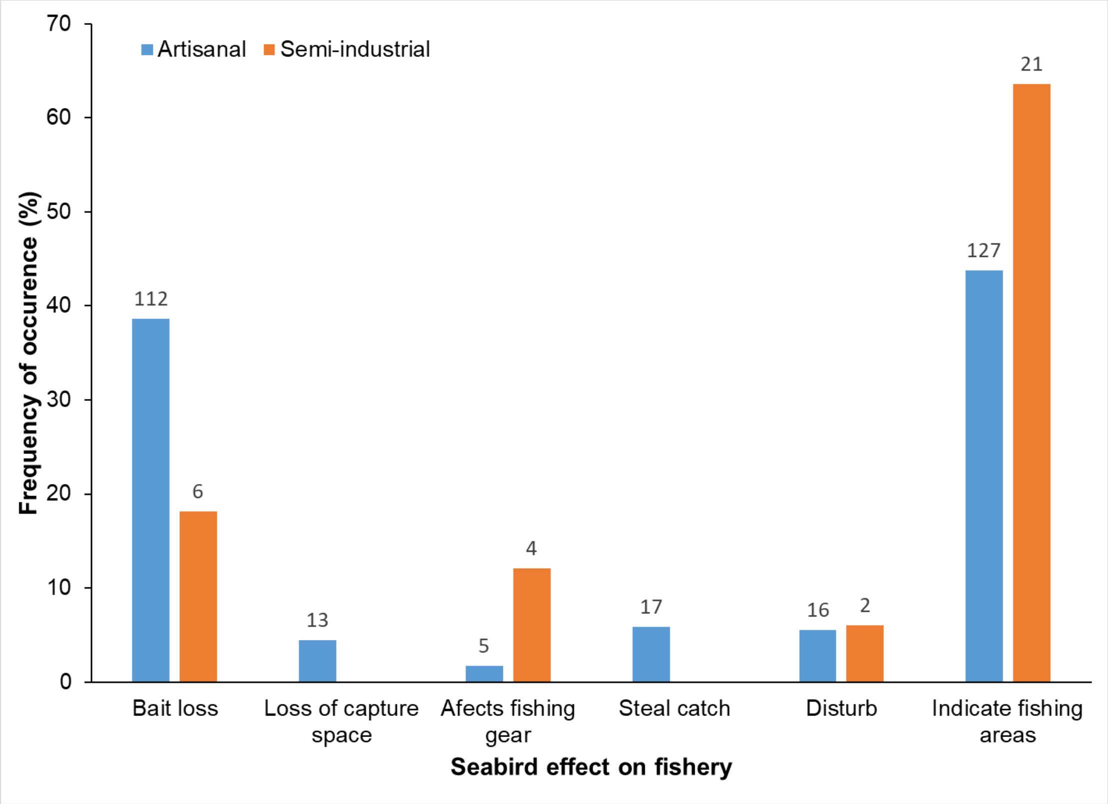


Figure 2.3. Frequency of occurrence different types of seabird effect on Cabo Verde artisanal and semi-industrial fishery activities. Sample size above each bar.

The model that better explained the seabird-bycatch probability (ZINB model with lowest AICc value, Table 2.4) was the one that included the following variables: species, fishing type, fishing gear and the combined variables fishing type *vs.* species and fishing gear vs species. By comparing each species with the reference species with low vessel interaction (Bulwer´s petrel), results showed a higher interaction probability for Cape Verde shearwaters, brown boobies, and red-billed tropicbirds, while for instance the Cape Verde petrel (*Pterodroma feae*) had a lower probability of interaction when compared to the reference species, but this was not significant (Table 2.5). Handlines and longlines were once again the most significant fishing gears influencing seabird bycatch, while gear retrieval had a significantly lower probability of catching seabirds when compared to the

Table 2.4. Summary statistics for zero-inflated negative binomial (ZINB) models testing the effect of the independent variables: species, month, island, fishing type and gear, fishing moment (gear set or retrieval) and their interactions on fishery by-catch events within the Cabo Verde Economic Exclusive Zone (EEZ). Fishermen ID included as a random effect to control for pseudo-replication issues. df = degrees of freedom, logLik = loglikelihood ratio statistic, AICc = Akaike's information criterion corrected for small sample size, w_i = Akaike weight.

Count component	**df**	**logLik**	**AICc**	**w_i**
Species + Fishing type + Fishing gear + Fishing type*Species + Fishing gear*Species	12	398.14	500	0.69
Species + Month + Fishing type + Fishing gear + Fishing type*Species + Fishing gear*Species	17	400.01	519	0.79
Species + Month + Island + Fishing type + Fishing gear + Fishing type*Species + Fishing gear*Species	23	402.23	555	1.10

Table 2.5. Statistics from zero-inflated negative binomial (ZINB) models testing the effect of the independent variables: species (Cape Verde shearwater-CVSh, Cape Verde storm petrel-CVSPt, white-faced petrel-WFPt, red-billed tropicbird-RBTr, Cape Verde petrel-CVPt, Cape Verde little shearwater-CVLSh, brown booby-BBo, Bulwer's petrel-BPt), month (January – December), Island (São Vicente, Sal, Boavista, Santiago, Fogo, Brava), fishing type (artisanal, semi-industrial) and gear (gillnet, handline, purse-seine and longline), fishing moment (gear set, gear retrieval) and their interactions on fishery by-catch events within the Cabo Verde EEZ. Reference categories set as the first category of the mentioned (6) before. Significant effects are shown in **bold**. Fishermen ID included as random effect to control for pseudo-replication

Parameters	Count component	
	β ± SE	P (>|z|)
Species (CVSh)	**4.14±0.24**	**<0.001**
Species (CVSPt)	-0.30±0.30	0.30
Species (WFPt)	-0.58±0.32	0.07
Species (RBTr)	**2.33±0.24**	**0.01**
Species (CVPt)	-2.15±0.54	0.08
Species (CVLSh)	-0.70±0.33	0.09
Species (BBo)	**2.59±0.24**	**0.01**
Fishing type (semi-industrial)	0.69±1.04	0.07
Fishing gear (handline)	**3.24±2.11**	**0.01**
Fishing gear (purse-seine)	0.53±0.32	0.25
Fishing gear (longline)	**1.99±0.65**	**0.02**
Fishing moment (gear retrieval)	**-3.23±1.23**	**0.001**
Fishing type (semi-industrial) * Species (CVSh)	**3.48±1.28**	**0.01**
Fishing type (semi-industrial) * Species (CVSPt)	-0.30±1.47	0.84
Fishing type (semi-industrial) * Species (WFPt)	1.31±1.30	0.31
Fishing type (semi-industrial) * Species (RBTr)	**2.24±1.16**	**0.03**
Fishing type (semi-industrial) * Species (CVPt)	2.15±1.54	0.16
Fishing type (semi-industrial) * Species (CVLSh)	0.7±1.48	0.63
Fishing type (semi-industrial) * Species (BBo)	**1.94±1.15**	**0.03**
Fishing gear (handline) * Species (CVSh)	**4.65±0.98**	**<0.001**
Fishing gear (handline) * Species (CVSPt)	-0.32±0.24	0.34
Fishing gear (handline) * Species (WFPt)	0.45±0.34	0.43
Fishing gear (handline) * Species (RBTr)	**3.09±2.77**	**0.02**
Fishing gear (handline) * Species (CVPt)	0.98±0.55	0.75
Fishing gear (handline) * Species (CVLSh)	-0.13±0.23	0.67
Fishing gear (handline) * Species (BBo)	**3.69±2.01**	**0.01**
Fishing gear (purse-seine) * Species (CVSh)	0.68±0.65	0.44
Fishing gear (purse-seine) * Species (CVSPt)	0.76±0.88	0.64
Fishing gear (purse-seine) * Species (WFPt)	-0.87±0.22	0.23
Fishing gear (purse-seine) * Species (RBTr)	-0.45±0.53	0.34
Fishing gear (purse-seine) * Species (CVPt)	-0.34±0.32	0.63
Fishing gear (purse-seine) * Species (CVLSh)	0.63±0.92	0.46
Fishing gear (purse-seine) * Species (BBo)	1.01±0.43	0.09
Fishing gear (longline) * Species (CVSh)	**1.83±0.65**	**0.03**
Fishing gear (longline) * Species (CVSPt)	-0.53±0.34	0.25
Fishing gear (longline) * Species (WFPt)	-0.44±0.56	0.43
Fishing gear (longline) * Species (RBTr)	1.07±0.98	0.07
Fishing gear (longline) * Species (CVPt)	-0.45±0.23	0.25
Fishing gear (longline) * Species (CVLSh)	-0.87±0.97	0.44
Fishing gear (longline) * Species (BBo)	1.55±0.59	0.05

reference category (gear set). In fact, most fishermen stated that bycatch occurred mainly during hook settlement in both fisheries. Although bycatch probability was higher for semi-industrial vessels, there was no significant interaction difference between both types of fisheries. Nevertheless, Cape Verde shearwaters were significantly more caught than the reference species, followed by red-billed tropicbirds and brown boobies in semi-industrial vessels. Handlines caught significantly more Cape Verde shearwaters, brown boobies, and red-billed tropicbirds, while longlines caught only Cape Verde shearwaters (Table 2.5).

Most fishermen claimed that birds are often alive when spotted caught and are released either dead or alive. Few of them think accidental catches are an inconvenience by disturbing fishing activities, on the contrary, most of them stated that it is not relevant (40-50%), and that incidental and intentional catches have decreased, except for sharks, with 50% of them stating that an increase in intentional shark catches is attributed to foreign vessels.

2.3.3. The influence of environmental predictors on fishery landings and chick growth parameters of Cape Verde shearwater

The best models concerning landings of tuna species included variables such as month, marine productivity, and zooplankton biomass (Table 2.6). The effect of month on tuna landings was significant for the months of July to December (Table 2.7), while zooplankton biomass seems to have a more significant effect on tuna landings than marine primary productivity, with a proportional increase of tuna landings with zooplankton biomass (Fig. 2.4).

Table 2.6. Best candidate Generalized Additive Models (GAMs) on the effect of different ecological drivers of marine productivity (i.e. month, monthly NAO, depth of euphotic zone (zeu, m), net primary productivity (npp, mg m^{-2} day^{-1}), biomass of zooplankton (zooc, g m^{-2}) and biomass of micronekton in the epipelagic layer (epi, g m^{-2}) on the amounts of (a) tuna, (b) pelagic predators and (c) small pelagic fish landed on the Cabo Verde archipelago.

Model structure	χ^2	df	AICc	ΔAIC	Akaike weight	Dev. Expl. (%)			
a) Tuna									
Tuna landings ~ month + npp + zooc	0.63	15.00	101.79	0.00	0.41	63.0	npp: p= 0.06	zooc: p< 0.001	
b) Pelagic fish									
Pelagic fish landings ~ zeu + zooc + epi	0.19	6.00	41.07	0.00	0.11	19.0	zeu: p= 0.05	zooc: p= 0.03	epi: p= 0.12
c) Small pelagic fish									
Small pelagic fish landings ~ npp + zeu + epi	0.24	6.00	348.34	0.00	0.32	24.4	npp: p= 0.001	zeu: p< 0.001	epi: p= 0.02

Table 2.7. Results from the model showing the effect of month on tuna landings (month was retained as an important variable in the model selection process). All months (categorical variable) are compared with Month 1 (January).

	β ± SE	t value	Pr(>|t|)
(Intercept)	4.89±0.31	15.90	<0.001
Month2	-0.45±0.34	-1.32	0.19
Month3	0.06±0.48	0.13	0.89
Month4	-0.23±0.47	-0.48	0.63
Month5	-0.01±0.43	-0.03	0.98
Month6	0.34±0.41	0.83	0.41
Month7	1.19±0.37	3.24	0.001
Month8	1.89±0.46	4.09	<0.001
Month9	2.51±0.52	4.84	<0.001
Month10	3.13±0.53	5.86	<0.001
Month11	2.66±0.49	5.47	<0.001
Month12	1.90±0.37	5.17	<0.001

For pelagic predatory fish landings, the best model showed the importance of the euphotic zone, biomass of zooplankton and micronekton in the epipelagic layer, however this last variable was not significant. Pelagic fish landings decreased with the increasing depth of the euphotic zone and increase of zooplankton biomass (Fig. 2.4).

The amount of small pelagic fish landed was significantly influenced by the depth of the euphotic zone, primary productivity and micronekton biomass in the epipelagic layer (Table 2.6). Landings increased with a higher depth of the euphotic zone and marine primary productivity, while a decrease was observed with the increase of micronekton biomass (Fig. 2.4).

Regarding the variables affecting the linear growth rate of Cape Verde shearwater chicks, the GLMs showed that this growth rate increased with the increasing of the monthly tuna and small pelagic fish landings, as well as of the marine primary productivity.

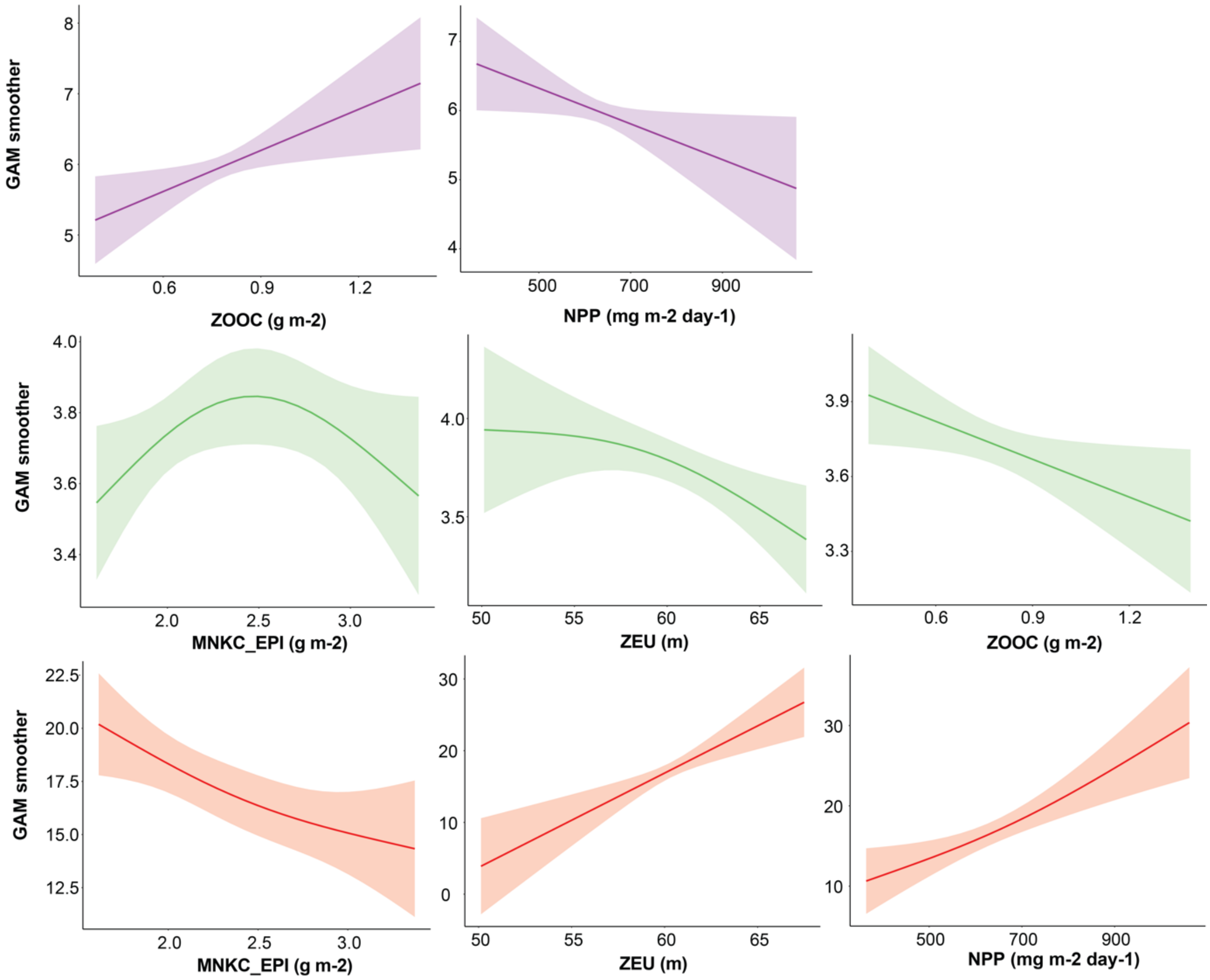


Figure 2.4. Generalized Additive Model (GAM) smoothers from the best models (see Table 1) showing the relation between landings of tuna (purple), pelagic predatory fish (green) small pelagic fish (red) with mass content of epipelagic micronekton (MNKC_EPI; g m^{-2}), euphotic zone depth (ZEU; m), mass content of zooplankton (ZOOC; g m^{-2}) and net primary productivity (NPP; mg m^{-2} day^{-1}).

The same landing variables contributed positively for the increase of the asymptotic mass of chicks, as well as the biomass of micronekton in the epipelagic layer (Table 2.8).

Table 2.8. General Linear Models (GLM) testing the effect of monthly (1) tuna, (2) pelagic predatory fish and (3) small pelagics landed and (4) depth of the euphotic zone, (5) net primary productivity, (6) zooplankton biomass and (7) biomass of micronekton in the epipelagic layer on the linear growth rate and asymptotic mass of Cape Verde shearwater chicks from Raso Islet, between May-October of 2013-2019. Significant results marked in **bold**.

	Linear Growth Rate			Asymptotic mass		
Parameter	$\beta \pm$ SE	t value	Pr(>|t|)	$\beta \pm$ SE	t value	Pr(>|t|)
Landings						
Tuna	**3.69±0.45**	**3.87**	0.01	**2.19±0.23**	**4.33**	**0.001**
Pelagic predatory fish	-0.25±0.34	1.32	0.19	-0.13±0.45	0.76	0.14
Small pelagic fish	**1.66±0.48**	**3.13**	0.01	**1.99±0.76**	**3.01**	**0.02**
Environmental predictors						
Depth of the euphotic zone (m)	0.64±0.56	0.87	0.12	0.07±0.06	0.54	0.31
Net primary productivity (mgC^{-1}day^{-1})	**1.99±0.65**	**2.67**	0.03	-0.14±0.23	0.45	0.39
Zooplankton biomass (g m^{-2})	-0.45±0.55	1.01	0.25	0.13±0.20	0.65	0.25
Micronekton biomass (g m^{-2})	0.45±0.31	0.77	0.19	**1.89±0.56**	**1.99**	**0.04**

2.4. DISCUSSION

2.4.1. Characterization of fisheries

The Cabo Verde national fishing fleet is composed mostly of artisanal boats that are allowed to fish within 3 nautical miles (hereafter referred to as n.m.) and semi-industrial and industrial domestic boats fishing within 12 n.m. Outside the 12 n.m. foreign vessels operate longlines and purse seines with fishing agreements to catch large pelagic fish (González et al. 2020). As previously observed by Fortes (2019) and Montrond (2020), artisanal boats operated a higher diversity of fishing methods, with the identification of six methods on this survey (Handlines, Snorkelling, Purse Seine, Gillnets, Traps and Longlines), while only three methods were identified for semi-industrial vessels (Purse Seine, Handlines and Longlines).

Our results were in line with previous descriptive studies, with artisanal boats using mainly handlines to catch demersal, large and small pelagic fishes, while some boats practicing diving to catch lobsters, crustaceans, and molluscs. Montrond (2020) also showed a similar tendency for artisanal boats to catch a more diverse array of fishes, targeting more demersal species compared to semi-industrial vessels that targeted mostly small pelagics. Nevertheless, fish targets were similar for both sectors, composed mainly of small pelagics and tunas, as observed in other countries in the west African region (Belhabib et al. 2014, 2016, 2018).

2.4.2. Seabirds-fisheries interactions

The Cape Verde shearwater, brown booby and red-billed tropicbird continue to be the most recognized and bycaught species by fishermen in Cabo Verde (Melo and Monteiro 2016; Montrond 2020). Our values of seabird bycatch for the islands (30%) are obviously underestimated due to the number of unanswered questions; previous studies indicated 66% seabird bycatch around the EEZ (Montrond 2020). This was possibly due to the higher number of fishermen interviewed from semi-industrial fisheries (44 fishermen), including industrial foreign vessels (22 fishermen) that showed increased bycatch compared to the smaller vessels. Additionally, interviews were anonymous, which would put fishermen at ease while answering questions. According to our results, bycatch was mainly related to artisanal handlines, with the Cape Verde shearwater attaining the highest level of bycatch as observed previously (Montrond 2020). Indeed, seabird bycatch has been shown to occur mainly in fishing vessels using hooks (Anderson et al. 2011), and since handline is practically the only representative of this gear-type in our sample, this result was expected. In the Mediterranean sea, other congenerous species (*Calonectris diomedea*) have been associated with high bait loss of operating gears using hooks (e.g. longline) (Sánchez and Belda 2003). The Mediterranean Sea, however, is a more closed and coastal environment compared to the Cape Verde islands, and heavily impacted by fisheries, increasing the probability of seabirds associating with fisheries. Nevertheless, the oligotrophic nature of the tropical waters of Cabo Verde and the high density of shearwaters may explain interactions with handlines (Weimerskirch 2007; Semedo et al. 2020).

Although results showed no significant difference between both types of fisheries in terms of interactions, bycatch seems to occur more while using the handline fishing gear, in line with what was previously reported by (Montrond 2020). Perhaps the higher number of artisanal fishing boats operating in Cabo Verde offers more opportunities for seabirds to access fish-baits when compared with a smaller fleet of semi-industrial vessels operating in the area. Nevertheless, industrial fishing boats from foreign countries, not included in this study but also operating in the area, might pose a bigger threat as they are usually responsible for much higher numbers of seabirds bycaught, especially in longlines (Anderson et al. 2011), and including to the fact that shearwaters and sulids (boobies and gannets) bycatch have been recorded in 11 different types of gear (Pott and Wiedenfeld 2017).

According to fishermen, the timing to which most bycatch events occurred was during hook settlement, a behaviour consistent with what is observed around the world (Brothers 1991; Huin and Croxall 1996; Sánchez and Belda 2003; Brothers et al. 2010; Wiedenfeld 2016; Hamm 2021), possibly explained by the type of bait that fishing vessels use, which consists of small pelagic fish targeted by seabirds naturally (e.g. mackerel) (Neves et al. 2006; Wiedenfeld 2016; Oliveira et al. 2020; Hamm 2021). However, hooked seabirds are often discovered during hauling, which by intuition, are deduced to be caught during hook setting and drowned afterwards (Brothers et al. 2010). When this happens, the number of bycaught birds can be underestimated as dead birds may be predated underwater and unaccounted for (Brothers 1991; Brothers et al. 2010).

The spotting of often alive seabirds when caught is probably true in our study because most Cape Verde boats are very small and handline gears are not very long (20-500m), allowing to keep track of seabirds when caught on lines. Although 40-50% of fishermen did not think this was a problem during interviews, off the record many spoke about the inconvenience that shearwaters incite during fishing, by stealing baited hooks, and sometimes handling them with aggression (Neves et al. 2006; Gianuca et al. 2020).

The release of birds either dead or alive is however arguable, as shearwater bycatch might be an opportunity for an additional monetary gain, given that some people still ask for shearwater meat.

Most fishermen agreed that handlines and longlines are the fishing gears that catches more seabirds accidentally around this area, a tendency that has been observed in other studies around Brazil, where some of our species occur naturally during the non-breeding period (Bugoni et al. 2008a; Gianuca et al. 2019). Hook size and shape has been suggested to play an important role in seabird bycatch. Larger hooks have a high probability of catching larger seabirds (Li et al. 2012), coincidently being the mostly caught species on gears (shearwaters, brown boobies and red-billed tropicbirds) (Montrond 2020). Larger seabird species usually have a larger bill size, which increases the ability to swallow hooks (Jiménez et al. 2012; Zhou et al. 2019; Heswall et al. 2021) when compared to smaller species. For Cape Verde shearwaters, brown boobies and red-billed tropicbirds, body size makes them the most vulnerable species to bycatch in Cabo Verde, as they are equally capable of being caught on smaller hooks, frequently used by artisanal boats, as well as larger hooks used on semi- and industrial boats (Montrond 2020). As procellariforms use their olfaction capabilities to detect odours at large scales leading them to their prey (e.g. dimethyl sulfide is produced by phytoplankton and detected by procellariforms), it might be possible that Cape Verde shearwaters use olfaction to find their prey near vessels and even be attracted to bait's odour (Nevitt 2008; Heswall et al. 2021).

The abundance of Cape Verde shearwaters is much higher than that of brown boobies and Red-billed Tropicbirds (Semedo et al. 2020), which increase their bycatch probabilities (Zhou et al. 2019). However, brown boobies and red-billed tropicbirds reproduce all year-round and forage mainly inside the EEZ (del Hoyo et al. 1992; Semedo et al. 2020; Almeida et al. 2021), increasing the probability of encounters with fishing boats, especially at coastal areas. Bycatch reports for sulids occur at south-eastern Brasil and other locations in a much higher frequency compared to Red-billed Tropicbirds (Pott and Wiedenfeld 2017; Gianuca et al. 2019). The breeding period of Cape Verde shearwaters (May-October) is also the same as the tuna fisheries operate, which is related to the upwelling seasonality off West Africa (Foreign Fishery Developments 1981; Paiva et al. 2015). Other seabirds breeding around this area, are either small and/or nocturnal, feeding on small crustaceans (e.g. krill), fishes (e.g. myctophids) and squids brought to the surface during the night through diel vertical migration, most likely decreasing interaction probabilities with the Capeverdean domestic fishing fleet (*Bulweria bulwerii, Hydrobates jabejabe; Pterodroma feae; Puffinus lherminiery boydi; Pelagodroma marina eadesorum*) (Neves et al. 2011, 2012; Underwood 2012; Ramos et al. 2015, 2016).

The fishermen's perception that incidental and intentional catches have decreased must be due to increasing laws and regulations defended by local NGO´s and enforced by national authorities in recent years, as well as awareness raising campaigns in fishing communities, which has decreased poaching activities in certain locations or made fishermen more cautious. Despite this, the inexistence of legal frames to enforce the laws of protection of seabirds and other species is a clear gap in legislation living room for illegal practices to occur. It is also common knowledge between Capeverdean artisanal fishermen that any increases in catches (e.g., sharks) are due to foreign vessels (José Melo *pers. com.*). In the West African region, as well as other parts of the world, foreign vessels are known to compete with small-scale fisheries, perhaps not always on the same spatial scale but for the same resources. With the new Fishing Agreement between Cabo Verde and the European Union (2019), foreign vessels are allowed to fish 8000 tons of tuna and similar species in in the waters of Cabo Verde for 750,000 euros annually, a weak financial compensation compared to the price paid by national consumers (6 euros/kg). There are also no real catch limitations, as penalties for exceeding the 8000 tons threshold is the same as the one already paid, and additionally, it does not account for mitigation measures for bycatch (Tommy Melo *pers. com.*).

2.4.3. Environmental predictors explaining changes in fish landings and chick growth measures of Cape Verde shearwaters

The importance of the month on tuna landings was predictable because previous studies show that tuna occur in tropical marine areas from summer to autumn (Foreign Fishery Developments 1981). Moreover, as tuna rely on small fishes for their diet, tuna abundance may be influenced by the planktonic food web, and therefore viewed as a proxy of prey availability for pelagic predators. In this case, the increase of zooplankton biomass would guarantee foraging opportunities for tuna and would ensure the availability of this commercial group for fishery catches. On the other hand, landings were negatively influenced by the increase of NPP. Although this variable was not significant, tuna landings occur mainly during the warmer period, when marine productivity is lower in the oligotrophic waters of Cabo Verde (Foreign Fishery Developments 1981), suggesting that landings should be lower when NPP is higher, coinciding with the months influenced by the upwelling off the African Coast (Kouadio et al. 2021), when tuna are less available.

For large pelagic fish, the depth of the euphotic zone and zooplankton biomass were the most significant environmental predictors. Increasing depth will mean that photosynthesis and phytoplankton production occur at deeper levels (van Ruth et al.

2020), working as a proxy of vertical marine productivity. This would affect the availability of zooplankton feeding on phytoplankton and increase the number of their predators (e.g., micronekton) (Brodeur et al. 2002; Engelhard et al. 2014) which in turn are included in the diet of large pelagic fish (Sabatié et al. 2003; Potier et al. 2007). The micronekton include small species and juvenile stages of cephalopods, small crustaceans, mesopelagic fish and pelagic nekton (Brodeur et al. 2002). They are important intermediates between mesozooplankton and top predators (Receveur et al. 2020) and are also prey to nektonic commercial species, undertaking vertical migrations to the sea surface at night, where they are consumed by epipelagic predators such as tuna, sharks and billfishes (Brodeur et al. 2002).

For small pelagic landings, both the depth of the euphotic zone and NPP (proxies of marine productivity) were the most significant variables, once again affecting this group through cascading effects, causing an increase in the prey availability (e.g., zooplankton) (Engelhard et al. 2014; Holland et al. 2021; Kouadio et al. 2021) and at the same time increasing fish stocks accessible to fisheries. As a proxy of epipelagic predators, the effect of micronekton on small pelagic landings was not expected, but since this variable was the least significant to the model there might be a geographical mismatch between the fished species and the areas where micronekton biomass peaked, within the archipelago. All these correlations appear to be related to the food web complex, with changes in prey and intermediate species resulting in bottom-up biomass shifts related to the base of the marine food-web and top-to-bottom changes if predators are affected (Anela Choy et al. 2016).

As facilitators of prey to seabirds (Au and Pitman 1986; Weimerskirch 2007) or as prey (Engelhard et al. 2014; Pikitch et al. 2014), higher landings of these species can be translated into high availability in the sea, becoming also available to seabirds such as the Cape Verde shearwater. As stated previously, NPP and EPI are respectively proxies of marine productivity and prey availability, influencing the general marine food-web and hence the availability of prey to seabirds. Finally, chick development seems to be correlated with changes in fish-landings of tuna and small pelagics. During the chick-rearing period, progenitors perform daily foraging trips around the islands, returning at night to feed the chick (Paiva et al. 2015). The availability of facilitators and prey in this area (particularly inside the EEZ) is important to increase foraging opportunities to Cape Verde shearwater breeders, delivering high energy content meals to developing chicks (e.g., fish) (Clarke and Prince 1980). The asymptotic mass and linear growth rate of chicks appear to be affected by these external variables of marine productivity and prey availability, with the potential to cause development and fledging delay.

Overall, our bycatch results were underestimated due to a lack of confidence on fishermen responses related to the apprehension with the new regulations for species poaching, a result that was previously observed by (Montrond 2020). Therefore, studies with onboard observers would be imperative to assess the right estimation of bycatch, as it is expected to be of significant amount, considering simple off-record talks with fishermen and contradictory answers to different questions of the quests. Additionally, we suggest the adoption of mitigation measures for bycatch in artisanal and semi-industrial vessels, and the consideration and implementation of fishing closures in the main foraging areas of Cape Verde shearwater, brown booby and red-billed tropicbird inside the Cabo Verde EEZ, especially during the chick-rearing period of the Cape Verde shearwater, as successful results of these measures have been reported elsewhere (Goad et al. 2019; Swimmer et al. 2020; Gilman et al. 2021; Sydeman et al. 2021b). Fishing closures could also benefit the marine ecosystem as landings seem to be affected by shifts in the marine food-web complex. Fishing down food-webs, has been reported all over the world, caused by unsustainable fishing, declining the mean trophic level of fish targets (Pauly et al. 1998). There are also some recent solutions to mitigate bycatch of seabirds and other taxa in longline fisheries, with relevance for the effectiveness of mini-hookpods (Sullivan et al. 2018; Goad et al. 2019) and tori lines (Jiménez et al. 2020a; Gilman et al. 2021) in driving bycatch numbers to almost zero.

Chapter 3

SEABIRD-FISHERIES INTERACTIONS WITHIN THE CABO VERDE ECONOMIC EXCLUSIVE ZONE (EEZ)

Abstract

Fishing vessels and marine top-predators such as seabirds are known to target the same prey or simply fishing and foraging alongside one another. Thus, as food resources are patchily distributed in the oceans, particularly in tropical regions, fishing vessels and marine megafauna overlap in areas of high fish abundance. With the development of tracking methods and vessel monitoring tools (Vessel Monitoring Systems and Automatic Identification Systems) in the last decade, we have access to a vast array of information concerning seabird ecology inside and outside their breeding season as well as crucial information on areas of high fishing pressure. In the West African region both artisanal and industrial fisheries overlap greatly in coastal areas, and target tuna species and small pelagic fish, vastly consumed by local populations or and seabirds. In this study, we investigated the spatio-temporal overlap between the distribution of seabird species more exposed to fishing vessel interaction and the activity of industrial, semi-industrial and artisanal fisheries within the Cabo Verde EEZ, between 2017-2019. Results showed that Cape Verde shearwaters exhibited higher overlap with artisanal vessels inside Cabo Verde EEZ, compared to other species, while brown boobies overlapped more with longline fisheries. As Cape Verde shearwaters have a more pelagic distribution, travelling to and from the West African coast, we believe that low overlap is due to industrial vessels turning off their AIS signal when increasing their fishing effort, while brown boobies foraging areas are related to high vessel fishing activities near important fishing ports. Cape Verde shearwaters were also identified to change their behaviours near vessels, suggesting attraction, possibly related to bait-type, searching for easier meals to overcome the patchy constraints of an oligotrophic tropical marine area during the breeding period. Also, brown boobies, known for targeting vessels for discards, were attracted to vessels given its generalist feeding behaviour, foraging on different fish species, many of which are commercially targeted. Red-billed tropicbirds low attraction to fisheries was also expected possibly dependent on oceanographic features related to prey availability as well as red-footed boobies, who's less energetic constraints compared to breeders, and young age allows them to explore more and not being influenced by vessel presence. With these results, we believe that mitigation measures should be applied to fishing vessels in this area to decrease the risk of bycatch, considering, high seabird attraction during the breeding season, particularly for Cape Verde shearwater. And we believe that more attention should be given to the industrial sector to avoid Illegal Unregulated and Unreported (IUU) fisheries and potentially higher bycatch camouflaged by disconnected AIS devices at these vessels.

Keywords: Cape Verde shearwater; brown booby; red-billed tropicbird; red-footed booby; Fishing vessels; Cabo Verde EEZ; overlap; vessel attraction

3.1. Introduction

Humans have long shared space with other animals throughout millions of years of existence on this planet. Whether inland, inshore, or offshore, spatial, and temporal overlap with anthropogenic activities causes direct and indirect impacts on the surrounding biodiversity (Montevecchi 2001; Lewison et al. 2004; Pauly et al. 2005; Smith et al. 2011; Reeves et al. 2013; Arias-Del-Razo et al. 2020). However, sharing space is not always an indication of interaction, as species may overlap due to similar habitat and/or prey preference as well as resource richness and availability (Torres et al. 2013). Especially at sea, we humans often look for the presence of other marine predators in search of fish prey patches (Montevecchi 2001) and in such cases, fishing vessels and top-predators may target the same prey or simply target different marine taxa related to the present food web, fishing and foraging alongside one another. Thus, as food resources are patchily distributed in the oceans, particularly in tropical regions (Weimerskirch 2007), fishing vessels and marine megafauna overlap in areas of high fish abundance. This type of overlap may occur at large temporal and spatial scales without the occurrence of interactions whatsoever, which usually takes place at much finer scales (Torres et al. 2013). In the case of seabirds, they may fly over or forage in the same area where a vessel is fishing during a certain time, overlapping spatially and temporally, but they are not necessarily interacting with the vessel. Recent studies have defined vessel encounter to occur at a maximum of 30 km (Soriano-Redondo et al. 2016; Fox et al. 2021), based on the distance to which birds can be recruited visually to foraging flocks (Haney et al. 1992), while vessel associations occur at 3 km or less (Collet et al. 2015; Orben et al. 2021). By clearly differentiating overlap and interaction behaviours, we may be able to clearly establish management plans that can prevent or mitigate bycatch events.

Yet, none of this could have been possible without the development of methods to track the movements of marine predators. In the last decade, the development and miniaturization of tracking devices have increased rapidly, and today we have access to a vast array of information concerning species ecology inside and outside their breeding season. Nevertheless, to identify interactions, vessel tracking is also needed and luckily the development of technologies, such as the Vessel Monitoring System (VMS) and Automated Identification System (AIS), has helped to provide such crucial information. Although improvement is still needed in some fields, this data is available to all at any time (globalfishingwatch.org), with various information such as type of fishing vessel, type of gear used and so on (Torres et al. 2013; Robards et al. 2016; Kroodsma et al. 2018; Watson et al. 2018; Weimerskirch et al. 2018; Rowlands et al. 2019).

When talking about interactions, it is also important to understand that different species behave differently from one another, present specific behaviours that make them more vulnerable to bycatch (Zhou et al. 2019), the same way different fisheries attract different species and cause different impacts (Furness 2003). As such, industrial and artisanal vessels have different implications for associated species.

Industrial fisheries globally extract large amounts of fish biomass from the oceans, targeting mainly large predatory fish (e.g. tuna), pelagic fish (herrings, sardines, anchovies, etc) and krill, with the largest tuna catches in the world at the Pacific Ocean being over 25 million tons annually, while pelagic fish and krill landings in the last 25 years have ranged around 22 million tonnes per year (Williams and Terawasi 2009; Smith et al. 2011). Palomares and Pauly (2019) reconstructed marine catches in a period of 64 years until 2014 and showed a rapid and higher increase in catches for industrial fisheries. Less changes for artisanal fisheries were due to their insufficient fishing power incapable of overexploiting fish stocks, as well as their flexible behaviour allowing them to change targets and exploit other species if stocks decline. These two types of fisheries operate in different spatial scales, with small-scale vessels (artisanal, subsistence and recreational) fishing within 50 km from the coast or at 200m depth (Chuenpagdee et al. 2006), while large-scale vessels should fish outside this boundary. This, however, is not always the case, as many large-scale vessels compete with smaller vessels for space (illegally or not), causing friction between both sectors, and negatively impacting the latter (Leroy et al. 2016). There are other major differences, as industrial fisheries generate enormous amounts of discarded fish and other marine biota, consume as much as 20 tons of fuel compared to 5 tons for smaller vessels, employs 10 million less people and receives almost 3 times more government subsidies compared to small-scale fisheries (Palomares and Pauly 2019).

In the West African region, while gross catches from industrial fisheries are mainly intended for exports through private companies, artisanal fishery catches are often more modest and intended for local markets and communities or for subsistence purposes (MegaPesca 2010; Teh and Sumaila 2013; Belhabib et al. 2015; Fortes 2019), as it happens on other parts of the world (Dalzell et al. 1996). As such, the economic outcome of these vessels is very low, and with the added costs of fuel, they do not have the technology advantage that larger vessels own. However, in west Africa, fishing effort and size may vary greatly among countries. As expected, industrial vessels are normally larger and have a much higher fishing capacity compared to smaller artisanal vessels, yet there was an increase in fishing effort and size of artisanal vessels in countries such as Senegal, Guinea-Bissau, Gambia and Ghana in the years 2000's, sometimes surpassing domestic industrial vessels of surrounding countries from the 1950's (Belhabib et al. 2018). Other increase in vessel size and capacity produced vessels known now as semi-industrial, operating in this region, as part of the small-scale fishery fleet (Belhabib et al. 2018). Thus, it should be unwise to believe that small-scale fisheries do not have the power to affect marine fish stocks if left unregulated and unrecorded (Belhabib et al. 2018).

In tropical areas, such as the West African region, where prey patches are unpredictable, and marine productivity occurs very close to the coast (e.g. Canary Current Large Marine ecosystem) (Arístegui et al. 2009; Grecian et al. 2016), both artisanal and industrial fisheries overlap greatly in coastal areas, and target tuna species (*Katsuomys pelamis*, *Thunnus albacares*, *Thunnus obesus*) and small pelagic fish (e.g. sardinellas, jacks and horse mackerels), vastly consumed by local populations or intended for aquaculture fish-meals (Belhabib et al. 2014, 2016, 2018). Seabirds may also feed on small commercially targeted pelagic fish (Rodrigues 2014), or follow tuna which drive their pelagic prey to the sea surface, and thus frequently overlap with fishing vessels along this area and possibly interact with them. Longline fisheries were identified as posing the highest risk of bycatch for seabirds globally (Anderson et al 2011) and are operated by industrial and semi-industrial vessels in this region, alongside with handlines of the artisanal sector, which also attract seabirds possibly due to the use of fish and squid baits found on their diet (mackerels, sardines, anchovies, squid) (Oliveira et al. 2020).

Moreover, concerning spatial scales, species that forage closer to the coasts and their breeding grounds (e.g., boobies and tropicbirds), or during the chick-rearing period may interact more with artisanal vessels due to constraints of feeding the chick, performing mainly shorter trips closer to the colony (Paiva et al. 2009). While pelagic and long-distance travelling species (e.g., shearwaters and petrels), as well as incubating birds, known to perform longer trips during this period (Paiva et al. 2009), should interact more with industrial vessels using pelagic waters. In Cabo Verde however, domestic fisheries operate at smaller scales compared to the 50 Km area normally accessible to small scale-fisheries on other countries (Chuenpagdee et al. 2006; Palomares and Pauly 2019).

Domestic Capeverdean vessels operate within 12 nautical miles [n.m. hereafter] (22.2 km) comprising the Capeverdean territorial sea (decree law no 126/77 of December), with possible seabird-vessel interactions occurring very close to the coasts around the islands for coastal species, and during the chick-rearing phases for pelagic species. Chick provisioning parents need to forage for prey in the colony surroundings where they are likely to encounter and interact with artisanal and semi-industrial fisheries, which necessarily operate at a close distance from shore, especially artisanal fisheries. Outside this threshold, pelagic and incubating seabirds should interact more with foreign vessels fishing with tuna pole and line, and with purse-seiners and longliners operating from 18 n.m. (33.3 km) (Montrond 2020).

In this study, we investigated the spatio-temporal overlap between the distribution of seabird species more exposed to fishing vessel interaction and the activity of industrial, semi-industrial and artisanal fisheries within the Cabo Verde EEZ, between 2017-2019. Given the fact that Cape Verde shearwater (*Calonectris edwardsii*) is the species suffering higher bycatch rates within the Cabo Verde archipelago, followed by brown and red-footed boobies (*Sula leucogaster* and *Sula sula*) and red-billed tropicbirds (*Phaethon aethereus*) (Montrond 2020; Chapter 2), we expect shearwaters to exhibit a comparably higher spatial overlap with fisheries, especially with artisanal and industrial longliners, when compared to boobies and tropicbirds. Moreover, spatio-temporal interactions should be more prevalent during the chick-rearing period of all breeding seabird species and exhibit a comparably lower overlap with the foraging distribution of non-breeding red-footed boobies.

3.2. Methods

3.2.1. Seabird Tracking data collection

Previous studies identified Cape Verde shearwaters, brown and red-footed boobies and red-billed tropicbirds as the most bycaught species in Capeverdean fishing vessels (Montrond 2020); Chapter 1); therefore we used GPS tracking devices CatTraq Travel Loggers (Perthold Engineering LLC) to track individuals during incubation (June-July) and chick-rearing (August – September) for Cape Verde shearwaters, and during chick-rearing (breeding throughout the year) for boobies and tropicbirds between 2018-2019. These datasets collected on colonies from Raso Islet were complemented by data collected from other populations of the same species present in other islets and islands of Cabo Verde (Table 3.1). Each device tracking configuration was set in accordance with the species characteristics to collect positions between 5 to 10 minutes. Species were caught during the night and devices were attached to the four central tail feathers, using Tesa® tape, and retrieved 5-15 days after deployment. Each GPS weighted 15-19 grams, and respecting the 3% body weight threshold recommended not to cause negative effects on the bird's foraging behaviour (Phillips et al. 2003). Prior to further analysis, all seabird tracking data was resampled to 10-min intervals, to match the tracking data of Cape Verde shearwaters, using the *track_resample* function of the *amt* package (Figure 3.1) (Signer et al. 2019).

Table 3.1. Sample size of tracked individuals and foraging trips and maximum distance to colony (mean ± SD) by Cape Verde shearwater (*Calonectris edwardsii*), red-billed tropicbirds (*Phaethon aethereus*), and Brown (*Sula leucogaster*) and red-footed boobies (*Sula sula*) from different Cabo Verde colonies, during incubation and chick-rearing between 2017 – 2019. * All tracked red-footed boobies were non-breeders.

Species	Island	Colony	Year	Incubation (N birds) [N trips]	Chick-rearing (N birds) [N trips]
Cape Verde shearwater	São Nicolau	Raso	2017	382.4 ± 275.8 (16) [40]	229.1 ± 174.1 (27) [203]
			2018	589.4 ± 336.8 (20) [30]	236.4 ± 174.0 (35) [189]
			2019	606.1 ± 376.2 (10) [29]	210.8 ± 165.6 (29) [160]
	Boavista	Curral Velho	2017	387.7 ± 270.9 (35) [37]	—
			2018	562.0 ± 231.3 (32) [35]	232.6 ± 170.0 (23) [43]
			2019	565.2 ± 263.2 (56) [63]	391.5 ± 191.4 (27) [58]
Red-billed tropicbird	São Nicolau	Raso	2017	107.5 ± 78.3 (5) [27]	—
			2018	312.5 ± 176.0 (15) [36]	257.3 ± 154.6 (20) [45]
			2019	242.2 ± 189.8 (2) [8]	101.6 ± 68.0 (11) [39]
	Sal	Cadjitinha & Furna	2018	224.3 ± 133.0 (15) [38]	116.4 ± 93.6 (15) [39]
			2019	—	67.5 ± 36.8 (39) [47]
		Monte Leão	2018	171.5 ± 106.0 (3) [8]	75.6 ± 22.5 (4) [17]
			2019	128.2 ± 87.5 (3) [12]	46.3 ± 24.0 (5) [18]
		Serra Negra	2017	118.7 ± 82.3 (10) [20]	86.3 ± 46.0 (11) [27]
			2018	134.5 ± 109.9 (6) [26]	66.9 ± 51.7 (5) [27]
			2019	146.4 ± 105.8 (3) [10]	47.4 ± 28.3 (5) [12]
	Boavista	Ponta Rincon & Ponte sol	2017	125.2 ± 73.9 (24) [49]	137.3 ± 69.7 (14) [36]
			2018	193.0 ± 72.3 (53) [88]	144.1 ± 115.7 (41) [79]
			2019	156.3 ± 128.2 (10) [32]	111.4 ± 76.0 (10) [38]
		Ponte Roque	2017	216.9 ± 126.9 (7) [23]	—
			2019	94.2 ± 31.1 (2) [16]	—
	Brava	Ilhéu Cima	2019	193.7 ± 106.3 (12) [32]	61.6 ± 36.9 (10) [31]
Brown booby	São Nicolau	Raso	2018	—	29.1 ± 15.1 (38) [370]
			2019	—	28.6 ± 17.6 (54) [412]
	Boavista	Curral Velho	2017	—	24.0 ± 15.3 (9) [58]
	São Nicolau	Raso	2018	—	60.5 ± 31.7

Red-footed booby *					(11) [78]
			2019	—	73.0 ± 35.5 (26) [56]

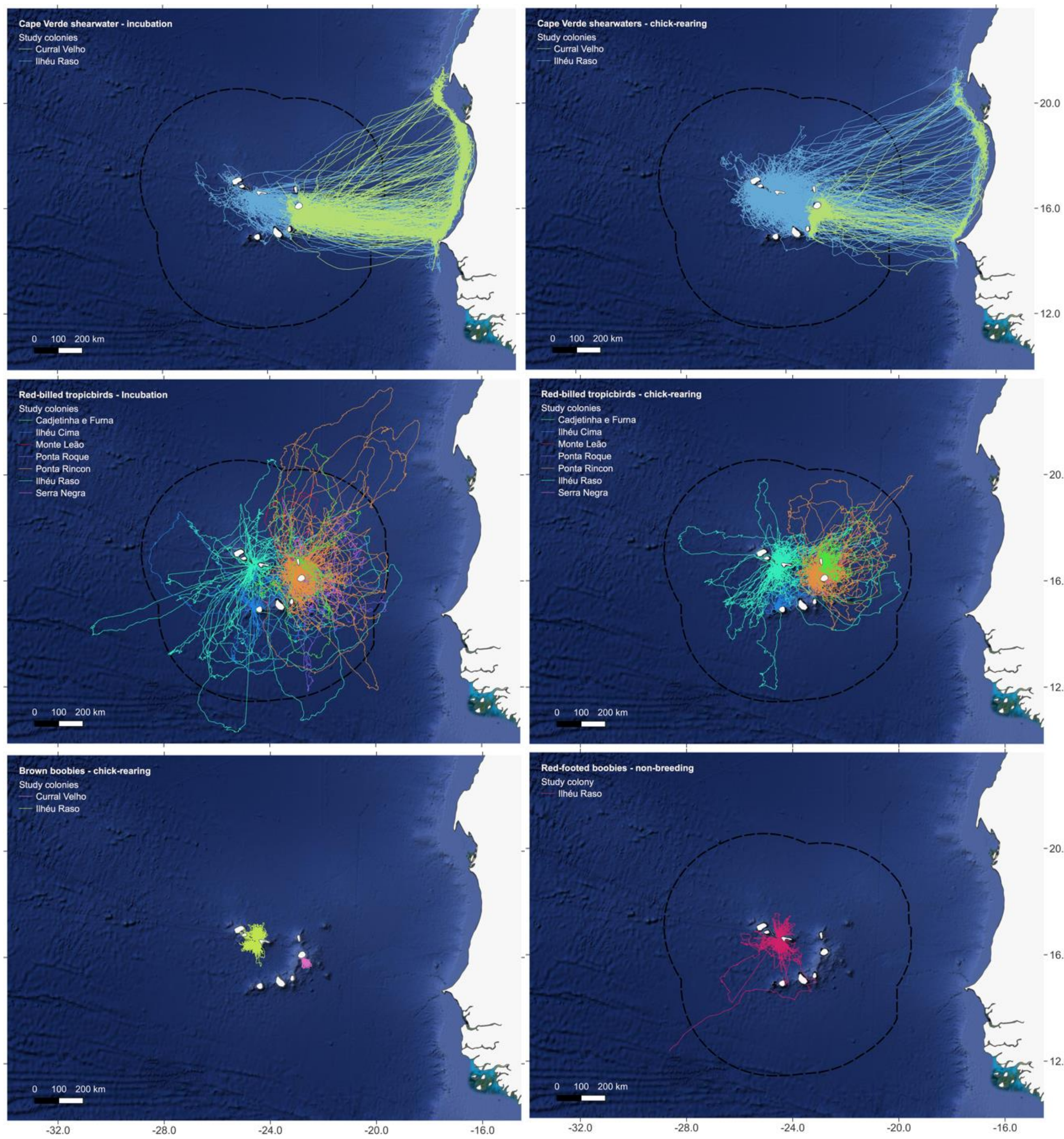


Figure 3.1. At-sea distribution of (1) Cape Verde shearwaters, (2) red-billed tropicbird, (3) brown and (4) red-footed boobies from different study colonies and during different phases of their annual life cycle, tracked between 2017-2019. Dashed black contour represents the Cabo Verde Economic Exclusive Zone (EEZ).

3.2.2. Tracking of artisanal (< 7m length) and semi-industrial (> 8m) fisheries

To locate and map fishing areas of artisanal vessels, we distributed similar GPS devices used to track seabirds, on fishing boats from different islands, to store location information on boat movements every 2 minutes. We also distributed a different version of these loggers, placed in tubular waterproof cases with 3 batteries, capable of collecting 3 months' worth of data with the same data configuration, to artisanal and semi-industrial vessels. Additionally, solar-powered transmitters were placed on semi-industrial fishery vessels from different islands, which came to the Fishing Complex of São Vicente to unload fish. Our final dataset consists of fishing tracks from 7 islands (5 from the "Barlavento" group and 3 from "Sotavento") and 15 fishing ports and communities. Both artisanal and semi-industrial fisheries used the methods 'handline' and 'pole fishing' (see chapter 1) (Figure 3.2).

3.2.3. Distribution of industrial fisheries

We collected data from the Global Fishing Watch database (https://globalfishingwatch.org), which uses the Automatic Identification System (AIS) to identify fishing activities, to have further information on the foreign vessel fleet fishing inside the Cabo Verde EEZ. According to (Kroodsma et al. 2018) this database contains a significant percentage of active vessels larger than 24 and 36 m, which is why it has been widely used in studies aiming to quantify fishing effort (Afán et al. 2018; Giménez et al. 2021; Pereira et al. 2021).

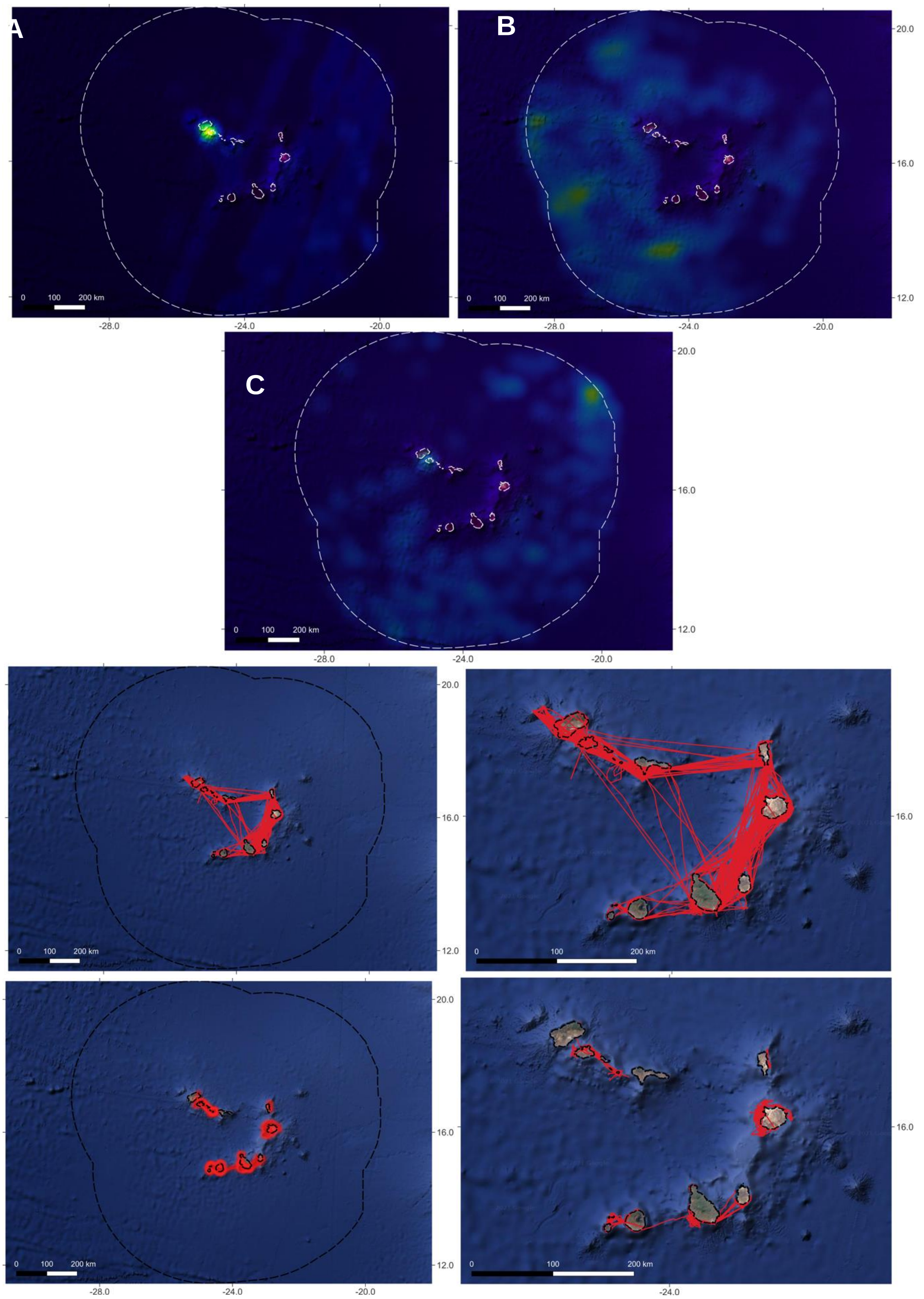


Figure 3.2. Average composites of the distribution of industrial (A) trawlers, (B) longliners and (C) purse-seiners, (D) semi-industrial vessels and (E) artisanal fishery boats between 2017-2019 within the Cabo Verde EEZ (dashed white/ black contour). In A-C fishing effort varies between 0.1 (blue) and 14.6 (yellow) fishing hours.

Thus, we extracted daily fishing effort data (fishing hours) from the GFW at 0.1° resolution, of the fishing activities of (1) trawlers, (2) longliners and (3) purse seiners.

3.2.4. Seabird-fisheries spatial overlap

The *kerneloverlap* function with Bhattacharyya's affinity (BA) method of the *adehabitatHR* package (Calenge 2006) was used to compute the overlap between the seabirds' foraging distribution and the fishing efforts of industrial, semi-industrial and artisanal fisheries. The BA Kernel Utilization Distribution (UD) overlap index ranges from 0 (no overlap) to 1 (identical UDs) (Kochanny and Fieberg 2005b). To test if birds' foraging distributions overlapped more than by chance with fisheries' distributions, correlated random walks within the individual home ranges were simulated using the *simm.crw* function from the *adehabitatLT* R package (Calenge, 2006). To generate each random track, we split the real track into two parts: one from the colony to the most distant location and one back to the colony. We generated 50 simulations per real track [after (Hindell et al. 2020), (Reynolds et al. 2021)] which were then combined to estimate the simulated kernel UDs. We then extracted the 50% and 95% kernel UDs for those random tracks (simulated UDs) and measured the overlap with the distributions of industrial (1) trawlers, (2) longliners (3) purse seiners and (4) semi-industrial (mostly handline and pole fishing) and (5) artisanal fisheries (mostly handline fishing).

3.2.5. Spatio-temporal seabird-fisheries interactions

For the periods where both seabirds and artisanal, semi-industrial and industrial fisheries were contemporaneously tracked, i.e., between January 2018 and November

2019 (see Table 3.2), we investigated the influence of fisheries on the foraging decisions of seabirds.

To obtain gridded maps of fishing effort for semi-industrial and artisanal fisheries, we computed the time spent per unit area by each tracked boat in each fishing event. We used the *tripGrid* function from the *trip* package which resamples each individual trip at a higher temporal resolution by linear interpolation (every 60 s) to approximate the time spent in each 0.1°-size cell. Then, we estimated the percentage of time spent in each cell relative to the total duration of the fishing trip and obtained a proxy of fishing effort (in hours), similar to that provided by the GFW for industrial fisheries.

Table 3.2. Number of artisanal (< 7m length) and semi-industrial (> 8 and < 12m) fishing vessels tracked with GPS-loggers in 8 of the main fishing ports of the Cabo Verde archipelago. Artisanal fishing boats from S. Vicente mostly operate within the Desertas Islands Natural Reserve, which includes the Raso Islet area.

Main Island	Tracking period	N vessels [N trips]	Max. dist. from harbour (km)
Artisanal			
São Vicente	Jul. 2018 – Nov. 2019	61 [90]	6.04 ± 2.47
Santo Antão	Jul. 2018 – Nov. 2019	4 [21]	8.03 ± 1.98
Sal	Oct. 2019 – Nov. 2019	3 [22]	13.66 ± 0.07
Fogo	Nov. 2018 – Jul. 2019	29 [69]	12.75 ± 9.19
Brava	Feb. 2019 – Oct. 2019	20 [57]	15.19 ± 7.66
Semi-industrial			
São Vicente	May 2019 – Nov. 2019	12 [35]	91.23 ± 87.22
Boavista	Jan. 2018 – Sep. 2019	16 [41]	56.51 ± 57.76
Santiago	Dec. 2018 – Aug. 2019	53 [75]	84.84 ± 86.77

For the seabird tracking information, three random steps were generated for each geographical fix using the 'random_step' function of the *amt* R package (Signer et al. 2019). Daily fishing effort was then extracted at the end of the foraging seabirds' steps, observed steps included, in order to conduct a step selection analysis and evaluate which fishing activity was likely driving a given step of the animal. Seabird-fishery interactions were tested as the probability of individuals choosing a specific path (step) within three other possible paths (random steps) in relation to the fishing effort (h) of industrial (1) trawlers, (2) longliners, (3) purse seiners (4) semi-industrial and (5) artisanal fisheries. This means that if birds changed their foraging direction, it will likely be driven by contemporaneously operating fisheries, through increasing fishing effort on contiguous grid cells. To model the used steps as a function of the variables, binomial generalized linear mixed models (GLMM) were built separately for each seabird species and breeding phase using the *lme4* R package (Bates 2015). Bird ID was included as a random factor to control for pseudo-replication issues, since each individual was tracked in multiple trips. All analyses were performed within the R Environment (R Core Team 2021).

3.3. Results

3.3.1. Seabird-fisheries spatial overlap

Overall, Cape Verde shearwaters were the species showing a higher than expected overlap with fisheries within the Cabo Verde EEZ, both considering their core foraging distribution (50% kernel UD) and home range (95% kernel UD). The overlap was particularly higher with the distribution of artisanal fisheries, with 66% of observed overlap, and at a lower extent with semi-industrial and industrial longliners (Table 3). Red-billed tropicbirds exhibited comparably lower overlaps with semi-industrial and artisanal fisheries, reaching a maximum of 42% of observed overlap with artisanal fisheries. Brown boobies overlapped significantly more than expected by chance with industrial longliners and semi-industrial and artisanal fisheries. Red-footed boobies exhibited rather comparably smaller overlaps with industrial longliners and the distribution of artisanal boats (Table 3.3).

Table 3.3. Metrics of Bhattacharyya's affinity (BA) overlap between core foraging distribution (50% kernel Utilization Distribution, UD) and home range (95% kernel UD) of seabird species and fisheries within the Cabo Verde EEZ, for the overall tracking period of foraging seabirds and fishery activities (see Tables 1 and 2 and methods section for further details). *P* represents the proportion of randomized overlaps that were smaller than the observed overlap. Significant differences are shown in **bold**.

	50% UD			**95% UD**		
Comparison	**Observed overlap**	**Permuted overlap (mean±SD)**	***P***	**Observed overlap**	**Permuted overlap (mean±SD)**	***P***
Cape Verde shearwater *vs.*						
Industrial fisheries						
Trawlers	0.23	0.29 ±0.11	0.33	0.45	0.51 ± 0.23	0.24
Longliners	0.41	0.34 ± 0.18	**0.02**	0.49	0.39 ± 0.17	**0.01**
Purse seiners	0.18	0.20 ± 0.09	0.45	0.20	0.17 ± 0.19	0.50
Semi-industrial fisheries	0.48	0.23 ± 0.12	**0.02**	0.32	0.40 ± 0.14	**0.02**
Artisanal fisheries	0.61	0.32 ± 0.23	**0.01**	0.66	0.39 ± 0.19	**0.001**
Red-billed tropicbird *vs.*						
Industrial fisheries						
Trawlers	0.19	0.31 ± 0.24	0.34	0.24	0.19 ± 0.34	0.28
Longliners	0.29	0.33 ± 0.25	0.07	0.33	0.28 ± 0.10	0.06
Purse seiners	0.25	0.29 ± 0.12	0.08	0.29	0.25 ± 0.15	0.06
Semi-industrial fisheries	0.33	0.26 ± 0.09	0.06	0.36	0.24 ± 0.18	**0.04**
Artisanal fisheries	0.40	0.30 ± 0.14	**0.05**	0.42	0.37 ± 0.14	**0.03**
Brown booby *vs.*						
Industrial fisheries						
Trawlers	0.18	0.15 ± 0.06	0.52	0.20	0.16 ± 0.13	0.46
Longliners	0.48	0.40 ± 0.07	**0.04**	0.51	0.42 ± 0.16	**0.03**
Purse seiners	0.18	0.20 ± 0.13	0.23	0.22	0.20 ± 0.16	0.19
Semi-industrial fisheries	0.42	0.31 ± 0.15	**0.05**	0.47	0.40 ± 0.09	**0.04**
Artisanal fisheries	0.40	0.37 ± 0.09	0.07	0.48	0.43 ± 0.13	**0.04**
Red-footed booby *vs.*						
Industrial fisheries						
Trawlers	0.23	0.16 ± 0.08	0.37	0.25	0.18 ± 0.11	0.25
Longliners	0.45	0.37 ± 0.12	**0.05**	0.49	0.42 ± 0.14	**0.04**
Purse seiners	0.25	0.20 ± 0.12	0.33	0.28	0.25 ± 0.16	0.28
Semi-industrial fisheries	0.28	0.26 ± 0.09	0.12	0.30	0.29 ± 0.21	0.09
Artisanal fisheries	0.49	0.40 ± 0.13	**0.04**	0.51	0.43 ± 0.08	0.02

3.3.2. Spatio-temporal seabird-fisheries interactions

Cape Verde shearwater changed foraging direction to interact with fisheries when in proximity of artisanal boats, semi-industrial vessels and industrial longliners (Table 3.4). The individuals that shifted chose their foraging direction in response to increasing fishing effort by artisanal fisheries, and in a less pronounced effect, the increasing fishing effort of industrial longliners and semi-industrial vessels, especially during the chick-rearing period. Red-billed tropicbirds responded in their foraging direction to the increasing fishing effort of artisanal fisheries, particularly during the chick-provisioning phase, although this response was less marked when compared to that of Cape Verde shearwaters. Chick-rearing Brown boobies shifted their foraging distribution in response to the increase in fishing effort by artisanal, semi-industrial and industrial vessels. While non-breeding red-footed boobies just responded to the increase in fishing effort by artisanal fisheries (Table 3.4).

Table 3.4. Coefficients and statistics from the Generalized Linear Mixed Models (GLMMs) testing the effect of fishing effort (h) of industrial (1) trawlers, (2) longliners, (3) purse seiners and (4) semi-industrial and (5) artisanal fisheries on the probability for seabird-fisheries interactions by four seabird species during their breeding period (incubation and chick-rearing). Bird ID was included as a random factor to control for pseudorelication issues. Significant differences are shown in **bold**.

Cape Verde shearwater	***Incubation***		***Chick-rearing***	
Parameters	***β* ± SE**	***P***	***β* ± SE**	***P***
Intercept	1.63 ± 0.65	0.06	3.42 ± 1.90	0.01
Industrial trawlers	0.32 ± 0.22	0.34	0.67 ± 0.56	0.27
Industrial longliners	**2.23 ± 1.43**	**0.02**	**3.19 ± 1.22**	**0.01**
Industrial purse seiners	0.12 ± 0.09	0.43	1.07 ± 0.67	0.15
Semi-industrial	**2.43 ± 1.34**	**0.04**	**1.84 ± 0.72**	**0.05**
Artisanal	**4.12 ± 1.01**	**0.01**	**5.21 ± 2.10**	**0.001**
Red-billed tropicbird	***Incubation***		***Chick-rearing***	
Intercept	1.34 ± 0.32	0.03	2.01 ± 1.98	0.02
Industrial trawlers	0.72 ± 0.63	0.14	0.53 ± 0.23	0.16
Industrial longliners	0.96 ± 0.35	0.08	**1.46 ± 0.77**	**0.03**
Industrial purse seiners	0.09 ± 0.12	0.23	0.17 ± 0.19	0.20
Semi-industrial	0.85 ± 1.04	0.10	0.89 ± 0.75	0.09
Artisanal	**2.48 ± 1.08**	**0.02**	**3.06 ± 1.55**	**0.001**
Brown booby			***Chick-rearing***	
Intercept	—		3.04 ± 2.17	0.01
Industrial trawlers	—		1.03 ± 0.99	0.13
Industrial longliners	—		**1.89 ± 0.65**	**0.05**
Industrial purse seiners	—		0.96 ± 0.60	0.16
Semi-industrial	—		**2.04 ± 1.07**	**0.03**
Artisanal	—		**2.77 ± 1.43**	**0.02**
Red-footed booby	***Non-breeding***			
Intercept	2.75 ± 1.44	0.01	—	
Industrial trawlers	0.15 ± 0.22	0.25	—	
Industrial longliners	1.67 ± 0.99	0.14	—	
Industrial purse seiners	0.95 ± 0.76	0.53	—	
Semi-industrial	1.74 ± 0.98	0.07	—	
Artisanal	**2.01 ± 0.53**	**0.05**	—	

3.4. Discussion

3.4.1. Seabird-fisheries spatial overlap

Cape Verde shearwaters exhibited a comparably higher overlap with fisheries inside Cabo Verde EEZ, particularly with artisanal vessels. Although at a lower extent, other species also displayed high overlap with artisanal fisheries at their core foraging distribution and home ranges, except brown boobies that overlapped more with longline fisheries. Even though this tendency was observed in previous studies (Montrond 2020), it is still surprising, as Cape Verde shearwaters, red-billed tropicbirds and red-footed boobies have a more pelagic foraging distribution or travel further distances from the colony, compared to brown boobies (Figure 3.2) (Paiva et al. 2015; Cerveira et al. 2020; Almeida et al. 2021). Brown boobies forage practically only inside the Cabo Verde territorial sea (12 n.m.), an area used exclusively by the domestic fleet (Figure 3.1) (Montrond 2020; Almeida et al. 2021). Cape Verde shearwater is the recognized species by fishermen to present a higher association with artisanal vessels and higher risk of bycatch, associated with handlines [(Chapter 2) (Montrond 2020)]. Considering that most semi-industrial vessels tracked were probably purse-seiners (Chapter 2), shearwaters should be attracted mainly to vessels using handlines, in this case artisanal boats. Additionally, the fleet size of artisanal vessels (N=1588 boats) compared to semi-industrial (N=119 vessels) (INE 2020) and foreign industrial vessels (61-88) [Source: Directorate General of Marine Resources, 2018 in (Montrond 2020)] could also be another reason to explain the high overlap with shearwaters. The most plausible reason why industrial longlines were not found to attract Cabo Verde shearwaters should be related to the fact that these vessels choose to turn off their AIS signal when increasing their fishing effort (Weimerskirch et al. 2020), especially in this African region where Illegal Unregulated and Unreported (IUU) fisheries occur in high frequency (Agnew et al. 2009; Belhabib et al. 2014), and lack of monitorization compromises policy efficiency (Belhabib et al. 2019). Comparing the number of licences attributed to foreign vessels by the Cabo Verde government between 2014-2017 (8-14 tuna pole and line, 26-36 purse-seiners and 27-39 longliners) [Source: Directorate General of Marine Resources, 2018 in (Montrond 2020)], with the number of available vessels obtained through the Global Fishing Watch website for this study (1 trawler, 2 longliners and 3 purse seiners), it seems that our values should be greatly underestimated and that vessels are indeed turning off their satellite tracking devices during the tracking period of shearwaters (May-October) (Paiva et al. 2015), coinciding with high availability of tuna in these waters (Foreign Fishery Developments 1981).

On the other hand, the high overlap of brown boobies with longlines could be related to their foraging distribution. Brown boobies from Raso explore a specific area between Santo Antão and São Nicolau Islands, including the marine reserve of Desertas (Figure 3.2), which is an area with high traffic of domestic (Figure 3.2D and E) and foreign vessels (Figure 3.1A), particularly to and from the two important ports in São Vicente Island (Porto Grande harbour and Fishing Complex of Cova d'Inglesa) where semi-industrial and foreign vessels deliver fish for private companies of canned fish (e.g. Frescomar and Atunlo CV) (González et al. 2020). On the other hand, brown boobies from Boavista, also forage in an area with high vessel traffic (Figure 3.1D and E), associated with high habitat and ecosystem structural diversity, as this is the only existing continental platform, containing important nearby seamounts and fishing banks, with high biodiversity hotspots and high fishing pressure (Monteiro et al. 2008; Graham et al. 2017; Wenzel et al. 2020).

3.4.2. Spatio-temporal seabird-fisheries interactions

By shifting their behaviours in proximity to artisanal boats, shearwaters appear to be attracted by these vessels. As previously stated, Capeverdean semi-industrial vessels use mainly purse-seines to fish, not attracting many seabirds as handlines do or other fisheries that use hooks such as longlines (Anderson et al. 2011). This possible attraction could be related to the type of bait used on vessels offering an easy-meal opportunity for seabirds (Soriano-Redondo et al. 2016). Scad species (*Decapterus spp.*) and bigeye scad (*Selar crumenophthalmus*) are used as bait on artisanal vessels using handlines (Chapter 2) and were identified in the diet of Cape Verde shearwater (Rodrigues 2014) and reported by fishermen to cause the majority of seabird bycatch (Montrond 2020). As this behaviour occurred especially during chick-rearing, when Cape Verde shearwaters change their foraging strategies to remain closer to the colonies to feed the chick (Figure 3.2) (Paiva et al. 2015; Cerveira et al. 2020), we may suggest that they could rely on artisanal vessels during this period, searching for easier meals to overcome the patchy constraints of an oligotrophic tropical marine area (Longhrust and Pauly 1987; Weimerskirch 2007), contrasting with results from temperate regions, where high prey availability was suggested to cause low spatial overlap with fisheries for Cory´s shearwaters (Pereira et al. 2021). On the other hand, they could simply be attracted by the feeding frenzy occurring around vessels, drawn visually by conspecific flocks and other megafauna involved (Sánchez and Belda 2003). Also, similar species such as Cory’s shearwater (*Calonectris borealis*) and Scopoli´s shearwater (*Calonectris diomedea*) in the North Atlantic and Mediterranean sea were reported to be bycaught (Calado et al. 2020) possibly in association with bait-loss in longline hooks baited (Sánchez and Belda 2003; Soriano-Redondo et al. 2016) with shearwater's prey-species such as sardines *Sardina pilchardus* (Dias 2011). Additionally, bait may indirectly affect seabirds by attracting fish species which are then swallowed by seabirds after being caught on hooks (Oliveira et al. 2020).

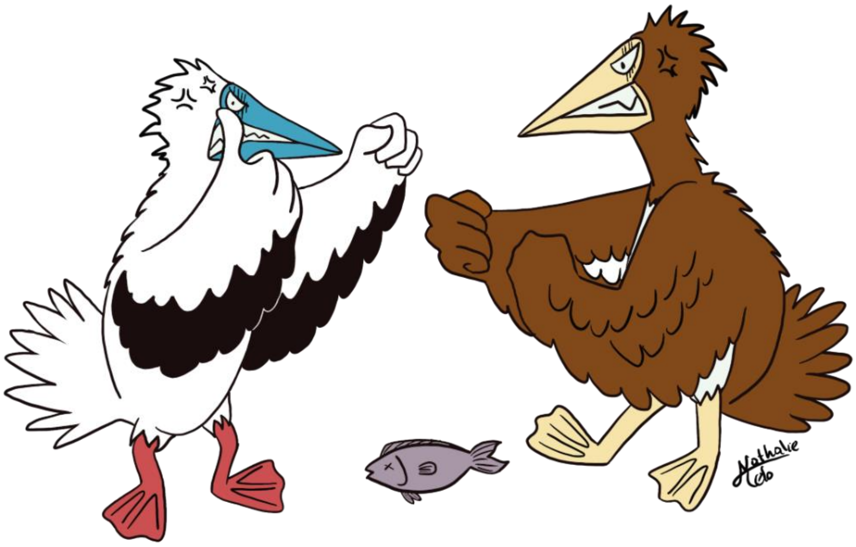
Brown boobies' response to all fisheries was also expected as their behaviour has been described as "fearless toward human activities" (López-Ortiz 2009) targeting floating hooked baits or feeding on fish discards (Tasker et al. 2000). Frequently recorded bycatch has been observed at the Brazilian coast (Gianuca et al. 2019), given its generalist feeding behaviour, foraging on different fish species, many of which are commercially targeted (e.g., Carangidae, Exocoetidae, Engraulidae) (López-Ortiz 2009).

The low attraction of red-billed tropicbirds to fisheries complies with other studies. At Madeleine Islet, Senegal, they forage at the shelf slope and beyond, not relying on available fishery discards from artisanal gillnet and demersal trawlers, but instead possibly following subsurface predators (Diop et al. 2018). The St. Helena's population of red-billed tropicbirds appear to be dependent on oceanographic features related to prey availability, as they travel northward conceivably constrained by the oligotrophic oceanic waters around the island and are attracted by areas where Scombridae species occur and are protected by fishing regulations at the local MPA, which decreases their bycatch risk.

Similarly to its congener masked booby (*Sula dactylatra*), the non-breeding red-footed booby is not known to follow vessels or feed on discards (Tasker et al. 2000), which should explain why their responses to fishing boats were very low. Additionally, the non-breeding status of these birds while in Cabo Verde might give them more freedom to explore marine areas, without looking for easy-meals available near vessels, and less energetic constraints compared to breeders, that must feed the chick and replenish their own food reserves (Weimerskirch 1998). Furthermore, most individuals were juveniles, still acquiring foraging skills in a tropical environment and exploring different environments while doing so (Mendez et al. 2017b).

Chapter 4

YEAR-ROUND AT-SEA DISTRIBUTION AND TROPHIC RESOURCES PARTITIONING BETWEEN TWO SYMPATRIC SULIDS IN THE TROPICAL ATLANTIC



Abstract

In the oligotrophic tropical marine environment resources are usually more patchily distributed and less abundant to top predators. Thus, spatial and trophic competition can emerge, especially between related seabird species belonging to the same ecological guild. Here we studied the foraging ecology of two sympatric species – brown booby (BRBO) *Sula leucogaster* (breeding) and red-footed boobies (RFBO) *Sula sula* (non-breeding)– at Raso islet (Cabo Verde), across different seasons. Sexual segregation was only observed during Jun-Oct, when RFBO were present, with larger females BRBO remaining closer to the colonies, while males and RFBO travelled further and exploited different habitats. Overall, species appeared to prefer areas with specific oceanic features, particularly those related with oceanic currents and responsible for enhancing primary productivity in tropical oceanic areas (e.g., Sea Surface Height and Ocean Mixed Layer Thickness). Female BRBOs showed high foraging-site fidelity during the period of sympatry, while exploiting the same prey species as the other birds. However, during the months of co-existence (Jun.-Oct.), isotopic mixing models suggested that female BRBO would consume a higher proportion of epipelagic fish, whereas female RFBO would consume more squid compared to the other birds, possibly due to habitat-specific prey availability and breeding energy-constraints for BRBO. We conclude that divergent parental roles, environmental conditions, habitat preference and competition could be mechanisms simultaneously underlying sexual segregation for BRBO during a period of co-existence, while inter-specific foraging differences appear to be more affected by habitat preference and different breeding stages. These results support previous statements that BRBO can adapt their foraging ecology to different circumstances of environmental conditions and competition, and that marine physical features play an important role in foraging decisions of boobies.

Keywords: Living in sympatry; brown booby; red-footed booby; chick-rearing; non-breeding: foraging; diet; sexual segregation

1.1. Introduction

Competition for food resources occurs naturally between organisms living in communities (Huffaker 1966), and between close-related species sharing the same geographic area (sympatry) for breeding and/or foraging (Hardin 1960; Gause 1973). Higher levels of competition may occur particularly when resources are scarce (Jaeger 1974; Pettex et al. 2019), which is the likely scenario in oligotrophic tropical seas (Longhrust and Pauly 1987; Weimerskirch 2007; Catry et al. 2009; Young et al. 2010a). As an evolutionary strategy to avoid high levels of competition, allowing species and populations to thrive and co-exist in the same environment, adaptations between and within species are expected to exist, displacing each other in such a manner that each takes possession of a certain niche, in which it has an advantage over its competitor (Hardin 1960; Gause 1973).

Intra-specific competition can exist in large seabird colonies, especially during breeding seasons when adult seabirds are constrained by central place foraging (James Grecian et al. 2018; Pettex et al. 2019), with breeders of some species segregating sexually. This type of segregation can usually be explained by three factors: (1) Anatomic differences between males and females (sexual dimorphism) (Surman and Wooller 2003; Weimerskirch et al. 2006b, 2009a; Miller et al. 2018), most frequently related to size of seabird species (Weimerskirch et al. 2006b, 2009a), influencing flight speed, foraging range and flapping frequency, as well as diving depth and duration induced by body mass (Weimerskirch et al. 2009b); (2) Divergent parental roles, influencing nest fidelity; and (3) nutritional requirements (Miller et al. 2018). Thus, some sulids exhibit Reversed Sexual Dimorphism (RSD), where the bigger females are the main chick provisioners and the smaller males invest more in nest attendance and defence (Gilardi 1992; Lewis et al. 2005; Weimerskirch et al. 2009a, b, 2010b; Miller et al. 2018). Here, size difference, when present, work as a limiting factor, by excluding the smaller gender from productive areas closer to the colony or competing for better resources. Although many RSD sulid species show sexual segregation, this is not always the case (Weimerskirch et al. 2009a; Castillo-Guerrero and Mellink 2011; Mendez et al. 2017a; Lerma et al. 2020a), perhaps due to harsher environmental conditions at their colony surroundings, resulting in fish stock depletion, or when broods are larger and demand a higher foraging effort (Castillo-Guerrero and Mellink 2011).

Boobies and gannets are suitable species to study intra- and inter-specific competition, because most of the colonies around the world are very numerous, reaching numbers as high as 750 000 individuals in some places (Carboneras 1992). Additionally, these species are often found breeding and/ or co-existing in mixed colonies with conspecifics (Lewis et al. 2005; Weimerskirch et al. 2009a; Young et al. 2010a, b; Kappes et al. 2011). Although this co-existence could lead to inter-specific competition, this may also be an opportunity for foraging information exchange (Thiebault et al. 2019; Courbin et al. 2020) to locate ephemeral prey patches in tropical areas, as happens with other conspecifics (Weimerskirch et al. 2010b; Wakefield et al. 2013). This could be a potential foraging strategy for individuals to contour their patchily distributed prey, because studies of penguins in different sized colonies, confirmed foraging overlap between individuals of smaller colonies, while individuals from larger colonies segregated in their foraging areas (Ainley et al. 2004), possibly after causing prey depletion (Birt et al. 1987). The proposed (Ashmole 1963) 'Halo hypothesis', suggested that tropical and other seabirds populations are regulated by food supply, creating prey-depleted "halos" near the colonies which affect breeding success. These same density-dependent effects that shape seabird colonies (Ashmole 1963), were observed in Cape gannets (*Morus capensis*) and Masked boobies (*Sula dactylatra*) from larger colonies which exhibited a higher foraging effort, translating into higher levels of competition when compared to individuals from smaller colonies (Grémillet et al. 2004; Oppel et al. 2015).

Some sulid species can exhibit high repeatability in foraging behaviour (Zavalaga et al. 2010; Wilkinson et al. 2020), especially adult breeders, in terms of spatial and trophic ecology (Wakefield et al. 2015; Votier et al. 2017), which is dependent on oceanic physical structures such as fronts, shelf edges, seamounts and other processes that are related to marine productivity (Xavier et al. 2004; Paiva et al. 2010a; Scales et al. 2014). However, most studies on marine tropical realms, have connected the occurrence of tropical seabirds, such as boobies, with the presence of sub-surface predators in a 'facilitated foraging behaviour' (Weimerskirch 2007), which could translate into low foraging site fidelity due to prey unpredictability (Hamer et al. 2001; Kappes et al. 2011).

At Raso Islet, Cabo Verde, RSD brown boobies (hereafter termed BRBO) *Sula leucogaster* breed and inhabit the islet year-round. Between June – October of each year, a recently established population of red-footed boobies (hereafter termed RFBO) *Sula sula* also inhabit the islet for moulting (Semedo et al. 2020). This sets the ideal scenario to investigate spatio-temporal foraging, trophic and dietary segregation within and between closely-related species, during different periods of the year, using GPS tracking and stable isotope analysis. Studies between sympatric boobies have long been performed around the world in tropical waters, with results being influenced by colony and species size (Lewis et al. 2005; Young et al. 2010b; Kappes et al. 2011), productivity and environmental conditions of surrounding waters (Kappes et al. 2011; Lerma et al. 2020a, b), fish stock distributions and reproductive behaviour (Ponton-Cevallos et al. 2017; Lerma et al. 2020a, b). Most of these studies, however, have worked with sympatric breeding boobies, because it is much harder to retrieve tracking devices from non-breeding species.

Overall, we expect to observe (1) inter-sexual behavioural and spatial segregation of bigger-sized female BRBO and RFBO performing shorter trips and foraging near the colony, while smaller males should forage at a greater distance, driven by RSD size-based competition; (2) inter-species behavioural and spatial segregation when co-occurring at Raso Islet, due to differences in size and breeding stage, with RFBO being more pelagic and with lower repeatability in foraging behaviour given the absence of breeding duties; (3) the foraging activity of RFBO to be triggered by gradients in environmental predictors (e.g. gradient in depth), which are known to depict oceanic frontal regimes likely occurring in pelagic areas that they might exploit in the absence of breeding duties, while BRBO should rely on local-scale changes of marine productivity patterns (e.g. Sea Surface Temperature), occurring in the colony surroundings, to frequently return to the colony for chick provisioning; (4) broader isotopic niches and a more diverse diet composition of RFBO when compared to BRBO individuals, which may be a reflection of a more generalist and pelagic diet.

Methods

1.1.1. Study site and logger deployment

Our study took place in Raso Islet (16°36’40.63” N, 24°35’15.81” W) (Fig. 4.1), located at ~16km from S. Nicolau Island, on the Cabo Verde archipelago. With 5.76 km^2 of area, it is the biggest islet of the archipelago, located among the northern islands of

"Barlavento" and belonging to the Integral Natural Reserve (Natural Reserves, Decree Law 3/II/03 of February 24) that also includes Santa Luzia Island and Branco Islet [44]. The islet holds two established colonies of BRBO, with ~289 breeding individuals, and one small population of RFBO, with ~133 non-breeding individuals occurring between June and October (Biosfera, unpublished data). The BRBO breeds throughout the year, but a peak in breeding numbers occurs in December-January.

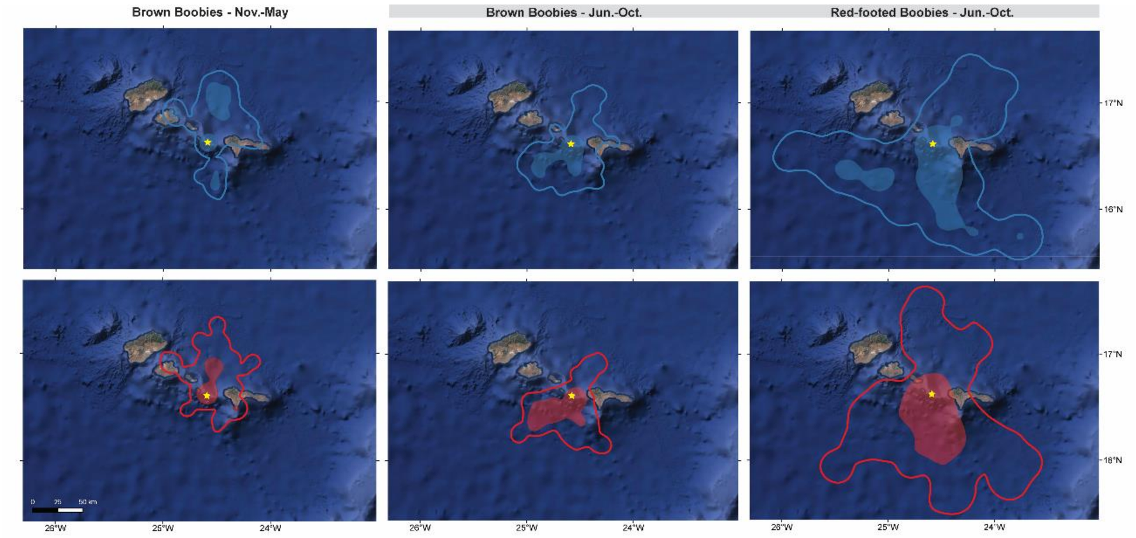


Figure 4.1. Kernel Utilization Distributions (UDs) of female (blue) and male (red) brown (BRBO) and red-footed (RFBO) boobies, tracked between November 2018 – October 2019 at Raso Islet (star), Cabo Verde. Bathymetric relief in the background (max. 4012m). Shaded area highlights the period when BRBO and RFBO co-occur in sympatry.

Both sulid species (BRBO and RFBO) were captured using a long pole and net, and CatLog2 devices (Perthold Engineering LLC) were attached to their four central tail feathers. Devices were secured using Tesa® tape, programmed to record locations every 5 minutes, and retrieved 5-7 days after deployment (see Table 4.1 for details on sampling numbers). Each GPS weighed 19 g, well below the 3% body weight (BRBO weight: 1246 ± 227 g; weight: RFBO weight: 1041 ± 178 g) threshold recommended to avoid causing

Table 4.1. Summary statistics (mean±SD, range in brackets) of trip characteristics, spatial distribution, trophic ecology and body condition of tracked brown (BRBO) and red-footed (RFBO) boobies from Raso Islet, Cabo Verde.

Species	Brown booby				Red-footed booby	
Season	Nov – May		June – October		June – October	
Sex	female	male	female	male	female	male
N tracks [N birds]	136 [22]	189 [29]	175 [17]	207 [48]	36 [11]	98 [26]
Mass (kg)	1.38 ± 0.12 (1.26 – 1.54)	1.19 ± 0.17 (1.00 – 1.42)	1.44 ± 0.20 (1.28 – 1.69)	1.18 ± 0.16 (1.09 – 1.49)	1.02 ± 0.11 (0.97 – 1.20)	0.95 ± 0.25 (0.85 – 1.03)
Trip duration (h)	4.08 ± 0.11 (3.87 – 4.34)	3.12 ± 0.34 (2.76 – 3.98)	4.11 ± 0.42 (3.52 – 4.60)	5.19 ± 0.21 (4.76 – 5.47)	4.99 ± 0.53 (4.02 – 6.16)	5.70 ± 0.23 (5.09 – 5.88)
Max. dist. colony (km)	24.7 ± 3.21 (20.42 – 33.11)	31.17 ± 3.32 (21.67 – 34.65)	22.83 ± 3.93 (21.55 – 32.09)	42.60 ± 3.20 (35.52 – 49.33)	63.14 ± 4.2 (56.87 – 69.11)	55.73 ± 5.14 (51.12 – 68.52)
Prop. Travelling (%)	0.30 ± 0.32 (0.13 – 0.49)	0.31 ± 0.20 (0.13 – 0.69)	0.29 ± 0.20 (0.07 – 0.65)	0.39 ± 0.13 (0.11 – 0.55)	0.38 ± 0.10 (0.13 – 0.59)	0.39 ± 0.35 (0.09 – 0.75)
Prop. Foraging (%)	0.24 ± 0.15 (0.08 – 0.65)	0.27 ± 0.11 (0.13 – 0.59)	0.26 ± 0.24 (0.08 – 0.69)	0.29 ± 0.62 (0.09 – 0.76)	0.31 ± 0.10 (0.11 – 0.45)	0.32 ± 0.33 (0.08 – 0.65)
Prop. Resting (%)	0.22 ± 0.25 (0.12 – 0.54)	0.23 ± 0.35 (0.11 – 0.74)	0.19 ± 0.40 (0.07 – 0.78)	0.17 ± 0.51 (0.10 – 0.85)	0.29 ± 0.19 (0.09 – 0.49)	0.31 ± 0.13 (0.09 – 0.45)
Distal latitude (º)	17.14 ± 1.06 (15.69 – 17.98)	17.27 ± 0.82 (15.55 – 17.86)	16.04 ± 1.01 (15.67 – 17.06)	16.47 ± 0.82 (15.45 – 17.70)	16.44 ± 1.14 (14.68 – 17.53)	16.49 ± 0.94 (14.72 – 17.76)
Distal longitude (º)	-24.49 ± 1.26 (-25.78 – -23.94)	-24.26 ± 1.01 (-25.15 – -24.08)	-24.60 ± 0.50 (-25.09 – -24.01)	-24.32 ± 0.69 (-20.22 – -25.69)	-24.20 ± 0.91 (-25.09 – -21.77)	-24.24 ± 1.76 (-26.10 – -22.87)
Distal bearing (º)	45.92 ± 2.98 (13.21 – 59.43)	56.60 ± 1.83 (49.43 – 58.04)	181.36 ± 1.72 (179.31 – 184.23)	146.23 ± 2.19 (141.65 – 149.23)	135.3 ± 2.87 (131.23 – 141.99)	137.46 ± 2.01 (132.01 – 139.62)
Plasma δ^{13}C (‰)	-17.51 ± 0.09 (-17.94 – -16.35)	-17.4 ± 0.12 (-18.19 – -16.10)	-16.59 ± 0.17 (-17.42 – -14.71)	-16.31 ± 0.10 (-17.52 – -14.63)	-16.25 ± 0.13 (-16.94 – -15.02)	-16.29 ± 0.13 (-17.66 – -13.70)
Plasma δ^{15}N (‰)	11.70 ± 0.10 (10.61 – 12.87)	11.5 ± 0.14 (10.50 – 12.53)	10.93 ± 0.08 (10.03 – 12.13)	11.03 ± 0.09 (10.23 – 11.97)	11.77 ± 0.11 (10.49 – 13.07)	11.37 ± 0.06 (10.04 – 12.44)
BodCondition Index (BCI)	0.23 ± 0.02 (0.17 – 0.28)	0.20 ± 0.01 (0.18 – 0.25)	0.20 ± 0.03 (0.17 – 0.27)	0.16 ± 0.04 (0.08 – 0.24)	0.12 ± 0.05 (0.04 – 0.26)	0.13 ± 0.02 (0.11 – 0.22)

negative effects on the bird foraging and feeding success (Phillips et al. 2003). GPS-loggers' deployment and retrieval were carried out after dark at the colony sites, and biometric data (wing-length, tarsus-width, body mass) were collected during logger deployment. At logger retrieval, data on body mass was collected once again to assess individual body condition, and blood (1ml) was drawn from the wing´s brachial vein and used for stable isotope analysis. Bird handling time did not exceed 10 minutes to avoid added stress to the animal. Body Condition Index (BCI) was obtained from the residuals of the linear regression of body weight on wing length – a measure of structural size (Brown 1996). BCI is, therefore, a measure of mass corrected for size and is considered an indicator of energetic reserves in seabirds (Chastel et al. 1995). Both species sex was identified using chest feather analysis with molecular markers, collected during field work (Weimerskirch et al. 2006b; Mendez et al. 2017a). Chick-rearing BRBO were tracked between September 2018 and August 2019, and non-breeding RFBO in September – October 2018 and June – August 2019, when this species inhabits Raso Islet (see further details on Table S4.1).

1.1.2. Characterization of at-sea behaviours

To define individual behavioural modes from movement trajectories of foraging trips we used the *Expectation Maximisation binary Clustering* (EMbC) R package (Garriga et al. 2016). This is a robust non-supervised multi-variate clustering algorithm leading to meaningful local labelling of each GPS location that can be easily linked to biological interpretations (Louzao et al. 2014). Two input variables (speed and turn angle) were used from successive individual locations to assign 4 behaviours by the *EMbC* algorithm: high velocity/low turning angle (HL), high velocity/high turning angle (HH), low velocity/low turning angle (LL) and low velocity/high turning angle (LH) (de Grissac et al. 2017). Following (Garriga et al. 2016), the behaviours were described as: (1) Resting, when locations showed low speed and low turn value (LL), indicating that the bird is resting at the sea surface; (2) Intensive foraging, representing Low speed while searching and High turn value (LH), when patches of prey are spotted; (3) Travelling, showing High speed and Low turn value (HL); and (4) Relocating, reflecting High turns at High speed (HH) as a change between restricted areas of intensive foraging. This technique has been previously used to interpret ecologically meaningful behaviours from movement data in sulids (Mendez et al. 2017b, a; Lerma et al. 2020b).

1.1.3. .Habitat use

GPS locations labelled as 'Intensive Foraging' were used to generate Kernel Utilization Distributions (Kernel UD) estimates, considering the 50% kernel UD contours as the core foraging region (FR) and the 95% kernel UD contours as the home range (HR), using the *adehabitat* package in R (Calenge, 2006). The most appropriate smoothing parameter (*h*) was chosen via least squares cross–validation for the unsmoothed GPS data, and then applied as standard for the other datasets. Grid size was set at 0.08° to match the grid of environmental predictors.

The extent of within-group foraging region (FR) and home-range (HR) overlap between (1) sexes of the same species and (2) between species when they co-occur (June-October) was estimated using the Bhattacharyya's affinity index (BA) kernel UD overlap index. This is considered the most appropriate measure of overlapping space use and BA index range from 0 (no overlap) to 1 (identical UDs) (Kochanny and Fieberg 2005a). We used a randomization technique (1000 randomizations of our dataset) to test the null hypothesis that there was no difference in the spatial distribution of different groups at test. If the null hypothesis is true, overlap between groups 50% and 95% kernel UDs should not differ significantly from that calculated if those groups were randomly assigned. *P*-values were determined by the proportion of random overlaps that were smaller than the observed overlap (see (Cleasby et al. 2015; Clay et al. 2016) for similar approaches).

1.1.4. Environmental predictors

To map the environmental conditions of the foraging areas and the surrounding colony, we used Seafloor depth as our static variable (DEP, blended ETOPO1 product, 0.01° spatial resolution, m), and the following dynamic oceanographic variables: Chlorophyll-a concentration (CHLA, 0.04°, mgm^{-3}), Sea Surface Temperature (SST, 0.04°, °C), Sea Surface Height (SSH, 0.08°, m), and Ocean Mixed Layer Thickness (OMLT, 0.08°, m). DEP was downloaded from http://ngdc.noaa.gov/mgg/global/global.html, SST and CHLA were extracted from http://oceancolor.gsfc.nasa.gov, while SSH and OMLT were downloaded from http://marine.copernicus.eu. Monthly averages composites were used for all dynamic predictors. Spatial gradients of all former variables (GDEP, GCHLA, GSST, GOMLT, GSSH) were obtained by estimating the proportional change (PC) within a surrounding 3 × 3 cell grid using a moving window as follows: PC = [(maximum value − minimum value) × 100/maximum value]. Gradients of dynamic variables are believed to be good indicators of oceanic fronts, while the GDEP was used as a proxy for slope. All oceanographic raster layers were rescaled at a spatial resolution of 0.08° prior to the habitat modelling exercise. Environmental predictors were processed with various functions within the *raster* package (Hijmans 2020).

1.1.5. Stable isotope analysis of bobbies' blood samples

Blood samples were separated into red blood cells (RBC) and plasma by centrifugation at 12000 rpm for 5 min. Plasma has a half-life of about 3-5 days (Cherel et al. 2005b) (i.e. fast turnover rate), therefore it represents prey ingestion and trophic ecology of tracked individuals during the last trips before sampling (Cherel et al. 2005b). We used plasma samples collected during field work to perform a stable isotope analysis (SIA) for $\delta^{15}N$ (^{15}N / ^{14}N) and $\delta^{13}C$ (^{13}C / ^{12}C). As $\delta^{15}N$ values increase continuously (3-5‰) in marine food webs, conferring different isotopic signatures to different prey consumed by seabirds, the trophic level is recognized, while $\delta^{13}C$ values increase at a slower step (~0.8‰), indicating birds feeding habitat (Quillfeldt et al. 2005; Inger and Bearhop 2008; Phillips et al. 2011). There is a gradient of high to low values of $\delta^{13}C$ from benthic and inshore to pelagic and offshore food webs, because the organic enrichment at the coast is gradually diluted towards the open ocean (France 1995). Each of the tracked birds was sampled upon return from a foraging trip, during logger retrieval.

In the laboratory, plasma samples were dried at 60 °C for 24 h and homogenized. Successive rinses with a 2:1 chloroform-methanol solution was performed on the plasma for dilapidation (Cherel et al. 2005b). Approximately 0.25-0.30 mg of each sample were weighed and encapsulated into tin foil cups for posterior processing. The carbon and nitrogen isotopic ratios of these were determined from continuous-flow isotope ratio mass spectrometry (CF-IRMS). Results were presented in the common δ notation as parts per mil (‰) and compared with values from the international standards Pee Dee Belemnite (PDB) for $\delta^{13}C$ and atmospheric N2 for $\delta^{15}N$. Replicate measurements of internal laboratory standards (acetanilide) indicate precision < 0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$.

1.1.6. Stable isotope analysis of prey samples

Prey species were collected in 2018 and 2019 in Cabo Verde waters, by local fishermen operating in the surroundings of Raso Islet or at local fish-markets, between June-October of each year, and therefore are contemporaneous with tracking of BRBO and RFBO. We selected the prey species that could be part of BRBO and RFBOs' diet, according to the data available in the literature for these and other similar taxa (Ancona et al. 2012; Connan et al. 2017; Miller et al. 2018; Donahue et al. 2020). All prey individuals were measured, weighted, and identified to the lowest possible taxonomic level. Fish species were identified with local guides, while squid specimens were identified using the lower beaks (Xavier and Cherel 2009). Approximately 0.5 gr of muscle of each prey were dried at 60 °C for 24 h, submitted to successive rinses with a 2:1 chloroform-methanol solution for tissue's dilapidation (Cherel et al. 2005b), and weighed and encapsulated into tin foil cups for SIA. Due to the high similarity between some prey isotopic signatures, we opted to pool them in three different groups: epipelagic fish, juvenile fish, and squid. Epipelagic fish was composed by fish species that inhabit in the epipelagic layers of the ocean (i.e., the upper 200 m): *Sardinella aurita* (N = 4), *Platybelone lovii* (N = 4), *Sardinella maderensis* (N = 4), *Selar crumenophthalmus* (N = 4), *Cephalopholis taeniops* (N = 4), *Cheilopogon* sp. (N = 4), *Sparisoma cretense* (N = 3), *Decapterus macarellus* (N = 4), *Myripristis jacobus* (N = 4; mean ± SD: δ^{13}C = –16.98 ± 0.50; δ^{15}N = 10.05± 0.78). Juvenile fish was composed by young fingerlings identified as epipelagic species (mean ± SD: δ^{13}C = –18.47 ± 0.24, δ^{15}N = 8.38 ± 0.43, N = 10). Squid comprised specimens of

Todarodes sagittatus (N = 6) and *Callimachus rancureli* (N = 4; mean ± SD: δ^{13}C = –17.02 ± 1.56, δ^{15}N = 11.66 ± 2.18).

1.1.7. Diet reconstruction using SI mixing models

Diet reconstruction of BRBO and RFBOs was carried out by combining predator and prey isotopic signatures, and computing Bayesian mixing models with functions within the *simmr* R package (Parnell 2020). Two models were run separately for each season (Nov.-May and Jun.-Oct.), computing the predicted consumption of three main groups of prey (epipelagic fish, juvenile fish and squid) for males and females BRBO and RFBO. We used adult plasma isotopic signatures as our predator data and prey muscle isotopic signatures as our sources data (Phillips et al. 2014; Parnell 2020), with no prior diet information being added to the model.

To the best of our knowledge there are no diet-tissue discrimination factor (DTDF) calculated for BRBO or RFBOs. These factors are often specific for taxon, tissue, and even diet-specific (Phillips et al. 2014; Jenkins et al. 2020), making them one of the largest sources of bias for isotopic mixing model practices (Phillips et al. 2014). In this study we used the DTDF calculated for Atlantic puffins (*Fratercula arctica*) in a captive experiment developed by (Jenkins et al. 2020); we chose the DTDF calculated for plasma δ^{13}C and δ^{15}N isotopic ratios (− 0.18‰ for δ^{13}C and + 1.72‰ for δ^{15}N) to compare directly with boobies' plasma δ^{13}C and δ^{15}N values and minimize the error of the models. Although puffins and boobies have different ecology and live in different environments (temperate vs tropics), we believe that these DTDF are the most adjusted values for this study, considering other values available in the literature (Cherel et al. 2005a; Ciancio et al. 2016). We considered a standard deviation of ± 1.0‰, in an attempt to further reduce the bias of DTDF, and account for possible differences between boobies and puffins (Votier et al. 2010).

1.1.8. Data analysis

Generalized Linear Mixed Models (GLMMs) were built to test the effect of the independent variables (1) sex, (2) season (Jun.-Oct. or Nov.-May), and (3) their interaction on the mean values of (1) trip duration (h), (2) maximum distance to colony (m), proportion of time (3) travelling (4) in intensive foraging and (5) resting, distal (6) latitude and (7) longitude of forays, plasma (8) δ^{13}C, (9) δ^{15}N values and (10) Body Condition Index. (i.e., dependent variables). Differences between sex and season on the (11) bearing of foraging trips (i.e. circular data) were tested with circular ANOVAs through the *circular* package (Agostinelli and Lund 2017). Dependent variables of GLMMs were transformed when they did not meet normality and homogeneity assumptions. Separate models were developed for BRBO and RFBOs aiming at simpler interpretations of their outputs (i.e., interactions with the variable sex would be difficult to interpret in complex models). Both (1) trip identity nested within bird identity and (2) month of sampling was included as a random effect to control for pseudo-replication and temporal variability in the productivity of the marine environment, respectively. This also helped to account for unbalanced sample sizes per month. Gaussian distribution of error terms and a log-link function were used in the modelling. Post-hoc multiple comparisons with Bonferroni correction were used to identify significant differences between categories of each independent variable. R packages used in the GLMMs were *lme4* (Bates 2015) and *lmerTest* (Kuznetsova et al. 2017).

GLMMs we also used to calculate "individual-level repeatability" (*R*) in each of the former behavioural and foraging parameters (except for distal bearings), with the *rptR* R package (Nakagawa and Schielzeth 2010; Stoffel et al. 2017) as:

$$R_{ind} = S^{2}_{A} / S^{2}_{ind} + S^{2}_{A}$$

where S^{2}_{A} is the inter-individual variance and S^{2}_{ind} the intra-individual variance of each individual over time. Thus, inter-individual and intra-individual variances reflect the variances between foraging trips between individuals and the same bird, respectively. Repeatability index (0 – 1) can be classified as low ($R_{ind} < 0.25$), moderate ($0.25 > R_{ind} > 0.5$) and high ($R_{ind} > 0.5$) (Potier et al. 2015; Traisnel and Pichegru 2019). For visual comparison, we also computed the "population-level repeatability", which is a variation of the former formula: $R_{pop} = S^{2}_{A} / S^{2} + S^{2}_{A}$; where S^{2}_{A} is the inter-individual variance and S^{2} is the global within-individual variance. We compared the adjusted repeatability (repeatability calculated in the full fixed- and random-effects models) with models including only the individual as random effect, without any fixed effect.

Generalized Additive Mixed Models (GAMMs) were used to test the effect of (1) sex and (2) all environmental predictors on the presence/ absence of foraging behaviour (grid cells with 'intensive foraging') by tracked BRBO during (model 1) Nov.-May and (model 2) Jun.-Oct. and RFBO during (model 3) Jun.-Oct. Sex was included as a categorical variable in the fixed effects part of each model using the argument "by" of the *mgcv* package (Wood 2017), allowing smoothers to be built for each sex and environmental variable combination. Smoothers were fitted to each environmental variable using 3 to 5 regression splines with shrinkage to avoid overfitting (Wood 2004; Wood et al. 2016).

Multi-collinearity among covariates was assessed using variance inflation factors (GVIFs, *AEDForecasting* library in R (Claster et al. 2016)), with variables exhibiting a value higher than 3 being excluded from the modelling exercise (Table S4.2). GAMMs were built with a binomial family and logit link function for presence/absence (of 'intensive foraging') data. Bird identity and sampling month were included to control for individual and monthly environmental variability effects, respectively. We started running models including all the main effects, and the best candidate model was selected based on the second-order corrected Akaike's information criterion (AIC). A difference of less than 2 was interpreted as competing models receiving a similar amount of support from the data (Burnham and Aderson 2002). As with GLMMs, the three separate models were developed to attain comprehensive interpretations of the outputs and easily compare the effect of different environmental predictors on foraging between study seasons (Nov.-May *vs.* Jun.-Oct.) and species (BRBO *vs.* RFBO).

To establish the isotopic niche between sexes, study species (BRBO *vs.* RFBO) and season (June-October *vs.* November-May) with the plasma stable isotope data, we used SIBER (Stable Isotope Bayesian Ellipses in R), which is based on a Bayesian framework that confers a robust comparison to be made among data sets concerning different sample sizes (Jackson et al. 2011). The area of the standard ellipse (SEA_C, an ellipse having a 40% probability of containing a subsequently sampled datum) was adopted to compare isotopic values among groups (sexes, species and seasons) and their overlap in relation to the total niche width (both groups combined), and a Bayesian estimate of the standard ellipse and its area (SEA_B) was used to test whether the isotopic niche of one group was narrower than that of other group (Jackson et al. 2011). We further compared other isotopic niche metrics between species, sex and seasons, such as (1) carbon range, the distance between max. and min. $\delta^{13}C$ values; (2) nitrogen range, the distance between max. and min. $\delta^{15}N$ values; (3) total area (TA), as the convex hull area encompassed by all values in a $\delta^{13}C$ - $\delta^{15}N$ bi-plot space; (4) mean distance to centroid (CD), as the average Euclidean distance of each isotopic value to the $\delta^{13}C$ - $\delta^{15}N$ centroid, where the centroid is the mean $\delta^{13}C$ - $\delta^{15}N$ value for all values in the food web; (5) mean nearest neighbour distance (NND), as the mean of the Euclidean distances to each value nearest neighbour in bi-plot space, and thus a measure of the overall density of 'values packing'; (6) SD nearest neighbour distance (SDNND), as a measure of the evenness of 'values packing' in bi-plot space that is less influenced than NND by sample size.

All data are presented as mean ± SD, unless otherwise stated. Results were considered significant at $P \leqslant 0.05$.

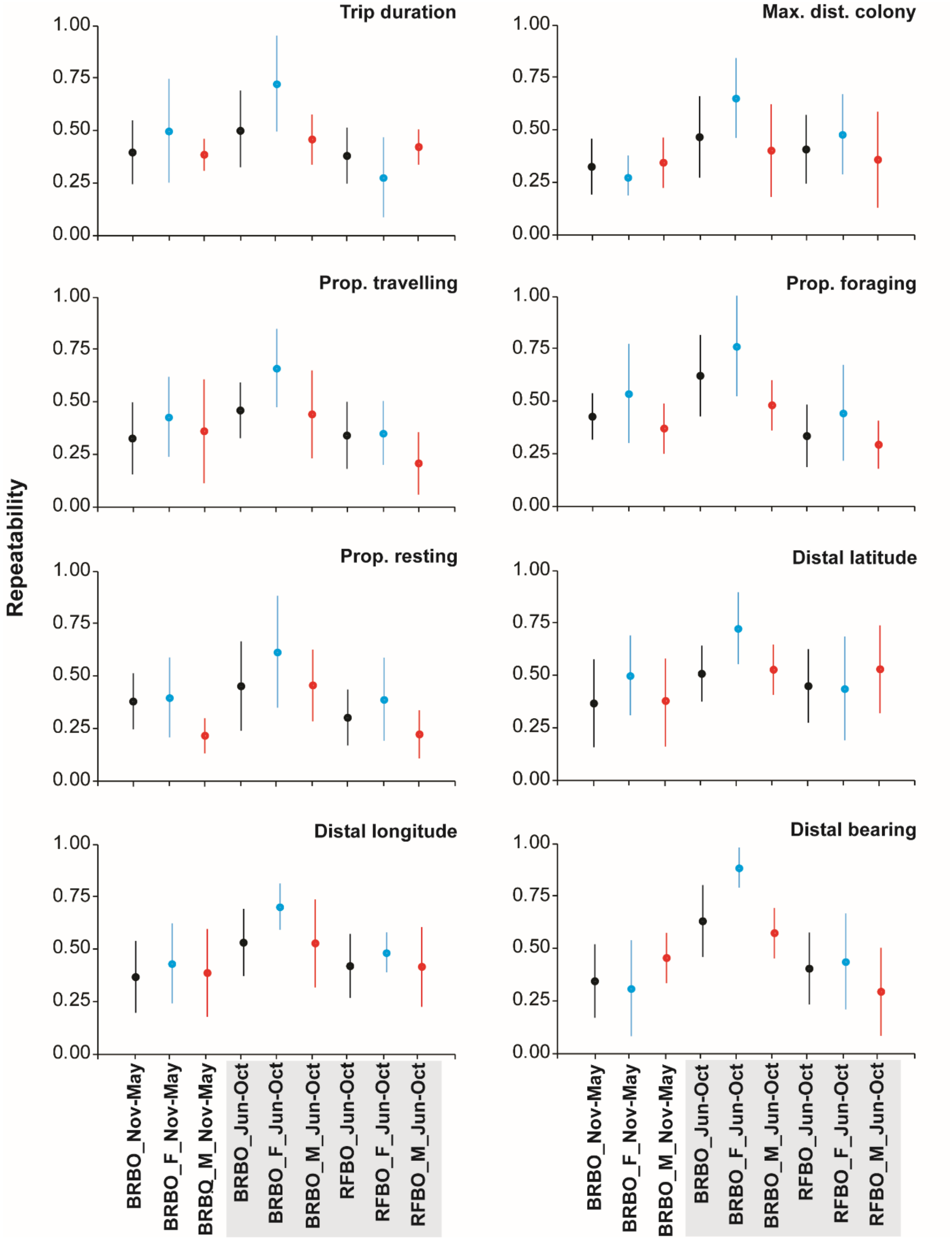
1.1.9. Compliance with ethical standards

This project was authorized by the "National Directorate of the Environment" of Cabo Verde (DNA) to be carried out at Raso Islet, Desertas Islands Natural Reserve. All sampling procedures and/or experimental manipulations were reviewed and specifically approved as part of obtaining the field license. All tracking information included in this publication is stored at BirdLife International Seabird Tracking Database (www.seabirdtracking.org) under IDs 1441 and 1442. Supporting data are available from the corresponding author upon reasonable request.

1.2. Results

1.2.1. Living without conspecifics

During Nov.-May, repeatability (*r*) of foraging behaviours and distribution was generally low ($r < 0.25$) to moderate ($0.26 < r < 0.5$) for most of the parameters, and it was similar between male and female BRBO (Fig 4.2).



Fig

Figure 4.2. Population-level ($R_{pop.}$; black) and individual-level (R_{ind}) repeatability values (±SE) of behavioural parameters for female (blue) and male (red) brown (BRBO) and red-footed (RFBO) boobies.

Overall, GAMMs showed a good predictive capacity, explaining 32.2%, 42.1% and 35.1% of the deviance in the probability of birds to switch between foraging and travelling behavioural modes (Table 4.2). Foraging probability of both female and male BRBO increased with decreasing ocean mixed layer thickness (OMLT) and increasing gradient in SST (GSST) and gradient in OMLT (GOMLT) (Fig 4.3).

Estimated diet composition of female and male BRBO was similar, with a higher estimated proportion of epipelagic and juvenile fish (including flying fish), and lower proportion of squids.

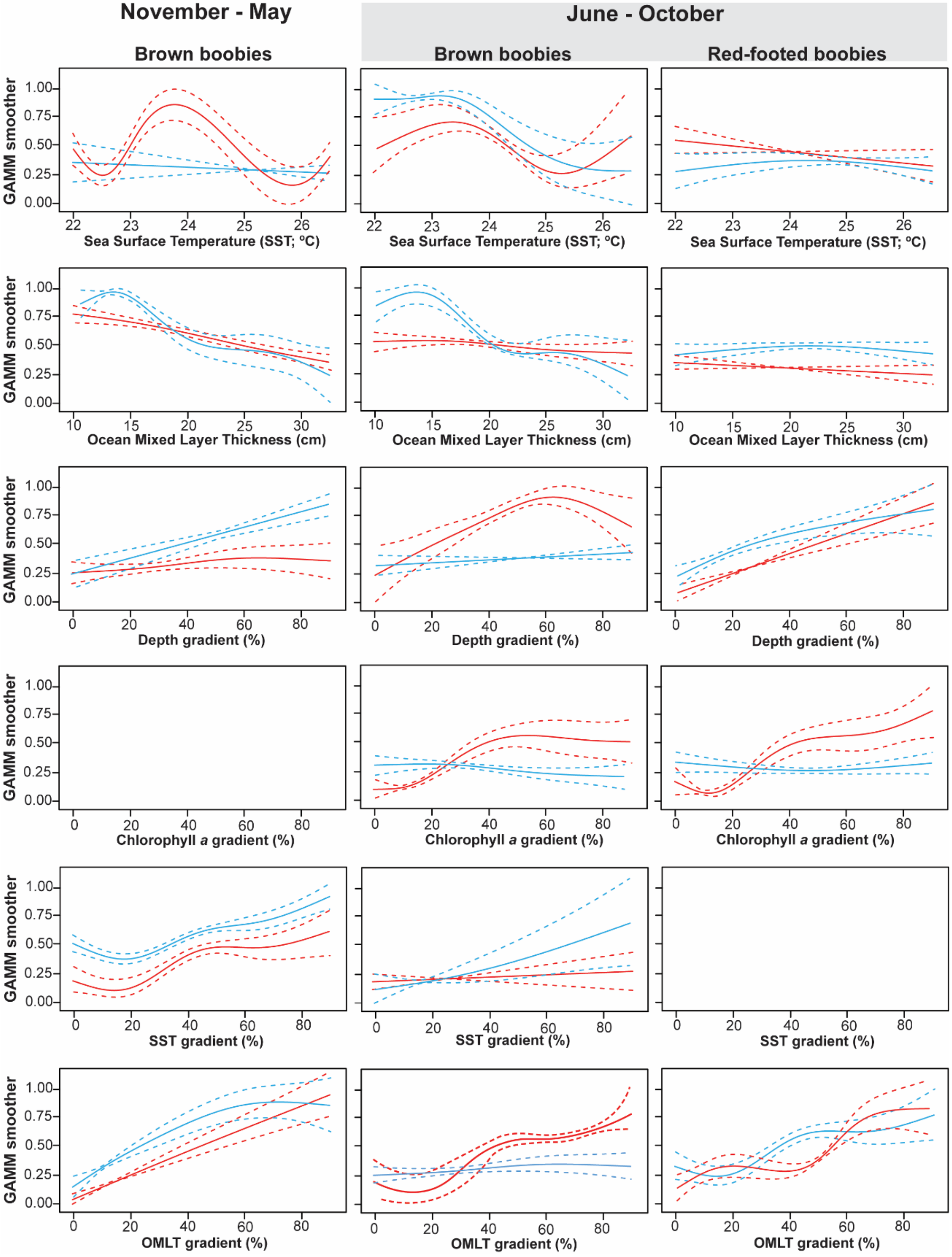
1.2.2. Living in sympatry

During Jun.-Oct., male BRBO spent on average 1.42 hours more during each excursion, travelled ~17 km significantly further from their colony, and spent respectively 10.0 % and 8.1 % more time travelling and foraging, when compared to female BRBO. Plus, male BRBO exhibited 1.1 ‰ significantly lower plasma $\delta^{13}C$ values and 7 % lower body condition when compared to female BRBO (Fig 4.1; Table 4.1 and 4.3A; Fig.S4.1).

Table 4.2. Generalized Additive Mixed Models (GAMMs) fitted to the probability to switch between foraging (1) and travelling (0) behavioural modes of tracked individual birds. Three different GAMM models were built: (A) brown boobies during Nov.-May, (B) brown boobies during Jun.-Oct. and (C) red-footed boobies during Jun.-Oct. All evaluated models included individual identity and month as a random factors, to control for pseudo-replication and environmental variability, respectively; DEP – depth (m); CHLA – chlorophyll *a* concentration (mgm^{-3}); SST - sea surface temperature (°C); OMLT – ocean mixed layer thickness (cm); SSH – sea surface height (m); GDEP – depth gradient (%); GCHLA – CHLA gradient (%); GSST – SST gradient (%); GOMLT – OMLT gradient (%); GSSH – SSH gradient (%). — Variables excluded after collinearity results. Significant results in **bold**.

	Nov.-May			Jun.-Oct.					
	Brown boobies (BRBO)			Brown boobies (BRBO)			Red-footed boobies (RFBO)		
Term	edf	Chi.Sq	*P*	edf	Chi.Sq	*P*	edf	Chi.Sq	*P*
s(DEP): female	—	—	—	—	—	—	—	—	—
s(DEP): male	—	—	—	—	—	—	—	—	—
s(CHLA): female	0.34	0.43	0.87	—	—	—	0.44	0.34	0.21
s(CHLA): male	1.12	0.65	0.10	—	—	—	1.49	1.51	0.11
s(SST): female	0.01	0.01	0.41	1.36	2.42	**0.001**	0.01	0.01	0.79
s(SST): male	2.93	25.45	**< 0.001**	2.53	9.28	**0.001**	0.64	4.78	0.10
s(OMLT): female	1.57	2.74	**0.01**	2.02	4.00	**0.001**	0.11	0.19	0.39
s(OMLT): male	0.75	0.86	**0.02**	0.14	0.60	0.92	0.01	0.17	0.65
s(SSH): female	0.99	0.43	0.23	0.09	0.30	0.57	0.06	0.09	0.96
s(SSH): male	0.80	0.47	0.08	1.95	2.73	**0.01**	0.77	2.51	**0.04**
s(GDEP): female	0.83	1.45	**0.01**	0.04	0.23	0.34	0.98	13.27	**< 0.001**
s(GDEP): male	0.38	0.16	0.19	2.31	8.53	**0.001**	0.97	18.82	**< 0.001**
s(GCHLA): female	—	—	—	1.11	0.70	0.12	0.14	0.19	0.35
s(GCHLA): male	—	—	—	1.33	1.02	**0.05**	2.19	14.83	**0.001**
s(GSST): female	2.44	10.99	**< 0.001**	1.31	1.20	**0.03**	—	—	—
s(GSST): male	3.12	26.69	**< 0.001**	0.69	0.72	0.06	—	—	—
S(GOMLT): female	1.16	20.12	**< 0.001**	0.12	0.09	0.48	2.50	24.23	**< 0.001**
s(GOMLT): male	1.54	20.41	**< 0.001**	2.64	22.61	**< 0.001**	2.64	12.74	**0.001**
s(GSSH): female	—	—	—	0.17	0.05	0.50	0.15	0.08	0.50
s(GSSH): male	—	—	—	1.63	1.69	**0.01**	0.76	1.24	**0.04**

Figure 4.3. Response curves of the most important smooths resulting from generalized additive mixed models (GAMMs), explaining the foraging distribution of male (red) and female (blue) brown boobies (BRBO) and red-footed boobies (RFBO), during November – May and June – October. Shaded area highlights the period when BRBO and RFBO co-occur un sympatry at Raso Islet, Cabo Verde.



The observed foraging overlap between sexes and the overlap of females' foraging distribution between seasons was similar to permuted overlap (Table 4.4). Yet, observed male-male foraging overlap between seasons and female-male foraging overlap during Jun.-Oct. was significantly lower than randomly expected (Table 4.4).

During this period, when both BRBO and RFBO inhabit Raso Islet, female BRBO spent 1.2 hours less during each excursion, travelled ~29 km closer to the colony, and spent respectively 9.3 % and 6.1% less time travelling and foraging, when compared to male BRBO and male and female RFBO. Moreover, female BRBO foraged over significantly lower latitude, longitudes, and distal bearings. Plus, they also exhibited 0.5‰ lower plasma $\delta^{13}C$ values, though a 4% higher body condition when compared to male BRBO and male and female RFBO (Fig 4.1; Table 4.1 and 4.3B; Fig S4.1). The observed foraging overlap between sexes and between species was generally significantly lower during Jun.-Oct. than permuted overlap (Table 4.4).

Repeatability of female BRBO generally increased significantly to high ($r > 0.6$), while male BRBO and both sexes of RFBO remained on low to moderate repeatability of foraging behaviours and distribution (Fig 4.2).

In terms of habitat preference, foraging probability in female BRBO increased with decreasing SST and OMLT and increasing GOMLT. However, male BRBO and male and female RFBO generally increased foraging probability with increasing sea surface height (SSH), and gradients in seafloor depth (GDEP), chlorophyll *a* concentration (GCHLA), OMLT (GOMLT) and SST (GSST) (Table 4.4, Fig 4.3).

Models suggest that female BRBO did increase the consumption of epipelagic and juvenile fish, and similar patterns were found for female RFBO. On the other hand, males of both species fed on a slightly lower proportion of these food items when

Table 4.4. Observed and randomized overlap (Bhattacharyya's Affinity) at the 50% and 95% Kernel utilization distributions (UDs) between (A) female and male brown boobies during November – May and June – October and (B) female and male brown (BRBO) and red-footed boobies (RFBO) during June – October. *P* represents the proportion of randomized overlaps that were smaller than the observed overlap. Significant differences are shown in **bold**.

	50% UD			**95% UD**		
Comparison	**Observed overlap**	**Permuted overlap (mean ± SD)**	***P***	**Observed overlap**	**Permuted overlap (mean ± SD)**	***P***
(A) Between sexes and seasons						
female BRBO Nov.-May *vs*. male BRBO Nov.-May	0.38	0.35 ± 0.04	0.69	0.71	0.75 ± 0.03	0.56
female BRBO Nov.-May *vs*. female BRBO Jun.-Oct	0.39	0.41 ± 0.05	0.61	0.68	0.70 ± 0.05	0.59
male BRBO Nov.-May *vs*. male BRBO Jun.-Oct	0.25	0.40 ± 0.03	**0.02**	0.51	0.79 ± 0.05	**0.01**
female BRBO Jun.-Oct. *vs*. male BRBO Jun.-Oct.	0.27	0.30 ± 0.05	0.06	0.49	0.76 ± 0.03	**0.04**
(B) Between sexes and study species						
female BRBO *vs*. male BRBO	0.29	0.36 ± 0.06	0.06	0.50	0.69 ± 0.04	**0.04**
female BRBO *vs*. female RFBO	0.22	0.38 ± 0.04	**0.02**	0.46	0.64 ± 0.06	**0.01**
female BRBO *vs*. male RFBO	0.26	0.41 ± 0.05	**0.02**	0.43	0.61 ± 0.05	**0.01**
female RFBO *vs*. male RFBO	0.42	0.33 ± 0.06	**0.05**	0.44	0.59 ± 0.04	**0.03**

Table 4.3A. Generalized Linear Mixed Models (GLMMs) testing the effect of (A) the interaction between sex and season (November-May *vs.* June-October) and (B) the interaction between sex and species (brown boobies-BRBO *vs.* red-footed boobies-RFBO) on trip characteristics, spatial distribution, trophic ecology and body condition shown in Table 4.1. Both (1) trip ID nested within bird ID and (2) Month of sampling were set as random effects to control for pseudo-replication and temporal variability on the environmental proxies of productivity, respectively. Significant results in **bold**. Effect was evaluated with Post-hoc multiple comparisons with Bonferroni correction. * Differences between means of circular data variables were analysed with circular ANOVAs.

Model A									
	Sex			Season			Sex : Season		
Variables	$F_{3,703}$	P	Effect	$F_{3,699}$	P	Effect	$F_{3,699}$	P	Effect
N tracks [N birds]	—	—	—	—	—	—	—	—	—
Mass (kg)	—	—	—	—	—	—	—	—	—
Trip duration (h)	2.17	0.09	—	2.77	**0.05**	Nov-May < Jun-Oct	2.83	**0.04**	male, Jun-Oct > all others
Max. dist. colony (km)	5.48	**0.001**	females < males	2.69	**0.05**	Nov-May > Jun-Oct	2.71	**0.05**	male, Jun-Oct > all others
Prop. Travelling (%)	3.39	**0.02**	females < males	2.29	0.08	—	2.80	**0.04**	male, Jun-Oct > all others
Prop. Foraging (%)	3.81	**0.01**	females < males	3.90	**0.01**	Nov-May < Jun-Oct	3.30	**0.02**	male, Jun-Oct > all others
Prop. Resting (%)	1.59	0.19	—	2.81	**0.04**	Nov-May > Jun-Oct	1.65	0.18	—
Distal latitude (°)	3.69	**0.04**	females < males	3.09	**0.03**	Nov-May > Jun-Oct	1.19	0.33	—
Distal longitude (°)	6.01	**0.001**	females < males	1.76	0.18	—	1.44	0.27	—
Distal bearing (°)*	1.11	0.33	—	3.88	**0.01**	Nov-May < Jun-Oct	2.26	0.08	—
Plasma δ^{13}C (‰)	3.89	**0.01**	females < males	3.85	**0.01**	Nov-May < Jun-Oct	2.73	**0.05**	male, Jun-Oct < all others
Plasma δ^{15}N (‰)	1.37	0.25	—	2.75	**0.05**	Nov-May > Jun-Oct	1.95	0.12	—
Body Condition Index (BCI)	2.78	**0.04**	females > males	3.41	**0.02**	Nov-May > Jun-Oct	2.62	**0.05**	male, Jun-Oct < all others

Table 4.3B. Continuation of Table 2.

Model B									
	Sex			Species			Sex : Species		
Variables	$F_{3,507}$	*P*	Effect	$F_{3,699}$	*P*	Effect	$F_{3,699}$	*P*	Effect
N tracks [N birds]	—	—	—	—	—	—	—	—	—
Mass (kg)	—	—	—	—	—	—	—	—	—
Trip duration (h)	3.33	**0.02**	females > males	3.82	**0.01**	BRBO < RFBO	2.63	**0.05**	female, BRBO < all others
Max. dist. colony (km)	8.02	**< 0.001**	females < males	5.60	**0.001**	BRBO < RFBO	7.18	**< 0.001**	female, BRBO < all others
Prop. Travelling (%)	2.19	0.09	—	1.85	0.14	—	3.09	**0.03**	female, BRBO < all others
Prop. Foraging (%)	1.78	0.15	—	3.35	**0.02**	BRBO < RFBO	5.61	**0.001**	female, BRBO < all others
Prop. Resting (%)	1.68	0.17	—	2.83	**0.04**	BRBO < RFBO	2.37	0.07	—
Distal latitude (°)	3.87	**0.01**	females < males	3.67	**0.04**	BRBO < RFBO	2.88	**0.03**	female, BRBO < all others
Distal longitude (°)	3.01	**0.01**	females < males	1.98	0.11	—	3.99	**0.01**	female, BRBO < all others
Distal bearing (°)*	1.52	0.21	—	5.59	**0.001**	BRBO > RFBO	5.59	**0.001**	female, BRBO < all others
Plasma δ^{13}C (‰)	2.10	0.10	—	2.69	**0.05**	BRBO < RFBO	3.00	**0.03**	female, BRBO < all others
Plasma δ^{15}N (‰)	1.15	0.33	—	3.14	**0.03**	BRBO < RFBO	1.91	0.13	—
Body Condition Index (BCI)	1.79	0.13	—	2.79	**0.04**	BRBO > RFBO	2.81	**0.04**	female, BRBO > all others

compared to females. The models also showed that while feeding on high proportion of epipelagic fish, female RFBO would rely also on comparable higher proportion of squid (Fig 4.4)."

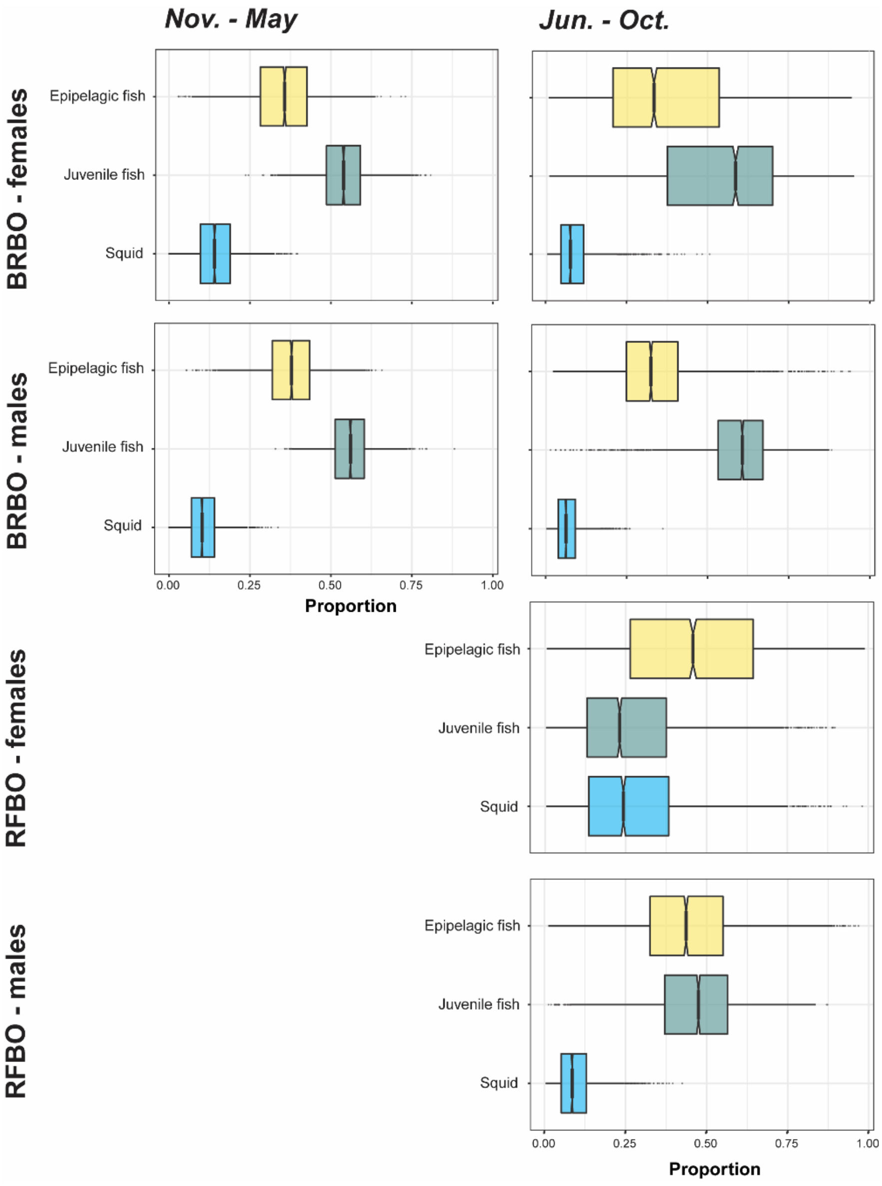


Figure 4.4. Estimated proportions of main prey items in the diet of male and female brown boobies (BRBO) and red-footed boobies (RFBO) from Raso Islet, Cabo Verde during a phase when only brown boobies occur on the colony (November-May; left panels) and when the two species co-occur in sympatry (June-October; right panels). Epipelagic fish – *Sardinella aurita*, *Platybelone lovii*, *Sardinella maderensis*, *Selar crumenophthalmus*, *Cephalopholis taeniops*, *Cheilopogon* sp., *Sparisoma cretense*, *Decapterus macarellus*, *Myripristis jacobu*; Juvenile fish – young fingerlings of epipelagic species; Squid – specimens from the Ommastrephidae and Onychoteuthidae families.

Both male and female BRBO enlarged their isotopic niches from Nov.-May to Jun.-Oct. Female RFBO exhibited the larger SEA_C (Table S4.3) and lower isotopic niche overlap in relation to male and female BRBO, but higher overlap with male RFBO isotopic niche (S2 Fig, S4 Table).

1.3. Discussion

1.3.1. Living without conspecifics

During Nov.-May, spatial segregation was very low between sexes of BRBO, a period when this is the only booby species occurring on Raso islet. Our results showed similar habitat use and repeatability of behavioural foraging parameters and distribution between sexes, as well as diet patterns, in line with brown boobies from islands in the Gulf of California (Castillo-Guerrero et al. 2016). There, colonies of BRBO are much larger (2,400-6,000 individuals) than those at Raso (~289 individuals) (S5 Table), but still no significant differences were observed in sexual foraging patterns in either place, meaning that density-dependent competition is not likely to drive sexual segregation.

Differences in sex-specific foraging patterns have mainly been related to marine productivity in the surrounding colonies (Weimerskirch et al. 2009b; Young et al. 2010b), allowing for flexible parental investment to occur during breeding (Weimerskirch et al. 2009b). In our case, neither differential parental roles (Thaxter et al. 2009), niche specialization associated with sexual dimorphism and competitive exclusion (Phillips et al. 2004), or nutritional requirements (Lewis et al. 2002) affected foraging behaviour between sexes (Castillo-Guerrero et al. 2016),because no segregation was observed. Other related species, such as Masked boobies have also shown similar foraging trip parameters, suggesting that local oceanic conditions and food distribution and availability are important factors leading to sexual segregation. Thus, these studies, imply that competition may not be an option when species are feeding on ephemeral prey, consequently compelling sexes to share food resources and foraging areas (Lerma et al. 2020a, b). Therefore, as tropical marine regions such as the Cabo Verde Islands, are associated with oligotrophic waters and patchily distributed fish (Longhrust and Pauly 1987), this equal sharing of resources and habitats within species can be expected here. Similar environmental conditions at Tromelin Island in the Western Indian Ocean (Kappes et al. 2011) and Palmyra Attol in the Central Pacific Ocean (Young et al. 2010b), have also been suggested to partly explain the lack of inter-sex differences observed in masked and red-footed boobies (Table S4.5). Additionally, we stress that during this period (Nov-May), a higher annual peak of breeding occurs for this species (Biosfera unpublished data), which could lead to a higher number of breeding pairs competing for food, but still, no differences were observed between sexes.

In terms of foraging habitat, as both sexes stayed relatively close to their colonies, certain physical features may occur around Raso Islet, allowing the occurrence of discrete productive habitats for subsurface and aerial predators year-round. Thus, both sexes of BRBO showed a preference for areas with decreasing OMLT and increasing gradients of SST and OMLT, during Nov. - May. The OMLT has often been related to the depth of the vertical temperature gradient (thermocline), located right beneath the Ocean Mixed Layer (OML), possibly working as a physical and biological barrier for fish species (Ballance et al. 2006; Pelletier et al. 2012). Gradients of SST have also been connected with ocean fronts, where prey is known to concentrate and made available to top-predators (Schneider 1990; Scales et al. 2014). Stretching from Cabo Verde Islands to the coast of Cape Blanc (West Africa), an important frontal system occurs, mixing waters coming from the north and south hemispheres with different gradients of temperature, salinity, and velocity (Peña-Izquierdo et al. 2012b). Even though, CHLA concentration was not identified by the models as a variable influencing foraging habitat preference during this period, it is important to note that at the adjacent African coast, the upwelling phenomena leads to a higher concentration of chlorophyll between 10-20°N (Thomas et al. 2001), especially during winter and spring, stretching long filaments and eddies of chlorophyll-rich waters to the open ocean and to the Cabo Verde archipelago (Pelegrí et al. 2005; Arístegui et al. 2009) (Fig S4.3). This could provide better foraging opportunities closer to the colonies during this period.

1.3.2. Living in sympatry

During this period (Jun.-Oct.), intra-specific segregation was observed within both sexes of BRBO, and inter-specific segregation occurred between two sulid species living in sympatry (Weimerskirch et al. 2009b; Young et al. 2010b; Kappes et al. 2011; Ponton-Cevallos et al. 2017) in Raso Islet. Although several studies concerning BRBO (Table S4.5) (Gilardi 1992; Weimerskirch et al. 2009b; Miller et al. 2018) and other sulid species (Weimerskirch et al. 2009b; Castillo-Guerrero and Mellink 2011) found that bigger females frequently perform longer and farther foraging trips than smaller males, our study showed the exact opposite, with female BRBO maintaining their previous foraging areas, whilst male BRBO and both sexes of RFBO looked for different foraging opportunities.

Many papers on sex-specific foraging behaviour have pointed out that males and females may adopt different foraging strategies in response to different factors, such as competition, prey and habitat preference, parental involvement, among others (Le Boeuf et al. 2000; Breed et al. 2006; Weimerskirch et al. 2006b, 2009b; Cleasby et al. 2015;

Miller et al. 2018; Pereira et al. 2018). Differences found in sexual foraging at Raso are in line with those found (Lewis et al. 2005) at Johnston Atoll, Central Pacific, where male BRBO foraged in far distant areas than females (Table S4.5). In our study, when both booby species were living in sympatry on Raso, inter-sexual differences in foraging behaviour and distribution may be explained by divergent parental roles, as females tend to stay closer to the colony, showing high repeatability to foraging grounds, feeding more rapidly and quickly returning to the colonies to feed their offspring. Several studies of boobies (Zavalaga et al. 2010) and other seabird species exhibiting high foraging site fidelity (Pettex et al. 2010; Passadore et al. 2018) were carried out in highly productive marine environments (temperate regions), where prey distribution is more predictable, while in tropical areas, it has been pointed out that the presence of bathymetric features may be an important variable in increasing site fidelity (Wilkinson et al. 2020). Social cues, by gathering information from previous foraging trips (Carroll et al. 2018), information transfer at sea (Weimerskirch et al. 2010b; Thiebault et al. 2016, 2019) and at the colony (Courbin et al. 2020), have also been suggested to increase site fidelity, however all were from studies in temperate areas. As females simply kept using the same areas, increasing repeatability of foraging parameters compared to the first period, and no important bathymetric features seem to be present or influencing utilized areas, this further suggests that parental involvement during this period, should be a factor explaining sexual segregation (Gilardi 1992; Weimerskirch et al. 2009b; Miller et al. 2018). As all tracked BRBO were rearing chicks, feeding on higher proportions of epipelagic and juvenile fish could explain female´s better body condition, and also mean high energetic meals delivered to the offspring, further supporting this conclusion and explaining site fidelity (Wojczulanis et al. 2006; Pereira et al. 2018).

Males on the other hand, would probably invest less on the chick, preferring to travel farther and using different foraging habitats, while taking advantage of winds to minimize flying costs (Shaffer et al. 2001) and increase flying efficiency (flight speed, foraging range and flapping frequency) (Lewis et al. 2005; Weimerskirch et al. 2009b). Intuitively, this could also indicate a male habitat preference (Cleasby et al. 2015) during a period of sympatry. Lower body condition in males could indicate that they have a harder time foraging, and therefore invest less in chick provisioning (Pereira et al. 2018). Additionally, low repeatability to foraging grounds could reflect prey-patch unpredictability in the oligotrophic waters of Cabo Verde (Weimerskirch 2007).

(Miller et al. 2018) also pointed out a possible division of labour between sexes at Reine Island (Great Barrier Reef, Australia), where males stayed longer at the nest and females travelled longer to bring food to the growing chick and returned later at sunset to avoid klepto-parasitism by frigate birds (Miller et al. 2018). This suggests that inter-specific competition could also play a role in affecting intra-specific segregation of sulids living in sympatry with other species. In our study, because other sulid species moves to the Islet, competition pressure may contribute to sexual segregation. Thus, we also suggest that the presence of other seabird species, such as the Cape Verde shearwater (breeding from June-October) (Paiva et al. 2015) and the Cape Verde little shearwater (prospecting) (Biosfera unpublished data), could also affect the foraging behaviour of BRBO. To further support this theory, at Raine island, BRBO were shown to exhibit intra-specific niche partitioning during breeding peaks (Miller et al. 2018), while during a period of low breeding effort no intra-specific niche segregation occurred (Ponton-Cevallos et al. 2017). This clearly demonstrates that BRBO can modify their intra-specific foraging behaviour to counterbalance possible competition for feeding resources. In our study, although the breeding peak of BRBO occurs between December-February, it is undeniable that the overall seabird breeding peak at Raso occurs during the summer period (Jun-Oct) (Hazevoet 2015; Paiva et al. 2015; Ramos et al. 2018; Cerveira et al. 2020; Semedo et al. 2020). Adding that a second colony of breeding Cape Verde shearwater and other species occur at less than 6.5 km away, in Branco islet (Hazevoet 2015; Semedo et al. 2020), is enough to suppose that competition is a possibility between species.

In summary, regardless of whether female BRBO travelled longer than males, or stayed closer to the colonies, all studies agreed that differential breeding involvement, division of labour or sex role partitioning, in addition to competition, could have a double effect on sexual segregation (Gilardi 1992; Weimerskirch et al. 2009b; Miller et al. 2018). Contrary to (Lewis et al. 2005), body size does not appear to be the factor explaining intra-specific segregation, because seasonal variations in foraging parameters and isotopic niches were observed for this species, implying foraging plasticity inferred by surrounding environmental characteristics affecting prey abundance and habitat preference, as well as inter-specific competition due to co-existence and breeding peaks.

Foraging patterns of RFBO were also generally similar between sexes, following with the former literature on this species (Lewis et al. 2005; Weimerskirch et al. 2006b; Mendez et al. 2016, 2017a). The similitude of these patterns might have been driven by low intra-specific competition due to the small population size of RFBO inhabiting Raso Islet (Ainley et al. 2004; Young et al. 2010b), or more likely driven by an unbalanced female:male sample size (N=4:17) (Ponton-Cevallos et al. 2017). Nevertheless, a difference in size does not seem to affect intra-specific foraging distributions here, and the lack of breeding seems to be a reasonable explanation for the low intra-specific competition.

Concerning inter-specific differences, RFBO showed a tendency to fly further and longer compared to BRBO due to its pelagic nature and smaller size (Young et al. 2010b; Ponton-Cevallos et al. 2017). Similarly, at Palmyra Atoll, in the Central Pacific Ocean, RFBO undertook more pelagic trips than bigger-sized Masked Boobies, although in this case there was an established breeding colony with a much greater number of RFBO (1000-2500 pairs) (Table S4.5) (Young et al. 2010b), which could imply a higher foraging effort. This higher effort was also observed in larger colonies of Cape gannets (17,000-70,000 pairs) (Grémillet et al. 2004) and Masked boobies (4,600 individuals) (Oppel et al. 2015), as competition is expected to be higher. On the other hand, at Tromelin Island (Indian Ocean), where colonies of both species are much smaller and fairly similar in numbers (RFBO=180 pairs; MB=250 pairs), Masked boobies travelled further than RFBO (Kappes et al. 2011), which was not expected, as the larger size of Masked boobies would probably confer them the ability to outcompete the smaller RFBO from foraging areas in the colony surroundings (González-Solís et al. 2000). In that case, environmental characteristics appeared to have a high influence on resource partitioning in an extreme oligotrophic environment (González-Solís et al. 2000).

In our study site, however, regardless of its tropical location and its less productive waters compared to the first period (Fig S4.3), foraging bigger-sized female BRBOs seem to have relied on locations near the colony during both study periods, while smaller male BRBO and RFBO individuals foraged farther from the colony, in a more diverse array of areas, and exhibited lower repeatability in their foraging behaviour. From June to October, female BRBOs foraging probability increased with decreasing SST and OMLT, depicting good environmental conditions in areas closer to the colonies and a thinner mixed layer, which should allow prey fish to be closer to the surface and more accessible to predators

(Ballance et al. 2001, 2006; Spear et al. 2001; Eeden et al. 2016; Cerveira et al. 2020). Contrastingly, male BRBO and both sexes of RFBO preferred areas with higher gradients of SST (i.e. ocean fronts), chlorophyll *a* concentration (CHLA) (i.e. upwelling phenomena), and seafloor depth (i.e. steep locations), possibly along seamounts or shelf edges. Birds also showed a preference for areas with higher SSH values. High values of SSH usually depict the presence of Anticyclonic Eddies (Weimerskirch et al. 2010a; Poli et al. 2017), which are also known to be associated with enhanced productivity (higher CHLA values), especially in tropical environments (Dufois et al. 2016). (Cardoso 2017) showed the frequent occurrence of eddies inside and outside the Cabo Verde archipelago, which drive CHLA-rich waters from off West Africa and enhance CHLA within the archipelago. (Meunier et al. 2012) also reported the formation of big anticyclonic eddies influenced by the Cabo Verde Frontal Zone (CVFZ). Similarly, studies in the Mozambique Channel (Europa Island) have shown the preference of the local seabird community (e.g. RFBOs) to forage in productive waters associated with the presence of mesoscale anticyclonic eddies, preferably around the edges of such oceanographic structures (Weimerskirch et al. 2004; Jaquemet et al. 2005; Mendez et al. 2016).

Both species explored the same prey species (squid, epipelagic and juvenile fish) which was expected, because sympatric tropical boobies studied in other locations exhibit similar dietary preferences (Table S4.5) (Weimerskirch et al. 2004; Cherel et al. 2008; Young et al. 2010b, a; Lerma et al. 2020a). During winter and spring months, both sexes of BRBO had a similar expected diet, however, during the months of co-existence female BRBO showed a higher consumption of epipelagic and juvenile fish. This may be related to a greater availability of fish than squid in their foraging areas (Clarke and Prince 1980), and as suggested before, a possible selection of higher energetic-content prey to provision their chicks (Kappes et al. 2011). Flying fish have also been described to occur at the edges of rapidly rotating eddies (Bakun 2006), a type of habitat present in the waters of the Cabo Verde Islands, used by male BRBO and both sexes of RFBO. Nevertheless, results shown here on diet preferences evaluated from isotopic mixing models should be interpreted with caution, given the small sample size for each prey species. Ideally, future studies should sample potential prey all year-round, and increase sample size of each prey species to ascertain BRBO and RFBO dietary preferences, if possible, at the family- or species-levels.

Although intra-specific and inter-specific isotopic niches overlapped during the Jun.-Oct. period, there was a significant difference in δ^{15}N values for females RFBO, as squid was expected to be more consumed by RFBO. This could be related to the higher abundance of squid during the summer months, main spawning and growth season (Arkhipkin et al. 2015), or even related to the use of different habitats (Kappes et al. 2011). Previous studies have connected the occurrence of squid (e.g. Ommastrephidae) with sea surface temperature and productivity connected to frontal zones (Pearcy et al. 1996; Ichii et al. 2004) such as the one occurring in Cabo Verde (Peña-Izquierdo et al. 2012b). A similar diet pattern was observed in two islands (Weimerskirch et al. 2006b; Kappes et al. 2011) of the Indian Ocean, where prey items of red-footed booby were mainly composed of squid, confirming the different trophic position of their prey. The fact that RFBO are not breeding may also be a contributing factor, because this species is not constrained by the need to feed chicks (Bugge et al. 2011).

While BRBO expanded their isotopic niches across seasons, perhaps due to enhanced inter-species competition, there was a lower niche overlap of female RFBO in relation to BRBO, but higher when compared to that of male RFBO. This confirms the expected broader isotopic niche in a more generalist species like the RFBO during the non-breeding phase. Also, a high overlap in RFBO may indicate low intra-specific competition due to low individual numbers and non-breeding phase if reproductive duties are relaxed (Ponton-Cevallos et al. 2017), or in this case inexistent, allowing adults to focus on their own nutritional needs.

1.3.3. Conclusion

The current study provides the first view over the foraging ecology of a resident booby in Cabo Verde, with a second overview of changes when the pressure of another similar species is added to the study area. We conclude that divergent parental roles, environmental conditions, habitat preference and inter-specific competition could be mechanisms simultaneously underlying sexual segregation for BRBO during a period of co-existence. These results agree with the idea that BRBO boobies have a certain foraging ecology plasticity (Castillo-Guerrero et al. 2016; Ponton-Cevallos et al. 2017; Miller et al. 2018), capable of adapting to different circumstances of environmental conditions and competition. Foraging similarities in RFBO sexes, although confirmed in other studies, could possibly be related to the non-breeding phase or even biased sex sampling (Ponton-Cevallos et al. 2017). As such, inter-specific foraging differences, appear to be more affected by habitat preference and different breeding stages between species.

The results obtained here, are also pivotal for the identification of core foraging areas of both species, as an important input for future conservation plans to be applied within the Natural Reserve of Desertas Islands.

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Chapter 5

QUANTIFYING THE SENSITIVITY OF IDENTIFIED IMPORTANT AREAS FOR MARINE TOP PREDATORS' ASSEMBLAGES (POTENTIAL MARINE PROTECTED AREAS; MPAS) TO ENVIRONMENTAL PRESSURES

Abstract

The ocean is a very dynamic and complex ecosystem, hosting a wide range of marine biodiversity, on which coastal human communities rely upon. Knowing that all the global ocean is influenced by human impacts and affected by multiple stressors, brought the need to create Marine Protected Areas (MPAs) for better management of marine ecosystems and resources. Seabird at-sea distribution has been used for designing MPAs, identifying "hotspots" of biodiversity and productivity in marine areas, as well as anthropogenic activity pressure. It has been 26 years since the Cabo Verde government compromised, through the Biodiversity Convention ratified in 1995, to a goal of achieving 10% protection of the national marine territory (12 n.m.), but only 5.8% has been declared since then. In this study we identified core foraging areas for each seabird population/species and described important seabird hotspots for the Cabo Verde EEZ while evaluating potential stress effects exerted by artisanal, semi- and industrial fisheries in the region. We also evaluated the suitability of existing MPAs, KBAs and a proposed LMPA for the Eastern side of the islands, concerning seabirds and fisheries distribution, using seven years' worth of 8 seabird species' tracking data (2013-2019) collected during field work in different colonies and islands of the Cabo Verde archipelago. Results showed moderate to high intra- and inter-annual variability in the at-sea distribution of the Cabo Verde seabird community, posing a challenge when delineating areas for applied conservation, as many factors must be taken into consideration (species, colony, and breeding phase). Key marine areas for seabirds in this study showed a clear lack of protection efficiency by the existing MPAs and recommends large area increase for current MPAs (157.2%) and KBAs (97.2 %) for effective conservation. Four important areas stood out, each containing at least one existing KBA and only one overlapped, to a small extent, with the proposed eastern LMPA. One major advantage to management is that these key areas fell well within the island's coastal surroundings, and very few locations were considered important in the pelagic marine EEZ, possibly due to the presence of island breeding colonies having a strong influence on species distribution. For wide-ranging species, like the Cape Verde shearwater, cross-nation marine spatial planning is needed during the incubation period, while most other species will only require national protection legislation, by the Cabo Verde government authorities. Temporal variability in foraging distribution was also observed within populations and between species recommending seasonal MPAs, known to provide socio-economic benefits while achieving ecological goals. Industrial fishing pressure overlap on key areas, was great for Bulwer´s petrel and Cape Verde shearwater during incubation. However, we suggest that for petrels, mitigation measures for artificial light pollution should be enough to avoid vessel collision, as well as bycatch mitigation measures for other species (shearwaters, boobies and tropicbirds) on vessel gears within the archipelago, particularly for artisanal fisheries

Keywords: MPA; KBA; hotspots; Marine EEZ; Cabo Verde archipelago

5.1. Introduction

Oceans cover 71% of the Earth surface, present a great variety of dynamic and complex ecosystems, and host a wide range of marine biodiversity, which coastal human communities have always relied upon. Thus, it is of major concern to acknowledge that all the global ocean is influenced by human impacts and 97.7% is affected by multiple stressors (Halpern et al. 2015). All these human impacts have brought the need to create important areas for conservation, i.e. Marine Protected Areas (MPAs), and to better manage the marine ecosystems and resources (Hooker et al. 2011; Lascelles et al. 2012; Ludynia et al. 2012). MPAs are described as *"a clearly defined geographical space, recognized, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values"* (Wilkinson 2008). There is a total of 16,409 designated MPAs representing 6.6% of the global ocean, however, 2,670 of these areas have almost no management regulations, and only 2.7% are fully/highly protected (Marine Conservation Institute, 2021). Additionally, there are still 244 areas that have already been proposed or committed (Marine Conservation Institute, 2021), and many more are needed to reach the 30% ocean protection target set by the IUCN for 2030.

Many MPAs are created for fisheries' management (Roberts et al. 2005; Stevenson and Tissot 2013), or even to protect species that are considered threatened, endemic or rare (Gilman et al. 2011). But the use of these areas for the conservation of multiple species, such as marine top-predators (Hooker and Gerber 2004; Hooker et al. 2011), also provides protection to associated species and to the overall ecosystem (Hooker and Gerber 2004). Thus, the decline of these marine top predators may cause cascading effects on lower trophic levels of coastal or open waters, with negative effects such as the spread of disease, carbon sequestration, among others (Scheffer et al. 2005; Estes et al. 2011).

Among the marine top predators, the use of seabird at-sea distribution as a primary source of information for designing MPAs has increased in recent years (Lascelles et al. 2012; Le Corre et al. 2012; Dias et al. 2017; Krüger et al. 2017; Beal et al. 2021; Davies et al. 2021a, b), providing also important knowledge on their distribution, abundance, breeding biology and behaviour (Furness 1982). Seabirds have high longevity (20-60 years), delayed maturity (up to 10 years), small clutch size, of which the majority only lays one egg per year and have long periods of chick rearing (up to 6 months) (Schreiber and Burger 2001). They are also very conspicuous animals, and for all these reasons, many studies have considered them as sentinel species of the marine environment, and any changes they may suffer in terms of numbers, breeding success or health, indicates marine environmental issues directly related to human stressors, such as pollution or overfishing (Furness and Camphuysen 1997) but also related to climate and ecosystem changes (Hazen et al. 2019; Sydeman et al. 2021a; Paiva 2022). Other taxa may also be related to the presence of seabirds, for instance by sharing the same prey and/ or habitats, further recognizing seabirds as umbrella species (Bugoni et al. 2008a; Catry et al. 2009).

The presence and role of seabirds as bio-indicator species, might not only identify “hotspots” of biodiversity and productivity in marine areas (Karpouzi et al. 2007), but also, marine ecological problems and environmental changes in the oceans (Weimerskirch et al. 2003; Hazen et al. 2019), as well as changes in prey stocks (Barrett and Krasnov 1996), making them suitable species for MPA design and implementation (Lascelles et al. 2012; Ludynia et al. 2012). Nevertheless, long-distance travelling and multiple-ecosystem reliance are challenging attributes when it comes to effectively protecting ‘static’ MPAs, especially when pelagic species cross jurisdiction boundaries (Block et al. 2011; De Santo et al. 2019; Dunn et al. 2019). Nonetheless, site fidelity has been exhibited by many species and populations regardless of their foraging movements (Baylis et al. 2015; Wakefield et al. 2015; Patrick and Weimerskirch 2017; Wilkinson et al. 2020), thus validating the use of multiple seabird taxa for the identification of candidate Large Pelagic Marine Protected Areas (LMPA), inside national waters (Lubchenco and Grorud-Colvert 2015) or at "high seas" in Areas Beyond National Jurisdiction (ABNJ) (Lubchenco and Grorud-Colvert 2015; Brooks et al. 2021; Davies et al. 2021a). LMPAs have increased in number over the years since their emergence in 2005, with various sizes, some exceeding 2 million km^2 (Alger 2021; Brooks et al. 2021).

Yet, MPAs have been the object of much criticism by the scientific and environmental community, with growing concerns on whether these areas are indeed created to effectively protect marine biodiversity and achieve sustainable global use of marine resources, or simply to achieve political goals (e.g., Aichi Target 11) (Singleton and Roberts 2014). For instance, the establishment of MPAs in remote areas where fisheries are not a problem, does not mitigate fish stock declines (Leenhardt et al. 2013; Singleton and Roberts 2014; Devillers et al. 2015; Langton et al. 2020); prioritizing no-take areas over fisheries management or effects of climate change does not promote sustainable development (Caveen et al. 2013; Leenhardt et al. 2013); creating "untouchable" MPAs does not take in consideration the needs and rights of local and indigenous communities (De Santo 2013; Singleton and Roberts 2014; Sowman and Sunde 2018).

MPA size is also important, allowing spillover (biomass export) to occur, by transporting egg/larva and adult commercial species to adjacent areas where fisheries are permitted (Roberts et al. 2001; Goñi et al. 2008). Small areas, for example do not effectively protect highly mobile species, introducing the idea of MPAs' networks being the most effective way to protect and sustainably exploit marine resources (Palumbi 2003; Gaines et al. 2010; Singleton and Roberts 2014; Hilborn 2018). As such, it appears intuitive to say that MPA size and species mobility are critical variables for effective MPA function and fishery success if we are to achieve sustainability as well as conservation. According to Cabral et al. (2019), for species with low mobility and low-commercial interest, small to moderately-sized MPAs are sufficient to optimize fisheries and food provision, while maintaining ecosystem integrity and resilience, whilst highly mobile and targeted species might benefit from MPAs that are 50% larger than the total area used for fishing them. It is, however, unwise to say that small MPAs, with open-access and low budgets, cannot be capable of securing ecological and economic benefits, as the use of aspatial policies such as gear restrictions, taxes, licenses restrictions, livelihood programs can be important if some level of enforcement exists, to redirect fishing efforts when necessary (Albers et al. 2021).

Therefore, the biggest challenge is to know how effective these areas are for conservation and sustainable use of resources in the marine realm (Jones and De Santo 2016). According to (Hilborn 2018) no-take areas do not particularly reduce fishing effort, but simply displace it to somewhere else. Additionally, the author argues that the increase of fish abundance outside MPAs will increase only in cases where fishing pressure is very high and fish stocks have been highly affected, thus fisheries management is probably the best way to ensure the decrease of overfishing, bycatch, and habitat damage (Hilborn 2018). Particularly at high seas, MPAs in Europe have been shown not to reduce harvesting when fishing management is dependent on international agreements (Dureuil et al. 2018). On the other hand, well enforced surveillance within EEZs have been suggested as a much more effective way to protect marine resources when compared to large MPAs. Thus, in multizone LMPA, negative impacts on marine food webs were clear inside the MPA and the EEZ, implying a larger effort in terms of management and enforcement for such areas (Dureuil et al. 2018). The same study also suggests that it would be much easier to perform monitorization and surveillance in these areas if Automatic Identification tracking Systems (AIS) were enforced on all industrial fishing vessels. Also, creating MPAs with no restrictions whatsoever when it comes to domestic industrial fisheries is the same as creating "Paper parks" where domestic vessels have the same capacity to generate harm in local fish stocks, food webs and habitats, as foreign vessels (Relano et al. 2021). Clearly, more studies are necessary to evaluate the conservation effectiveness of MPAs, while taking into consideration that effective fishing management, monitorization, surveillance and enforcement seem to be the key to success towards marine conservation and sustainability.

In Cabo Verde, Protected Areas were recognized by the Decree-Law nº3/2003 of February 24, designating a National Network (RNAP), classified in 6 categories. Of the 46 designated areas, 22 are Marine Protected Areas with a total of 1.321 km^2 of marine areas. These include all the major reproductive seabird colonies on the islands, except for Rombos islets, which, despite all the conservation and protection work performed by local NGOs from Fogo and Brava, still does not have a delineated protection area designated or an elaborated management plan to support their effective protection. It has been 26 years since the Cabo Verde government compromised, through the Biodiversity Convention ratified in 1995, to a goal of achieving 10% protection of the national marine territory (12 n.m.), but only 5.8% has been declared since then. Though 44% (8 MPAs) have an approved plan and implementations have been undergoing with or without approvals, the majority is not effectively protected due to many problems, such as the lack of law enforcement, human resources, funding, or effective funding management, etc. Additionally, while these protected areas do exist in Cabo Verde, there is no correspondence between the national categories and the Council of the International Union for Conservation of Nature's (IUCN) Protected Areas, which shows a clear gap in legislation (PNUD 2010). Some of these areas, however, are located inside Key Biodiversity Areas (KBAs) recognized for the islands by the IUCN through applied criteria (11) and thresholds (IUCN 2016). These are sites that contribute significantly to the global persistence of biodiversity, but contrastingly to Protected Areas, they have no legal status and are not managed by any type of governance.

Seabird species breeding in these islands are mostly pelagic species, foraging within the Cabo Verde EEZ or travelling to the coast of Africa to feed during the breeding season (Paiva et al. 2015; Ramos et al. 2016, 2017; Cerveira et al. 2020). Cabo Verde EEZ area is fairly large (804,694 Km^2) with species feeding on pelagic waters to the North, influenced by the productivity of the Canary Current (Peña-Izquierdo et al. 2012b; Almeida et al. 2021); to the East, where many important seamounts occur and the upwelling phenomenon from the African coast stretches long filamented fingers to the islands seasonally (Pelegrí et al. 2005; Monteiro et al. 2008; Arístegui et al. 2009); as well as to the South and West, with other important seamounts and ocean features (Monteiro et al. 2008; Benchimol et al. 2009a). Since the MPAs implemented here are very small and almost exclusively coastal, the only seabirds that might benefit from them spatially would be species with a marked coastal foraging behaviour, such as the brown booby (*Sula leucogaster*). However, even rather coastal species might move outside the boundaries of these MPAs (Almeida et al. 2021) and their core foraging grounds may be under stress if fishing activities are high there. Therefore, we believe that the identification of larger and pelagic MPAs in Cabo Verde might be crucial for the conservation of its rich and endemic marine biodiversity (Freitas 2014; Rocha et al. 2015; Semedo et al. 2020). Considering that Cabo Verde relies greatly on the ocean for food resources and employment (FAO 2018), it is also important to improve surveillance and enforcement in this area, and promote governance to local communities to manage their own resources to achieve sustainable use.

In this study, we identified core foraging areas for each seabird population/species and described important seabird hotspots for the Cabo Verde Islands while evaluating potential stress effects exerted by artisanal, semi-industrial and industrial fisheries in the region. Overall, this information contributed to test the protection efficiency conferred to seabirds by the current MPAs and KBAs around the Cabo Verde EEZ. Additionally, we evaluated the suitability of a proposed LMPA for the Eastern side of the islands, concerning seabirds and fisheries distribution. To do this, we used seven years' worth of seabird tracking data (2013-2019) collected during fieldwork in the main breeding colonies and islands of the Cabo Verde archipelago. This tracking data includes information from the eight seabird species breeding in Cabo Verde (Cape Verde shearwaters *Calonectris edwardsii*, brown boobies *Sula leucogaster*, red-billed tropicbird *Phaethon aethereus*, Bulwer´s petrel *Bulweria bulwerii*, Cape Verde little shearwater *Puffinus lherminieri boydi,* Cape Verde petrel *Pterodroma feae,* white-faced storm petrel *Pelagodroma marina eadesorum;* Cape Verde storm petrel *Hydrobates jabejabe*), and one non-breeding species (red-footed booby *Sula sula*). Contemporaneous information on the at-sea distribution and effort of industrial, semi-industrial and artisanal fisheries was also gathered as one of the main Human-related sources of stress imposed on the foraging seabirds, either through competition for food or bycatch.

5.2. Methods

5.2.1. Tracking data: deployment and processing

Nine seabird species from 12 breeding locations were tracked during their incubation and chick provisioning periods and one species during non-breeding period, during the last 7 years (2013 – 2019), totalizing 1239 individuals and 3682 foraging excursions (see Table S5.1 and Figs. S5.1 – S5.8 for further details). Birds were tracked either with CatLog2 devices (Perthold Engineering; http://www.mr-lee.com/science.htm) for bigger species (Cape Verde shearwaters, red-billed tropicbird, brown and red-footed boobies) or with nanoFix mini-GPS (Pathtrack Ltd; https://www.pathtrack.co.uk/products/product-range.html) for smaller species (Cape Verde petrel, Cape Verde storm-petrel, Cape Verde little shearwater, Bulwer's petrel and white-faced storm petrel). Devices were attached to the bird's back feathers using TESA tape model 1640 and the overall process did not take more than 10 minutes (see Table S5.1 for further details). Prior to further analysis, all seabird tracking data was resampled to 10-min intervals, to homogenize tracking data periodicity among study species, using the *track_resample* function of the *amt* package (Signer et al. 2019).

To define individual behavioural modes from movement trajectories of foraging trips we used the *EMbC* (Expectation Maximisation binary Clustering) R package (Garriga et al. 2016). Four behaviours are assigned to each location by the *EMbC* algorithm: high velocity/low turning angle (HL) – travelling, high velocity/high turning angle (HH) – extensive foraging, low velocity/low turning angle (LL) – resting and low velocity/high turning angle (LH) – intensive foraging (de Grissac et al. 2017). This technique has been previously used to interpret ecologically meaningful behaviours from movement data in different seabird species (Cerveira et al. 2020; Almeida et al. 2021). All locations except travelling (HL locs) were used to analyse the use of KBAs and MPAs areas of Cabo Verde (see below).

5.2.2. Interannual consistency of area use

To assess the consistency in area use (1) within and (2) between study years by diverse populations of different seabird species, the *kerneloverlap* function and Bhattacharyya's affinity (BA) method of the *adehabitatHR* package (Calenge 2006) was used to compute the overlap between the seabirds' foraging distribution (all at-sea locations except travelling, see previous sub-chapter). We analysed populations that had been tracked in multiple years to compare the distribution of the core foraging areas (50% Kernel UD) of the birds from the same year with the distribution of the core areas in different years with an ANOSIM (analysis of similarity) analysis from the *vegan* package in R (Oksanen et al. 2013). ANOSIM uses a bootstrap randomization procedure (1,000 repetitions) to test for differences between groups (i.e., years). Results vary between -1 (when within-year is more variable than between-years distributions) and 1 (when between-years is more variable than within-year distributions). A value of 0 reveals no difference between and within year distribution.

5.2.3. Level of coverage offered by current KBAs and MPAs within the Cabo Verde EEZ

Shapefiles of current KBAs within the Cabo Verde EEZ were provided by BirdLife International upon request (https://www.keybiodiversityareas.org) and MPA files within the Cabo Verde EEZ were obtained from the Cabo Verde governmental authorities (*INGT – Instituto de Nacional de Gestão do Território*) and from different organizations (e.g., University of Cabo Verde, Lantuna). To quantify the use of current KBAs and MPAs and proposed KBAs, custom build R scripts were built using functions from the *sp* (Bivand et al. 2013) *sf* (Pebesma 2018), *raster* (Hijmans 2021) and *spatialEco* (Evans 2021) R packages.

5.2.4. Identifying important sites for biodiversity – Key Biodiversity Areas (KBAs)

We used the *track2KBA* R package (Beal et al. 2021), based originally on the method to identify Marine Important Bird and Biodiversity Areas (mIBAs) (Lascelles et al. 2016), to delineate areas of importance to local seabird populations from tracking information, and assess how important these locations are for the overall regional biodiversity against standardized criteria (KBA standard; https://www.keybiodiversityareas.org) (IUCN 2016).

The first part of our analysis was to identify individual core areas using the Kernel Density Estimation (KDE), a nonparametric technique more accessible to different users, using animal point locations to calculate the probability of an animal occurring in space, known as the Utilization Distribution (UD). To do this, we used the function *estSpaceUse* to set the smoothing parameter *h* to reflect the resolution of our data and species ecology. Using the *findScale* function, several *h* values are calculated, giving us a wide range of *h* values to be selected as the best representative for our species. Afterwards, we used 50% UD as reflecting track core areas ('UDLev') (Dias et al. 2017, 2018).

The second part of our analysis addressed whether our tracking data is representative of local population distributions (Lascelles et al. 2016). Because it is hardly feasible to track the entire population, only a small part is tracked and thus it is necessary to evaluate the level of representativeness of the sample population to capture the variability that naturally occurs within individuals (Lindberg and Walker 2007). Thus, very small samples are likely to miss the identification of important areas for species/populations with a more variable distribution and habitat preference (Delord et al. 2014). Using the *repAssess* function, the program iteratively selects a subsample of random individual trips, pooling them into a 50% UD, and calculate all out-of-sample tracking located within this area (i.e., 'inclusion rate'). A nonlinear least squares regression is then fitted showing a relationship between the sample size and inclusion rate until it reaches a plateau (horizontal asymptote), indicating the sample size which best represents the population distribution. This means that no matter how many more individuals are added to the sample, the space use of the population will remain the same. The estimated representativeness must be > 80% to confidently say that the sample is representative of the population. Samples with representative values lower than 70% must be treated carefully or eliminated.

Finally, using the *findSite* function we delineated areas substantially used by the sampled population, identifying regions where individual core areas (50% kernel UDs) overlap in each grid cell, multiplied by the representativeness of the sample, giving us an estimate of the proportion of the whole population that uses each grid cell both spatially and temporally. We then identified important areas by aggregating grid cells used by a significant amount of the source population. Small, isolated polygons were removed and wholes within a large polygon (5% smaller than the overall area) were filled. Additionally, we multiplied the population size (when known) by the population estimated to use each grid cell to estimate the predictable number of individuals or species using this site.

When tracking information from a breeding phase (incubation or chick-rearing) of a specific population did not reach the minimum sample size for KBA estimation, data was polled for the overall breeding phase (see Dias et al. 2019 for a similar procedure).

5.2.5. Identification of candidate MPAs off west Africa

To identify priority areas for conservation off west Africa, the proposed KBAs (see Figs. S5.9 – S5.29), obtained through the Track2KBA method (see above), were included in the spatial conservation prioritization algorithm 'Zonation' (Moilanen et al. 2005; Moilanen 2007), which has been used successfully to prioritize conservation efforts in coastal (Oppel et al. 2012) and pelagic (Krüger et al. 2017) regions using the distribution of seabird species. Since species distributions tend to overlap over time and space, it is important to highlight the need to identify areas that maintain high connectivity for a vast array of species. For this purpose, the Zonation algorithm starts by protecting the landscape as a whole, and progressively removes locations (grid cells) of least conservation value, leaving the areas or cells that are more relevant to conservation, with the most important areas remaining last (Moilanen et al., 2005; Leathwick et al., 2008). The method is designed to work with multiple species, which adds weight when justifying the designation of marine reserves (Nur et al. 2011).

We added species' weight to the Zonation exercise based on the IUCN Conservation Status, with endangered species with a higher value: least concern (LC) = 1; near threatened (NT) = 2; vulnerable (VU) = 3; endangered (EN) = 4 and critically endangered (CR) = 5 (Pereira et al., 2018a). Areas of high fishing effort were also included in the analysis as cost layers, because fisheries constitute one of the most impactful Human-related stressors for seabirds (see Chapters 1 and 2). Gridded maps of average annual fishing effort (2013 – 2019) were built following methods described in Chapter 2 to map the distribution of (1) artisanal, (2) semi-industrial and (3) industrial fisheries and included in the Zonation analysis. Zonation outputs should find areas where pelagic reserves should be generated, as well as areas with high impact of stressors, although very productive and ecologically rich, where management measures should be applied (further details on Krüger et al. 2017).

5.3. Results

5.3.1. Interannual consistency of area use

The spatial ecology of all Cabo Verde seabirds varied greatly among data-group combinations (i.e., seabird-colony-breeding phases), with Bulwer's and Cape Verde petrels usually engaging on longer and more distant forays when compared to the rather coastal brown boobies and Cape Verde little shearwaters (see Table S5.1).

Cape Verde shearwaters and brown boobies were the species revealing higher intra and inter annual variability in space use, across populations and different phases of their breeding period. Different populations of red-billed tropicbirds revealed an intermediate level of inter-annual consistency in space use, during different phases of their breeding cycle (see Fig. 5.1). Comparably, lower interannual consistency was a pattern for almost all populations and breeding phases of Bulwer's petrels and Cape Verde – petrels and – little shearwaters. While Cape Verde storm petrels, brown – and red-footed – boobies exhibited higher intra-annual variability in their at-sea area usage (Fig. 5.1).

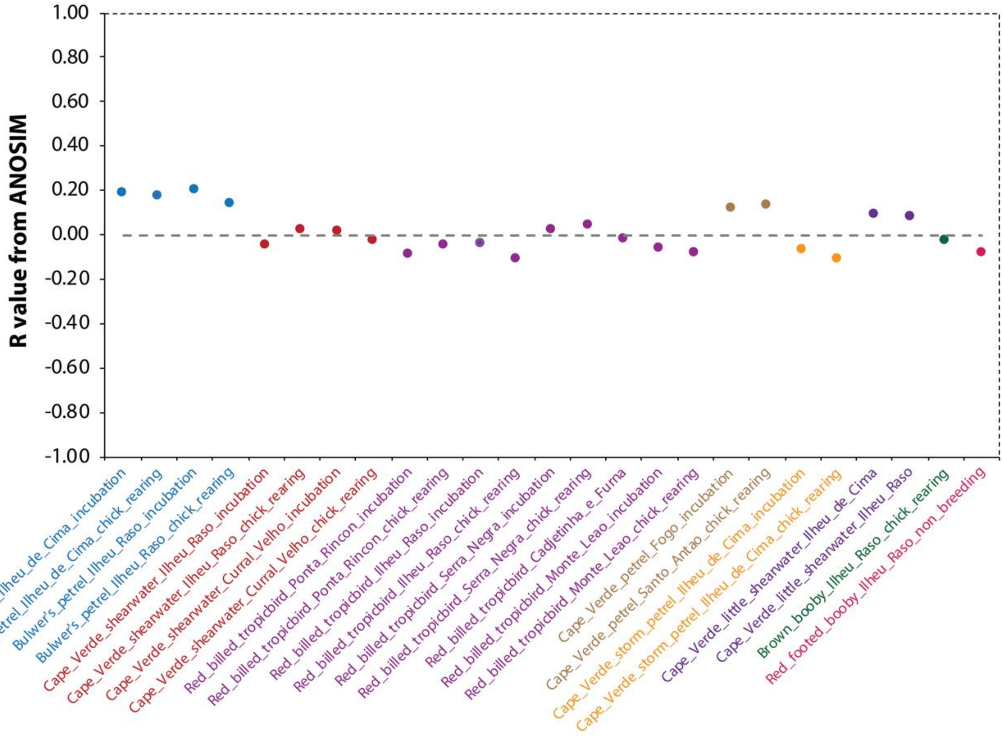

Figure 5.1. Results of the ANOSIM analysis, showing the variability in R values in the datasets analysed for the Bhattacharyya's affinity index. ANOSIM R values can potentially vary between -1 (within-year variability > between-years variability) and 1 (between-years variability > within year-variability). Data-groups of single year tracking or lower annual sample sizes were excluded from these analyses (see Table S5.1)

5.3.2. Level of coverage offered by current MPAs and KBAs within the Cabo Verde EEZ

The protection offered by the current network of MPAs within the Cabo Verde EEZ is generally low for all data-group (i.e., seabird-colony-breeding phases) combinations. The at-sea distribution of brown boobies from Raso Islet had the highest coverage by the MPA network, while Cape Verde – petrels, – storm petrels and – little shearwaters presented the lowest overlap with existent MPAs (Fig. 5.2). The current network of KBAs offered moderate to high protection to the at-sea seabirds' distribution, especially in terms of the % of birds overlapping with KBAs (see Fig. 5.3). Nevertheless, different populations of red-billed tropicbirds showed the lowest coverage by KBAs and brown– red-footed– boobies and the two populations of Cape Verde shearwaters were the species that benefited more from the current network of KBAs (Fig. 5.3).

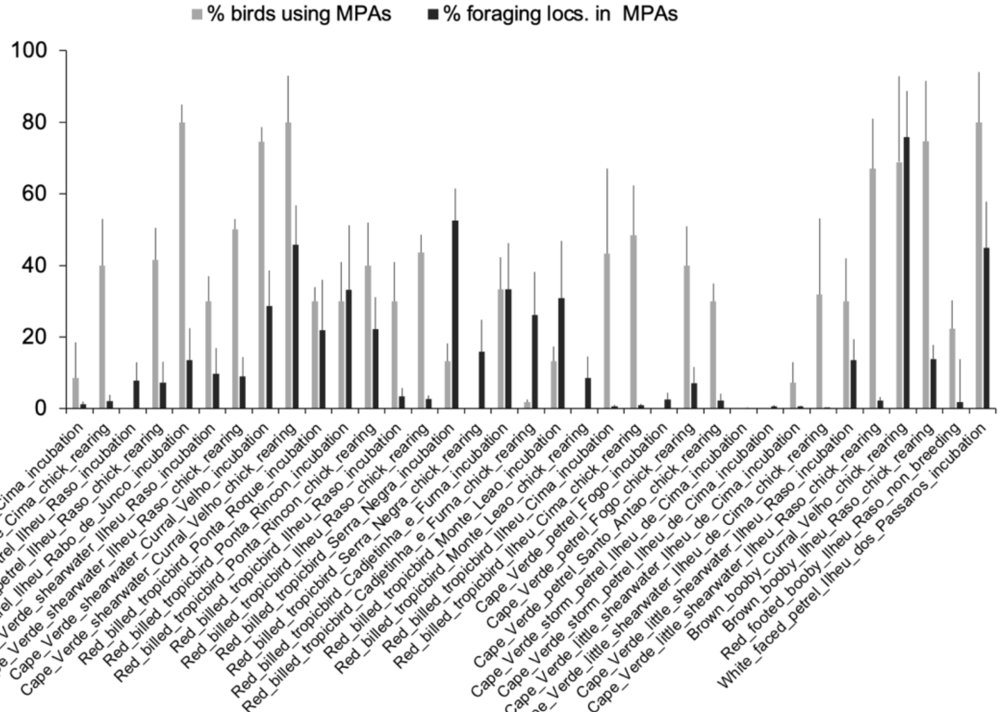

Figure 5.2. Percentage of birds (grey) and foraging locations (black) within the current network of Marine Protected Areas (MPAs).

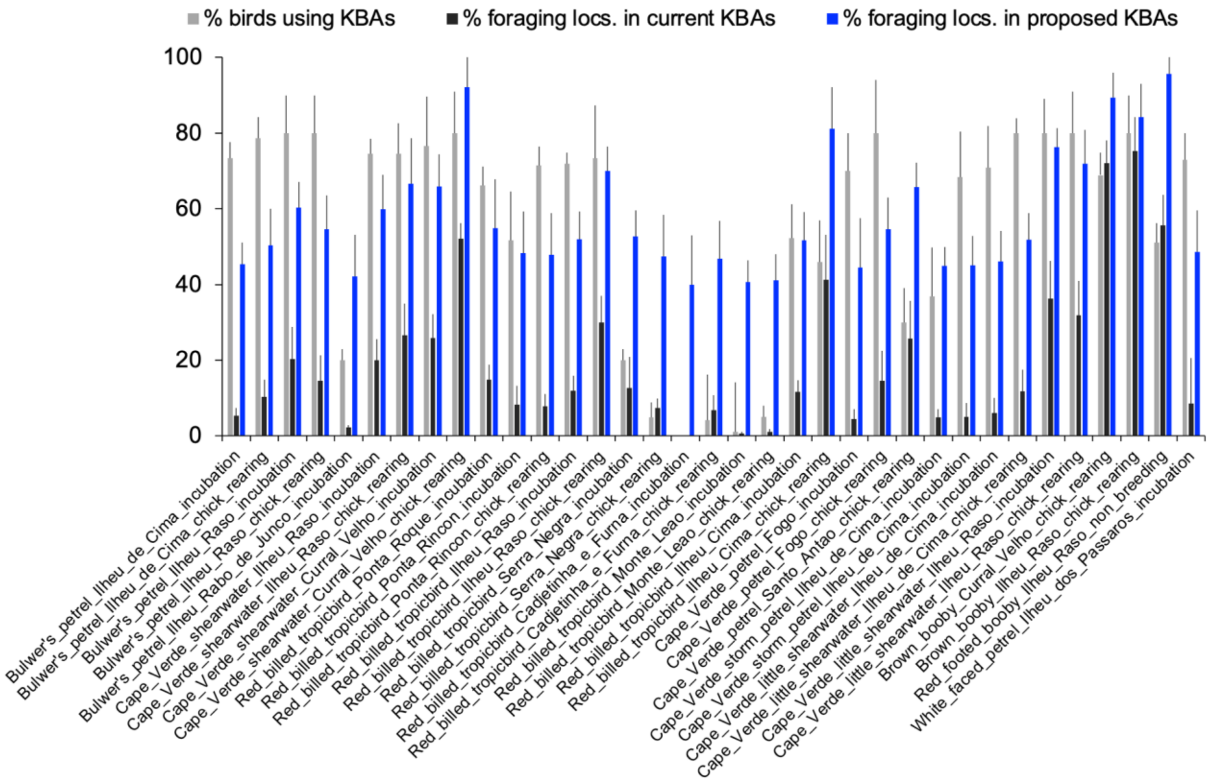

Figure 5.3. Percentage of birds (grey) and foraging locations (black) within the current network of Key Biodiversity Areas (KBA) and percentage of foraging locations covered by the (new) proposed network of KBAs (blue)

5.3.3. *Identification of candidate MPAs off west Africa and protection coverage by proposed KBAs*

Almost all seabird species and populations benefited in their foraging distribution (foraging locations) with the protection coverage offered by proposed/ candidate KBAs, with increases in coverage varying between 9.8 % for brown boobies breeding on Ilhéu Raso and 40.1% for red-billed tropicbirds breeding in Cadjetinha and Furna, during the incubation period. Noticeably, different populations of red-billed tropicbirds were among the taxa benefiting more from the proposed network of KBAs, both during their incubation and chick-rearing phases (Fig. 5.3). The Zonation exercise drew an extension of rather coastal areas and some regions between islands, with an increase in area of 97.2% from the current network of KBAs and 157.2% from MPAs within the Cabo Verde EEZ (see Fig. 5.4).

KBAs estimated from the distribution of Bulwer's petrels showed comparably higher overlaps with industrial fisheries, while those estimated from the foraging distribution of red-billed tropicbirds exhibited higher overlaps with artisanal fisheries. Brown and red-footed boobies' KBAs showed higher overlaps with the areas of higher fishing effort by the artisanal fleet. Cape Verde shearwaters' KBAs exhibited higher overlap with artisanal fisheries, especially during the chick-rearing period, and increased the overlap with semi-industrial and industrial fisheries' during the incubation phase. (Table 5.1).

5.4. Discussion

Here we provide empirical evidence on where the seabird community of Cabo Verde concentrate its core foraging range inside the national Exclusive Economic Zone (EEZ), to inform the design of Marine Protected Areas and evaluate possible fisheries' management actions. These areas act as indicators of biological importance, and if well managed, can lead to effective conservation of the local seabird community and other marine-taxa inhabiting those areas (Lascelles et al. 2016; Krüger et al. 2017; Requena et al. 2020), whilst providing economic gain for local communities (Masud et al. 2017).

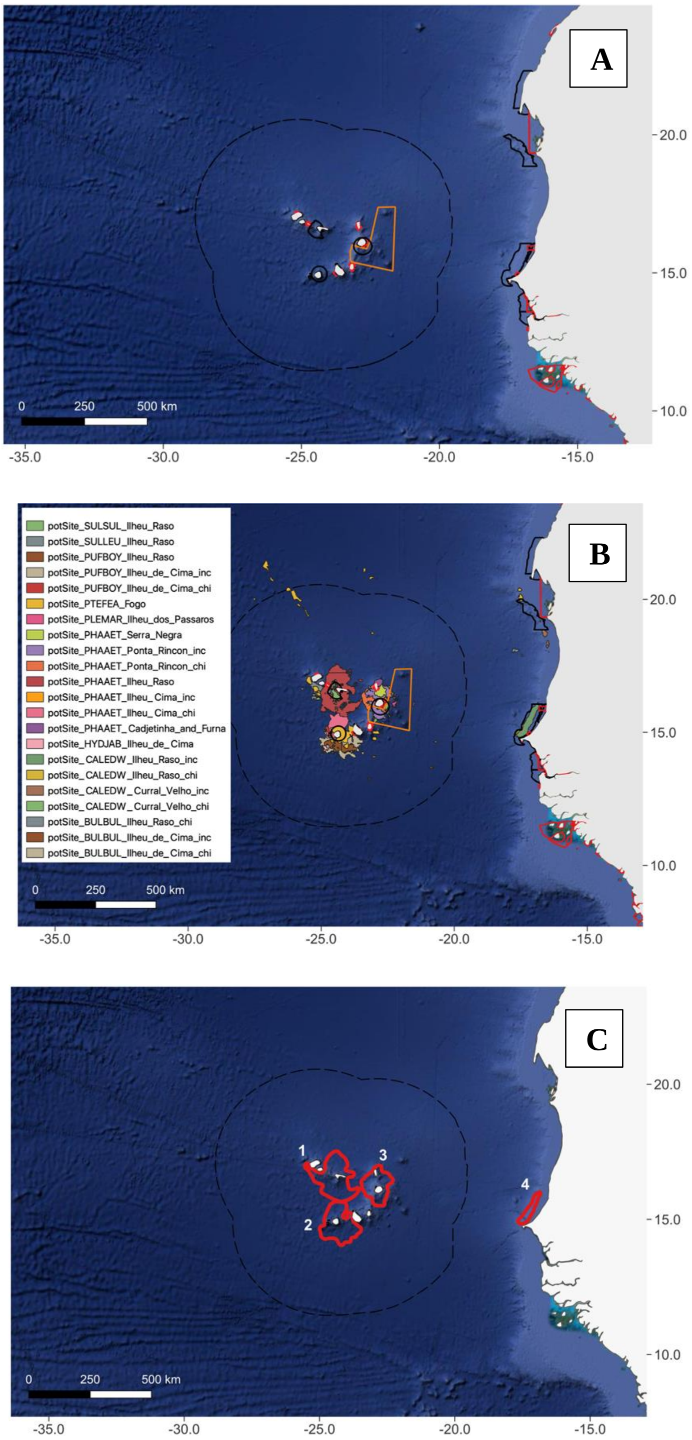

Figure 5.4. (A) Current network of Key Biodiversity Areas (KBAs) and Marine Protected Areas (MPAs) off west Africa; (B) marine areas off west Africa with the highest value for the conservation of nine seabird species breeding/ inhabiting the Cabo Verde archipelago; outputs of the *track2KBA* method (Beal et al. 2021) and (C) Four areas identified as the 10% most important regions (i.e. scoring ≥ 0.9, for a max. of 1) using the systematic conservation-planning 'Zonation' algorithm. Dashed black contour represents the Cabo Verde EEZ, black polygons are current network of Key Biodiversity Areas (https://www.keybiodiversityareas.org), red contours are Marine Protected Areas of Cabo Verde and off West Africa and the orange polygon sets a potential pelagic MPA (Oceania) under designation. Bathymetry in the background

Table 5.1. Spatial overlap of Key Biodiversity Areas (KBAs) with the artisanal, semi-industrial and industrial fishing effort off west Africa.

Species	Main Island	Colony	Breeding phase	% of KBA overlapping with artisanal fisheries	% of KBA overlapping with semi-industrial fisheries	% of KBA overlapping with industrial fisheries
Bulwer's petrel	Fogo	Ilhéu de Cima	incubation	15.8	2.7	31.1
Bulwer's petrel	Fogo	Ilhéu de Cima	chick-rearing	10.7	1.8	33.4
Bulwer's petrel	S. Nicolau	Raso	incubation	11.9	1.7	25.7
Bulwer's petrel	S. Nicolau	Raso	chick-rearing	10.9	2.3	29.6
Cape Verde shearwater	S. Nicolau	Raso	incubation	21.2	28.7	41.7
Cape Verde shearwater	S. Nicolau	Raso	chick-rearing	46.9	22.7	10.9
Cape Verde shearwater	Boavista	Curral Velho	incubation	19.7	21.8	38.6
Cape Verde shearwater	Boavista	Curral Velho	chick-rearing	41.8	24.0	11.5
Red-billed tropicbird	Boavista	Ponta Rincon	incubation	38.7	11.4	6.8
Red-billed tropicbird	Boavista	Ponta Rincon	chick-rearing	33.6	15.7	11.4
Red-billed tropicbird	S. Nicolau	Ilhéu Raso	breeding	31.0	18.6	19.8
Red-billed tropicbird	Sal	Serra Negra	breeding	24.8	16.9	11.5
Red-billed tropicbird	Sal	Cadjetinha e Furna	breeding	26.9	10.0	8.4
Cape Verde petrel	Fogo	Fogo	breeding	14.3	26.7	10.7
Cape Verde storm petrel	Fogo	Ilhéu de Cima	breeding	18.9	2.4	2.9

Cape Verde little shearwater	Fogo	Ilhéu de Cima	incubation	26.7	18.7	3.1
Cape Verde little shearwater	Fogo	Ilhéu de Cima	chick-rearing	22.4	11.6	5.4
Cape Verde little shearwater	S. Nicolau	Ilhéu Raso	breeding	29.7	8.7	6.9
Brown boobies	S. Nicolau	Ilhéu Raso	breeding	51.9	39.6	8.1
red-footed boobies	S. Nicolau	Ilhéu Raso	non-breeding	48.7	33.7	10.7
white-faced storm petrel	Boavista	Ilhéu dos Pássaro	breeding	31.8	25.7	6.7

The moderate to high intra- and inter-annual variability in the at-sea distribution of the Cabo Verde seabird community poses a challenge when delineating areas for applied conservation, as many factors must be taken into consideration (species, colony, and breeding phase), and are possibly influenced by interannual variation in oceanographic conditions (Ballance et al. 2006). Additionally, we must also consider the high distribution variability between species, belonging to diverse ecological guilds, and ranging from coastal to long distance travellers.

Our results show a clear lack of protection efficiency by the existing MPAs inside the archipelago. Apart from the coastal brown booby, whose foraging range may benefit to some extent from these areas (Almeida et al. 2021), the foraging ranges of most seabird species/populations/ breeding phases fell way beyond these boundaries, especially for Cape Verde petrel, storm-petrel, and little shearwaters.

Additionally, although brown, red-footed boobies and Cape Verde shearwaters foraging ranges overlapped more with KBAs, these areas are not supported by legislation and thus not managed by any kind of governance. Thus, proposed KBAs in this study dictate a large area increase for current MPAs (157.2%) and KBAs (97.2 %) for effective conservation. Other studies have also shown the unsuitability of existing protected areas for the conservation of specific species and justified the expansion or additional key area designation (Fuentes et al. 2019; Heerah et al. 2019; Giménez et al. 2021). Recent public list of measures and estimated needs of finance for the implementation of the 2020-2030 target (Paris Agreement and United Nations Framework Convention on Climate Change) pinpoints the expansion of Marine Protected Areas in Cabo Verde as one of the adaptations needed to achieve this goal (Resolution nº 107/2021).

Four important areas stand out, each containing at least one existing KBA and only one overlapping, to some extent, with the proposed eastern Pelagic Marine Protect Area. Two areas are located at the Barlavento group, one to the west another to the east. The first area comprises the south-western parts of Santo Antão, São Vicente and surrounds the marine reserve of Desertas and São Nicolau Island, stretching southward and northward. Here we find two important islets which are breeding sites for several and numerous seabird populations (Semedo et al. 2020). The Raso Islet, located in the Desertas marine reserve, holds colonies of 7 species of seabirds, of which 6 are breeders and comprising perhaps the largest colony of Cape Verde shearwaters (Almeida 2014; Semedo et al. 2020). Adjacent to this area, a second islet (the Branco Islet, not included in our sampled population) contains important colonies of 5 of the species found at Raso Islet (Hazevoet 2015). This area is also characterized by high vessel traffic, due to the presence of important fishing and cargo vessel ports located in the island of São Vicente (González et al. 2020).

The second area surrounds the islands of Sal and Boavista, where other important colonies occur, specifically red-billed tropicbird, brown boobies, and white-faced storm petrels (Semedo et al. 2020). The island of Sal and Boavista contains many protected areas, and Sal holds today the largest known colony of red-billed tropicbird (Semedo et al. 2020). However, red-billed tropicbirds and brown boobies suffer from habitat loss, predation of invasive species and likely human harvesting (Semedo et al. 2020). Both islands are located in the vicinity of very important bathymetric features, congregators of marine species diversity and productivity (Monteiro et al. 2008; Mangas et al. 2015; Graham et al. 2017; Wenzel et al. 2020), and because they are the most important islands for tourism in the archipelago (INE 2020) they are frequently explored by fishing vessels and game fishing vessels (Freitas et al. 2018).

The third important area is located around the westward islands of Sotavento surrounding the islands of Brava, Fogo and west of Santiago. Here, another important group of islets occur (the Rombos islets), which hold important breeding colonies of 5 species (Semedo et al. 2020). The island of Fogo holds an important population Cape Verde petrel, breeding mainly at high altitude in Chã das Caldeiras (Militão et al. 2017) and foraging in marine areas surrounding the island. Additionally, the newly designated marine protected area of Baía do Inferno in Santiago (Decree-regulation nº 3/2021), is now being surveyed to characterize the seabird community (personal observations). This area holds important breeding populations of brown boobies and red-billed tropicbirds (Semedo et al. 2020) and was recently reported the first breeding attempt recorded by red-footed boobies in the archipelago (Loureiro et al. 2021). Overall, this area contains breeding colonies of all seabird species occuring in Cabo Verde (Teresa Militão *Pers. Comm.*).

The fourth area is located on the west African coast, close to Senegal. This area is highly used by species from the African coast, Macaronesia islands and wintering seabirds from the northern hemisphere (Wynn and Knefelkamp 2004; Camphuysen and Van Der Meer 2005b; Gremillet et al. 2015; Paiva et al. 2015; Grecian et al. 2016; Monteiro 2019), attracted by the marine productivity driven by the Canary Current and coastal upwelling (Laurans et al. 2004; Camphuysen and Van Der Meer 2005b; Worm et al. 2009), and the scenario for intense year-round industrial fishing activities (Agnew et al. 2009; Belhabib et al. 2018; Li et al. 2021).

Key marine areas for seabird species fell well within the island's coastal surroundings, and very few locations were considered important in the pelagic marine

EEZ. This result was also observed for other archipelagos in the south Atlantic (Falkland and Tristan da Cunha islands) (Augé et al. 2018b; Requena et al. 2020) and Australian waters (Kerguelen islands) (Thiers et al. 2017), with core areas of species distributions falling within the countries EEZ. Similarly, this was mostly due to the strong influence of the island breeding colonies location on the species distribution. While breeding, many seabird species are central place foragers, commuting between the colony and the foraging patches (Paiva et al. 2010b, 2015). Pelagic, long travelling species use areas closer to the colonies as commuting corridors when travelling from the colonies to foraging areas, although they might feed opportunistically along the travelling path (Weimerskirch et al. 2007). Movement corridors have been proposed by Hooker et al. (2011) as overlooked potentially important areas for seabird protection. However, in the case of wide-ranging species, like the Cape Verde shearwaters (Paiva et al. 2015), cross-nation marine spatial planning is imperative to provide the necessary protection (Augé et al. 2018a) during their long excursions in the incubation period and less frequently during chick-rearing phase (Paiva et al. 2015; Cerveira et al. 2020). Coastal species, on the other hand, mostly use their colony surroundings as foraging areas (Almeida et al. 2021) and will thus benefit from national protection legislation defined by the Cabo Verde government authorities.

Moreover, species main foraging areas have been associated with seamounts diversity hotspots (Lascelles et al. 2016; Requena et al. 2020). Cabo Verde has a considerable amount of seamounts (Mangas et al. 2015) and although most of them were not included in the final designated key areas, the seamount located south of Brava appeared to be frequently used by seabird populations of the southern Islands, as well as the João Valente fishing bank located at the eastward island's platform, suggesting some degree of association with marine bathymetric features. This is also observed by species travelling to the coast of Africa to the highly productive continental shelf and slope (Cerveira et al. 2020).

Concerning temporal use, the Cabo Verde seabird community presents different breeding strategies among species and colonies, suggesting temporal variability in foraging distributions. Red-billed tropicbirds and brown boobies, for instance, breed all year round (Hazevoet 2015), and although the tropicbirds perform longer and wider trips to pelagic areas inside the EEZ, designated KBA were mainly coastal and between islands, similar to the KBAs highlighted for brown boobies. This suggests that these species could benefit from MPAs that are not very extensive and still very much coastal around the main island breeding colonies.

Other species in this study should benefit from seasonal MPAs with protection during the breeding period which mostly occurs from January to April (winter breeders) and May-December (summer breeders) depending on the population (Semedo 2020). Krüger et al. (2017) found that the use of seasonal protected areas would cost less to human activities, ensuring at the same time high conservation value by simply decreasing fishing densities by half. Species breeding during the first part of the year include year-round breeders (brown boobies, red-billed tropicbirds), smaller species with possibly two breeding populations (Cape Verde storm petrel), and winter breeders (white-faced storm petrel, Cape Verde petrel and little shearwater) (Semedo 2020).

In terms of fishing pressure on key areas, industrial vessels overlapped greatly with Bulwer´s petrel and Cape Verde shearwater during incubation. For Bulwer´s petrels, fishing pressure may not cause a significant impact because this species feeds mainly during the night, targeting bioluminescent prey migrating to the surface during the night (Zonfrillo 1986; Neves et al. 2011). This type of fish is not usually targeted by fisheries and vessel impacts might be related to artificial light at night, disorienting birds which might collide against vessels (Glass and Ryan 2013; Ryan et al. 2021), causing injuries, possibly due to their phototrophic feeding behaviour. Procellariiformes, such as petrels and shearwaters, have been identified as the most attracted species to artificial lights, especially fledglings (Le Corre et al. 2002; Troy et al. 2011; Rodríguez et al. 2014, 2015). In such cases, simple mitigation measures during the fledging period, such as reduced lighting or avoiding fishing in the proximity of seabird colonies, and the use of shielded light to illuminate smaller areas should suffice to avoid these events, without compromising vessel crew safety (Lukies et al. 2019).

Cape Verde shearwaters overlapped with the distribution of industrial vessels, and require protection over the African continental shelf, which demands actions between countries, particularly between Cabo Verde and Senegal during the incubation period. During chick-rearing, their key foraging areas are included in two of the designated areas, overlapping with artisanal vessels inside the EEZ and industrial vessels beyond its boundaries. For these and other species overlapping with fishing vessels, mitigation measures should be important to decrease bycatch risk, such as the use of mini-hookpods and tori-lines (Sullivan et al. 2018; Goad et al. 2019; Jiménez et al. 2020a; Gilman et al. 2021). Particularly for artisanal fisheries, blue-dyed bait might potentially be a cost-effective mitigatory effect, though trials with the Cabo Verde fishing fleet are advisable, since its efficacy is dependent on the bait used and fishing context (Cocking et al. 2008).

Breeding species from Brava, Rombos, Fogo and Santiago should benefit from protected areas in the southern waters of these islands, where fishing activity is probably less marked and overlap with fisheries was generally low.

In legal terms, this work shows that Implementation of an effective legislation is still needed is needed to designate MPAs to effectively protect and manage seabird populations breeding in the Cape Verde archipelago. It is important that local authorities regard that this as a priority to ensure that marine resources are used sustainably and will be available for future generations.

Chapter 6

GENERAL DISCUSSION

6.1. Overview of the thesis and main results

From the findings of this work, I highlight the following:

(1) According to fishermen's' observations Cabo Verde shearwaters have the highest risk of bycatch in Cabo Verde, associated with artisanal handlines, followed closely by Brown boobies and Red-billed tropicbirds. Additionally, while fish-landing changes occurred due to variables affecting the marine food web, shearwater chick development was also correlated with changes in fish-landings influenced by prey availability in the ocean (Chapter 1); (2) confirming fishermen's reports, overlap and foraging response-changes to vessel proximity was higher for Cape Verde shearwaters often attending artisanal boats using handlines, while brown boobies attended more industrial vessels and red-billed tropicbirds and red-footed boobies had low response to vessels (Chapter 2); (3) Boobies exhibit plasticity in foraging ecology, adapting to different circumstances of environmental conditions and competitors, while breeding stage and presence of marine physical features play an important role in their foraging decisions (Chapter 3); (4) The current network of MPAs does not cover a high percentage of the foraging distribution of the Cabo Verde seabird community. This scenario would shift to a comparably higher protection if the KBAs emanating from this study contribute to update the current network of MPAs. More insight on each chapter is discussed below.

6.2. Chapter 2

This chapter gives us good insight on the fishing sector of the Cabo Verde islands and renewed certainty when it comes to identifying indicator-species of marine and fishing changes around this area. The connection between fish-landings, environmental features related to marine productivity and prey availability, to changes observed in chick development, ensures the potential of the Cape Verde shearwater being a good indicator of marine and fishing changes around this area and it´s sensitivity to overfishing.

Fishermen have life-long experience and ancestral Local Ecological Knowledge (LEK) of the marine environment and its species (Silvano and Valbo-Jørgensen 2008; Silvano and Begossi 2012). By going directly to the source, we not only have a better picture of what is happening at sea, but we can also have a better understanding of the struggles that these men face during fishing in terms of monetary losses, especially when competing with large-scale vessels (Leroy et al. 2016) and the impact of bait-loss by seabirds (Sánchez and Belda 2003; Kumar et al. 2016). Yet, even though fishermen's interviews continues to be used and is a common method for bycatch assessment (Moore et al. 2010; Oliveira et al. 2015; Lopes et al. 2016; Montrond 2020), the real bycatch scenario can only be quantified in addition with direct visual methods, such as onboard observers (Jiménez et al. 2020a; Da Rocha et al. 2021) and electronic monitoring (EM) videos (Glemarec et al. 2020). Because fishermen, are sometimes reluctant to answer questions honestly, in fear of losing fishing spots or infracting regulations (Torres 2018; Montrond 2020), unwanted catches can be somewhat underestimated. On board observers or EMs would give us direct observation access of bycaught species, near-vessel interactions and the attitude of fishermen towards bycaught species (Neves et al. 2006; Gianuca et al. 2020). Additionally bird-borne video cameras would give us clear certainty on whether species are indeed attracted to vessels or simply overlap spatially and temporally due to the attraction of other visual cues such as seabird flocks or subsurface predators (Tremblay et al. 2014). Taking into consideration off record talks with fishermen, and existing video recordings showing the amount of Cape

Verde shearwaters around operating fishing vessels it might be wise to use these methods in the future.

Concerning bycatch, many studies have focussed on finding solutions to mitigate such events. The design of protected cases for hooks as safety measures for seabirds (mini hookpods), was trialled in New Zealand allowing baited hooks to be sunk to certain depths that are safe for diving seabirds, maintaining target catch rates and reducing seabird bycatch (Goad et al. 2019). Other methods involve the use of scaring devices such as tori-lines (Jiménez et al. 2020b; Gilman et al. 2021), and bird-scaring kites keeping birds away from baited gear (Oliveira et al. 2020). Integrated weight longlines have also been adopted in demersal longlines (Dietrich et al. 2008), or by switching fisheries to operate during the night or at midday have also been shown to decrease bycatch by avoiding hours of high seabird activity (sunrise and sunset) (Sánchez and Belda 2003). A combination of some of these measures could also have a better effectiveness on seabird bycatch (Jiménez et al. 2020b). Many have been the developed tools and many more are still in development and should be adopted by vessels around this area.

Species and ecosystems have also been shown to benefit from the absence of fishing. Specific fishing closures in areas of primary foraging range of African penguins showed increased breeding productivity (Sydeman et al. 2021c). Studies based on simulations showed that choosing lightly fished areas for closure in addition with reduction of effort should reduce fishing impacts on benthic communities (Hiddink et al. 2006). Fishing closures can also be implemented periodically to allow ecosystem recovery while sustaining livelihoods. In the Indo-Pacific ocean, periodically-harvested closures are used to reduce fishing pressure, however, studies show that frequent and long duration openings, when paired with intense and destructive exploitation, can cause unsustainable harvesting (Cohen et al. 2013). Moreover, periodic fishing closures in the Bay of Bengal, Blangladesh, caused significant distress over fishing communities with significant loss of income and food security for fishing crew members, suggesting that the community involvement in decision-making of fishery changes is necessary (Islam et al. 2021). However, these measures can also benefit domestic fisheries with the potential to decrease foreign industrial fisheries' overexploitation of resources. This off course can never be possible without ensuring monitorization and surveillance to enforce legislation and keep illegal practices from happening.

6.3. Chapter 3

Results from this chapter are part of a continued research from the first chapter, assessing identified species with the highest risk of bycatch, interacting with tracked vessels. Using Cape Verde shearwaters, boobies, and red-billed tropicbirds we observed high overlap of Cape Verde shearwater related to artisanal vessels using handlines. Studies have shown that seabird overlap with fisheries can vary among seabird populations and species. Studies in temperate regions show low overlap related to high availability of food, with congeners preferring to forage instead of looking for easy meals (Pereira et al. 2021), while other areas with high fishing pressure and food competition, showed that similar species' population attend fishing vessels (Laneri et al. 2010; Louzao et al. 2011; Soriano-Redondo et al. 2016; Carle et al. 2019; Reyes-González et al. 2020) and others don´t (Cianchetti-Benedetti et al. 2018). This suggests an overlap variability among seabird populations. In the case of this study, in a tropical marine environment where resources are patchily distributed (Longhrust and Pauly 1987), species could search for easier meals near vessels specially when constrained by breeding duties (Weimerskirch 2007).

Looking ahead, interaction studies should be performed at much finer scales, addressing maximum vessel encounter distance (Soriano-Redondo et al. 2016; Fox et al. 2021), based of visual recruitment (Haney et al. 1992), and minimum vessel association distance (Collet et al. 2015; Orben et al. 2021) in order to clearly differentiate between overlap and interactions (Torres 2018). Specific tracking tools, such as bird-borne video cameras (Tremblay et al. 2014) and GPS radar detector on seabirds should be important tools for verifying the extent of seabird-vessel overlap and identify interactions (Grémillet et al. 2019), while contouring AIS signal turn-offs by vessels and detecting IUU fishing activities (Weimerskirch et al. 2018). These would be important results to take in consideration when designing area's management plans and for specific-species conservation planning.

6.4. Chapter 4

This chapter delivers important information on conservation planning at the species level. When analysing species tracking data, we have close view on species ecology and phenology, which is imperative in informing MPA designers, stakeholders and managers (Hays et al. 2019; Augé et al. 2018; Requena et al. 2020). Knowledge on species foraging habitat preference and site-fidelity will aid on the identification of important habitats that should be included inside MPAs (Wilkinson et al. 2020). The representation and replication of different habitats is key to successfully insure the survival of the ecosystem and offer connectivity for highly mobile species (Watts et al. 2017). Inter-specific differences in at-sea distribution can address what species and what proportion of the population is being protected by existing MPAs and inform new MPA creation or expansion if the current one is not effectively protecting a significant proportion of the population. It should also inform species-specific vulnerability to anthropogenic activities (Soanes et al. 2016).

However, our results were solely related to the chick rearing phase, as the capture of boobies while incubating proved to be too risky for the egg, taking into consideration the catching method (e.g., pole-net) and the species aggressiveness. Tracking of birds during the incubating phase would probably give us a wider view of Brown boobies' home ranges since seabirds are known to forage farther during this period, when they are not yet constrained to feeding the chicks (Paiva et al. 2015; Cerveira et al. 2020).

Future studies should also make an effort on securing an even sample of females and males to better assess sexual segregation, as parental roles can also be important in spatial planning, knowing that sexes will sometimes have different strategies at sea, different space use and diet (Weimerskirch et al. 2009b; Miller et al. 2018). Species with wide distribution and habitat preference can also lead to area identification bias if population samples are too small (Delord et al. 2014).

Age and non-breeding stages, are also important matters to ponder on when planning (Mendez et al. 2017b; Lerma et al. 2020a), as species may benefit from seasonal MPAs or fishing closures during their breeding period, or benefit from MPA habitat connectivity for migration purposes.

Finer-scale studies of interactions of these species with fisheries should be imperative to address bycatch risk considering their frequent attendance to boats and boldness toward anthropogenic activities at sea (Tasker et al. 2000; López-Ortiz 2009; Gianuca et al. 2019). Methods such as GPS radar to detect vessel radar, should be an important tool for addressing illegal fishing (Weimerskirch et al. 2018) and bird-borne cameras should better give us and understanding of these interactions (Tremblay et al. 2014).

6.5. Chapter 5

Completing the main objective of identifying areas that are suitable for marine protection inside the Cabo Verde EEZ, this chapter gives gross information on species distribution hotspots (Ronconi et al. 2012) as well as the overall domestic and foreign fleet operating here.

Existing MPAs and KBAs were proven to be insufficient to cover a significant proportion of the seabird community, demanding substantial area increase to effectively have the potential to achieve species protection.

Interannual consistency variability observed between species, suggest seasonal variation in species distributions (Krüger et al. 2017; Thiebot et al. 2019), related to the species needs, colonies and breeding periods. This fact is indeed challenging for marine preservation and indicates that the best way to achieve conservation goals is to establish seasonal and dynamic MPAs, that take in consideration the best timing and associated key foraging habitats.

Designated key areas were mainly coastal, around and between islands, giving us a rather costal and less extensive area to work with, compared to the overall size of the Cabo Verde EEZ (734.000 km^2) This can have its own advantages and disadvantages for future management, as closer coastal areas are much easier to handle if all the necessary attributes of effective management and protection are met (Maxwell et al. 2020), while coastal areas require stronger fishing management but should always aim to find solutions that cause less impacts on sustenance anthropogenic activities (Krüger et al. 2017). To achieve this, partially protected areas have been implemented, however, although these areas are easier to implement, studies have shown that partially-protected areas exhibit significant increase in artisanal and recreational fisheries compared to fully protected MPAs and areas that are not protected (Zupan et al. 2018a). Knowing this, caution should be exercised when creating "partial MPAs", ensuring that effective regulations are accurately placed and enforced (Zupan et al. 2018a). Having a fully protected area nearby (no extracting anthropogenic activities) could also aid species conservation (Zupan et al. 2018b; Claudet et al. 2020). On the other hand Naidoo et al. (2019) showed that communities near protected areas and taking advantage of their resources for ecotourist, expressed lower degree of poverty, which is a goal that should be aimed by the Cabo Verde Marine protected areas, as most of the country depends on the sea for food and employment (Silva 2009).

Three of the designated areas only require national management and are associated with colony location. Some bathymetric features were important for the seabird community and should be included inside protect areas (Lascelles et al. 2016; Requena et al. 2020). The fourth area designated located in the coast of Africa was designated specifically to Cape Verde shearwaters, and agreements between involved countries (Augé et al. 2018a) should be imperative to protect the species during incubation period and alternating long trips during chick rearing (Paiva et al. 2015; Cerveira et al. 2020).

Most seabird-fisheries overlaps were associated with artisanal vessels, and we believe that mitigation measures in artisanal gear should be an important measure for bycatch evasion (Sullivan et al. 2018; Goad et al. 2019; Jiménez et al. 2020a; Gilman et al. 2021).

As most species in this area are not known for interacting with vessels, apart from the three larger birds identified in the second chapter. Other species, interacting with industrial vessels, are mainly nocturnal and to avoid the risk of vessel impact due to artificial light pollution, they would also benefit from simple deck-strike mitigation measures (Lukies et al. 2019), especially during the fledging period (Le Corre et al. 2002; Troy et al. 2011; Rodríguez et al. 2014, 2015).

Future studies should focus on using GPS radars on birds for detecting ship radars (Weimerskirch et al. 2018) to better understand the distribution of foreign vessels, as we feel that the industrial vessel impact here was underestimated due the low number of available vessels provided by the Global Fishing Watch website. Additionally, other species are underrepresented due to the small numbers of tracked birds (e.g., Cape Verde storm petrel, white-faced storm petrel, red-footed boobies), and more effort should be placed into tracking more individuals to better understand their foraging ranges. Incubating brown boobies should also give us a better view of their possibly wider foraging ranges.

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Table S2.1. Document used for fishermen interviews

Dados do entrevistador

Nº do Questionário________ Nome do entrevistador ____

Data __/___/201____ Local ____ Ilha ____________

DADOS GERAIS

1. Dados do entrevistado

NOME:____

Idade: ☐ 18-30 anos ☐ 31-50 anos ☐ >50 anos	Experiência: ☐ <de 2 anos ☐ de 2 a 5 anos ☐ de 6 a 10 anos ☐ > de 10 anos	Posição que ocupa no barco: ☐ Patrão ☐ Marinheiro ☐ Mergulhador ☐ Outra. Especificar: ____________________________

2. Características da embarcação

Potência (cv):________	Número de tripulantes: _____	Comprimento (m): _____

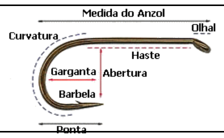
3. Artes de pesca utilizadas

		Variável (marcar com um X as artes utilizadas)			Nº questionário adicional
		Abril-Setembro	Outubro-Março	% anual	
Artesanal	Covos				
	Linha de mão				
	Mergulho de apneia				
	Palangre				
	Rede de arrasto de praia				
	Rede de cerco				
	Rede de emalhar				
	Outra: Qual?__________				
Industrial	Covos				
	Linha/Vara				

	Palangre				
	Rede de cerco				
	Rede de emalhar				
	Outra: Qual?__________				

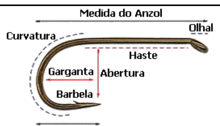
4. Características da arte (Preencher só para as artes de pesca que o pescador utiliza)

Covo	☐ Artesanal ☐ Industrial		
Número de linhas da calada			
Comprimento total da arte (metros)			
Número de covos por linha			
Tamanho (entrada dos covos – em cm)			
Material do covo			
Número de dias de pesca por mês	**Primavera/Verão:** **Outono/Inverno:**		
Isco utilizado Isco 1	Tipo de isco: ______	☐ 0-10 cm ☐ 10-20 cm ☐ > 20 cm	☐ Primavera/Verão ☐ Outono/Inverno
Isco 2	Tipo de isco: ______	☐ 0-10 cm ☐ 10-20 cm ☐ > 20 cm	☐ Primavera/Verão ☐ Outono/Inverno
Isco 3	Tipo de isco: ______	☐ 0-10 cm ☐ 10-20 cm ☐ > 20 cm	☐ Primavera/Verão ☐ Outono/Inverno
Observações:			

Linha de mão/Vara	☐ Artesanal ☐ Industrial		
Nº de linhas/varas da calada			
Comprimento total da arte (em metros)			
Número de anzóis em média			
Tamanho do anzol 	**Comprimento/Medida do anzol:** **Abertura:** **Garganta:** **Tipo:**		
Número de dias de pesca por mês	**Primavera/Verão:** **Outono/Inverno:**		
Isco utilizado Isco 1	Tipo de isco: ______	☐ 0-10 cm ☐ 10-20 cm ☐ > 20 cm	☐ Primavera/Verão ☐ Outono/Inverno
Isco 2	Tipo de isco: ______	☐ 0-10 cm ☐ 10-20 cm ☐ > 20 cm	☐ Primavera/Verão ☐ Outono/Inverno
Isco 3	Tipo de isco: ______	☐ 0-10 cm ☐ 10-20 cm ☐ > 20 cm	☐ Primavera/Verão ☐ Outono/Inverno
Observações:			

Mergulho de apneia	
Número de dias de pesca por mês	**Primavera/Verão:** **Outono/Inverno:**
Espécies alvo	

Observações:

Palangre	☐ Demersal (fundo) ☐ Pelágico (superfície) Usa bóias? Sim ☐ Não ☐		☐ Artesanal ☐ Industrial
Número de linhas de calada			
Comprimento total da arte (metros)			
Número anzóis em médio			
Número de dias de pesca por mês	**Primavera/Verão:** **Outono/Inverno:**		
Tamanho do anzol 	**Comprimento/Medida do anzol:** **Abertura:** **Garganta:** **Tipo:**		
Isco utilizado Isco 1	Tipo de isco: ______	☐ 0-10 cm ☐ 10-20 cm ☐ > 20 cm	☐ Primavera/Verão ☐ Outono/Inverno
Isco 2	Tipo de isco: ______	☐ 0-10 cm ☐ 10-20 cm ☐ > 20 cm	☐ Primavera/Verão ☐ Outono/Inverno
Isco 3	Tipo de isco: ______	☐ 0-10 cm ☐ 10-20 cm ☐ > 20 cm	☐ Primavera/Verão ☐ Outono/Inverno
Observações:			

Rede de arrasto de praia	
Tamanho (luz de la malha (poro) em cm)	
Comprimentos total da arte (em metros)	
Número de dias de pesca por mês	**Primavera/Verão:** **Outono/Inverno:**
Observações:	

☐ Rede de cerco ☐Rede de emalhar	☐ Artesanal ☐ Industrial
Comprimento total da arte (em metros)	
Tamanho (luz da malha (poro))	
Altura da rede	
Observações:	

Outras Descrever os dados que correspondam às outras artes de pesca utilizadas

ACTIVIDADE PESQUEIRA PARA A ARTE DE ____________________

<u>NOTA: esta parte é para preencher para cada tipo de arte de pesca que o pescador utiliza. Imprimir várias cópias desta parte do questionário (perguntas 5-16) para o caso do pescador utilizar mais do que uma arte de pesca</u>

Nº questionário geral relacionado com este questionário adicional: _____
Nº questionário adicional: _____

5. Duração das saídas:

☐ Inferior ou igual a 1 dia
☐ De 2 a 5 dias
☐ Superior a 5 dias. Especificar: _____

6. Tempo que a arte está na agua:

☐ <6 h ☐ 6-12 h ☐ 12-24 h ☐ >24h

7. Há limites de pesca em determinados dias?

☐ Sim ☐ Não ☐ Não sabe

Data inicio veda _____
Data final de veda _____

Outros períodos sem pescar _____

---

8. Horário de pesca:

☐ Horário flexível
☐ Horário fixo

	Calada	Içada
Noite [escura]	Hora aproximada: ☐ Raramente ☐ Frequentemente ☐ Sempre	Hora aproximada: ☐ Raramente ☐ Frequentemente ☐ Sempre
Alvorecer [±1h desde o nascer do sol]	Hora aproximada: ☐ Raramente ☐ Frequentemente ☐ Sempre	Hora aproximada: ☐ Raramente ☐ Frequentemente ☐ Sempre
Dia	Hora aproximada: ☐ Raramente ☐ Frequentemente ☐ Sempre	Hora aproximada: ☐ Raramente ☐ Frequentemente ☐ Sempre
Ocaso [±1h desde o pôr-do-sol]	Hora aproximada: ☐ Raramente ☐ Frequentemente ☐ Sempre	Hora aproximada: ☐ Raramente ☐ Frequentemente ☐ Sempre

9. Principais espécies alvo: (seleccionar máximo três das seguintes categorias)

☐ Pequenos peixes pelágicos Espécies: ______________________________
☐ Grandes peixes pelágicos Espécies: ______________________________
☐ Tubarão Espécies: ______________________________
☐ Peixes demersais Espécies: ______________________________
☐ Cefalópodes (ex. lula) Espécies: ______________________________
☐ Gastrópodes (ex. buzio) Espécies: ______________________________
☐ Bivalves (ex. mexilhão) Espécies: ______________________________
☐ Crustáceos (ex. lagosta) Espécies: ______________________________
☐ Outras Espécies: ______________________________

10. A que profundidade(s)s pesca? Pode indicar mais que uma opção

☐ <de 20 metros
☐ Entre 20 e 50 metros
☐ Entre 50 e 200 metros
☐ > de 200 metros

11. Número de lances/caladas por jornadas de pesca:

☐ 1-2
☐ 3-5
☐ > 5

12. Na calada nocturna, que tipo de iluminação utiliza?

☐ Só luzes de posição
☐ Iluminação extra na coberta
☐ Iluminação extra para atrair a espécie(s) alvo
☐ Não faz esta operação de noite

13. No içado nocturno, que tipo de iluminação utiliza?

☐ Só luzes de posição
☐ Iluminação extra na coberta
☐ Iluminação extra para atrair a espécie(s) alvo
☐ Não faz esta operação de noite

14. Costuma ter capturas acessórias de peixe ou cefalópodes?

☐ Não
☐ Sim. Neste caso preencher os dados da tabela debaixo

Motivo principal	Tamanho predominante	Quantidade por lance	Quando ocorrem?
☐ Não têm tamanho ☐ Excesso de quota ☐ Baixo valor comercial ☐ Vísceras ☐ Outro. Qual? ________	Rango: ☐ < 20 cm ☐ 20-30 cm ☐ > 30 cm	☐ 1-10kg ☐ 10-50 kg ☐ 50-100 kg ☐ 100-500 kg ☐ >500 kg	☐ Durante a calada ☐ Durante o içado ☐ Navegando ☐ Outro. Qual ___________

15. Zona onde opera esta arte de pesca (apontar os códigos (por ex: B7; D15, etc) de um máximo de 5 quadrados por mapa):

Mapa Global:
Mapa Barlavento (Santo Antão a São Nicolau):
Mapa Sal e Boavista:
Mapa Sotavento (Brava a Maio):

16. Nome da zona ou banco de pesca fora do âmbito dos mapas proporcionados: ____
_____

CONHECIMENTO SOBRE AVES MARINHAS E SUA INTERAÇÃO COM A PESCA (E CAPTURAS DE TARTARUGAS E TUBARÕES)

17. Consegue identificar a espécie das aves que estão nas fotos? (mostrar fotos aves)
☐ Identifica correctamente todas as espécies
☐ Identifica só algumas espécies. Quais? ____
☐ Não identifica correctamente nenhuma das espécies

18. Costuma observar aves associadas ao barco durante a sua actividade pesqueira?
☐ Nenhuma
☐ Poucas (1-5)
☐ Algumas (5-25)
☐ Muitas (>25)

19. Que espécie de ave se associa mais ao seu barco durante a sua actividade pesqueira?
☐ Nenhuma
☐ Alcatraz
☐ Rabo de Junco
☐ Cagarra
☐ Pedreiro/Baitu/Topetigude
☐ Gongon/Biôro
☐ João Preto
☐ Pedreiro azul
☐ Pedreirinho
☐ Outra:__________________

20. Que efeito têm as aves sobre a sua actividade profissional?
☐ Perda do isco
☐ Perda de espaço de captura
☐ Afecta a arte (por ex. flutuação)
☐ Rutura das artes
☐ Roubam as capturas
☐ Incomodam (ruido, dejectos…)
☐ Positivo. Indica locais com peixe
☐ Não é relevante
☐ Não tenho opinião/Não sabe
☐ Outros. Especificar: _____

21. Como quantifica a perda económica causada pelas aves?
☐ alta ☐ baixa ☐ inexistente ☐ não sabe
Estimativa da perda: _________ecv/ano

22. Que grupos de espécies considera mais prejudiciais? (por ordem decrescente)

1.__________ 2.__________ 3.__________
Alguma espécie concreta? _______________

23. Que grupos de espécies considera mais beneficiosas? (por ordem decrescente)

1.__________ 2.__________ 3.__________
Alguma espécie concreta? _______________

24. Alguma vez aconteceu que aves marinas ficassem feridas ou morressem, de forma acidental, como consequência da actividade pesqueira do seu barco? E tartarugas ou tubarões?

AVES MARINHAS	TARTARUGAS	TUBARÕES
☐ Não	☐ Não	☐ Não
☐ Sim	☐ Sim	☐ Sim

25. Quando é que se produzem as capturas acidentais das aves? E as tartarugas ou tubarões?

AVES	TARTARUGAS	TUBARÕES
☐ Durante a calada	☐ Durante a calada	☐ Durante a calada
☐ Com a arte já calada	☐ Com a arte já calada	☐ Com a arte já calada
☐ Içando	☐ Içando	☐ Içando

26. Como é que as aves ficam presas na arte? E as tartarugas ou tubarões?

Ficam presas no sistema de pesca (linhas, redes, anzóis, etc.) ☐ Aves ☐ Tartarugas ☐ Tubarões
Engolem o anzol ☐ Aves ☐ Tartarugas ☐ Tubarões
Colidem com o sistema de pesca ☐ Aves ☐ Tartarugas ☐ Tubarões
Outros. Especificar: __________________________________ ☐ Aves ☐ Tartarugas ☐ Tubarões

27. Qual é o estado das aves que ficam presas? e das tartarugas ou tubarões?

☐ Vivas: com frequência ☐ Aves ☐ Tartarugas ☐ Tubarões
☐ Vivas: raramente ☐ Aves ☐ Tartarugas ☐ Tubarões
☐ Mortas: com frequência ☐ Aves ☐ Tartarugas ☐ Tubarões
☐ Mortas: raramente ☐ Aves ☐ Tartarugas ☐ Tubarões

28. Que arte acha que provoca mais capturas acidentais de aves? E em tartarugas ou tubarões?

☐ Palangre ☐ Aves ☐ Tartarugas ☐ Tubarões
☐ Rede de cerco ☐ Aves ☐ Tartarugas ☐ Tubarões
☐ Rede de emalhar ☐ Aves ☐ Tartarugas ☐ Tubarões
☐ Rede de arrasto de praia ☐ Aves ☐ Tartarugas ☐ Tubarões

☐ Pesca à linha/Vara ☐ Aves ☐ Tartarugas ☐ Tubarões
☐ Outra. Especificar: ________________________________ ☐ Aves ☐ Tartarugas ☐ Tubarões

29. Se uma ave/tartaruga ou tubarão é capturado acidentalmente que faz?

☐ Se ainda está viva, solta-a ☐ Aves ☐ Tartarugas ☐ Tubarões
☐ Se ainda está viva, mata-a para comer ou vender ☐ Aves ☐ Tartarugas ☐ Tubarões
☐ Se já esta morta, atira-a para o mar ☐ Aves ☐ Tartarugas ☐ Tubarões
☐ Se já está morta, come-a ou vende-a ☐ Aves ☐ Tartarugas ☐ Tubarões
☐ Outro. Qual? ________________________________ ☐ Aves ☐ Tartarugas ☐ Tubarões

30. Qual é a sua percepção perante esta situação?

☐ É um incómodo
☐ É um problema grave para os animais
☐ Não é relevante
☐ Não tenho uma opinião

31. Considera que ao longo dos últimos 10 anos tem havido alterações importantes na captura acidental e intencional de aves marinhas? E tartarugas e tubarões?

Acidental

☐ Aumentou ☐ Aves ☐ Tartarugas ☐ Tubarões
☐ Diminuiu ☐ Aves ☐ Tartarugas ☐ Tubarões
☐ Não se alterou ☐ Aves ☐ Tartarugas ☐ Tubarões
☐ Não tenho uma opinião/Não sabe ☐ Aves ☐ Tartarugas ☐ Tubarões

Intencional

☐ Aumentou ☐ Aves ☐ Tartarugas ☐ Tubarões
☐ Diminuiu ☐ Aves ☐ Tartarugas ☐ Tubarões
☐ Não se alterou ☐ Aves ☐ Tartarugas ☐ Tubarões
☐ Não tenho uma opinião/Não sabe ☐ Aves ☐ Tartarugas ☐ Tubarões

No caso de ter havido alterações, pode explicar brevemente a quê que acha que se devem estas alterações?

____
____
__

32. Costuma capturar intencionalmente aves marinhas? E tartarugas ou tubarões?

Aves marinhas	Tartarugas	Tubarões
☐ Não	☐ Não	☐ Não
☐ Sim	☐ Sim	☐ Sim

33. Como captura activamente as aves no mar?

☐ Utiliza um pau com um anzol na ponta para apanhar as aves

☐ Utiliza luzes para atrair as aves
☐ Outro método. Qual? ____

PREENCHER A TABELA ABAIXO INDICADA CASO TENHA RESPONDIDO AFIRMATIVAMENTE À CAPTURA ACIDENTAL (Pergunta 24) E/OU INTENCIONAL DE AVES MARINHAS (Pergunta 32)

Espécie	Que captura?	Com que frequência?	Quantidade por ano?	Para quê?	Quando?
Aves em terra: que espécies ou grupo? __________ __________ _______	☐ Ovo ☐ Filhote ☐ Adulto no ninho	☐ 1 vez por ano ☐ 2-5 vezes por ano ☐ 6-10 vezes por ano ☐ >10 vezes por ano	☐ <10 aves ☐ 11-100 aves ☐ 101-1000 aves ☐ >1000 aves	☐ Consumir ☐ Vender ☐ Remédio ☐ Oferecer ☐ Outro. Qual?________ _______	☐ Primavera - verão ☐ Outono - inverno
Aves no mar: que espécies ou grupo? __________ __________ __________ _________		**Acidentalmente:** ☐ 1 vez por ano ☐ 2-5 vezes por ano ☐ 6-10 vezes por ano ☐ >10 vezes por ano **Intencionalmente:** ☐ 1 vez por ano ☐ 2-5 vezes por ano ☐ 6-10 vezes por ano ☐ >10 vezes por ano	**Acidentalmente:** ☐ <10 aves ☐ 11-100 aves ☐ 101-1000 aves ☐ >1000 aves **Intencionalmente:** ☐ <10 aves ☐ 11-100 aves ☐ 101-1000 aves ☐ >1000 aves	☐ Consumir ☐ Vender ☐ Remédio ☐ Oferecer ☐ Outro. Qual?________ _______	☐ Primavera - verão ☐ Outono - inverno
Tartarugas em terra	☐ Ovos ☐ Adulto	☐ 1 vez por ano ☐ 2-5 vezes por ano ☐ 6-10 vezes por ano ☐ >10 vezes por ano	**Adultos:** ☐ 1 ☐ 2-5 ☐ 6-10 ☐ >10	☐ Consumir ☐ Vender ☐ Oferecer ☐ Outro. Qual?_____	☐ ☐ Primavera - verão ☐ Outono - inverno
Tartaruga no mar		**Acidentalmente:** ☐ 1 vez por ano ☐ 2-5 vezes por ano ☐ 6-10 vezes por ano ☐ >10 vezes por ano **Intencionalmente:** ☐ 1 vez por ano ☐ 2-5 vezes por ano ☐ 6-10 vezes por ano ☐ >10 vezes por ano	**Acidentalmente:** ☐ 1 ☐ 2-5 ☐ 6-10 ☐ >10 **Intencionalmente:** ☐ 1 ☐ 2-5 ☐ 6-10 ☐ >10	☐ Consumir ☐ Vender ☐ Oferecer ☐ Outro. Qual?________ __________	
Tubarão		**Acidentalmente:** ☐ 1 vez por ano ☐ 2-5 vezes por ano ☐ 6-10 vezes por ano ☐ >10 vezes por ano **Intencionalmente:** ☐ 1 vez por ano ☐ 2-5 vezes por ano ☐ 6-10 vezes por ano ☐ >10 vezes por ano	**Acidentalmente:** ☐ <10 ☐ 11-50 ☐ 51-100 ☐ >100 **Intencionalmente:** ☐ <10 ☐ 11-50 ☐ 51-100 ☐ >100	☐ Consumir ☐ Vender ☐ Remédio ☐ Oferecer ☐ Outro. Qual?________ __________	☐ Primavera - verão ☐ Outono - inverno

34. Estaria de acordo em levar um aparelho GPS no barco quando for pescar para identificar as principais áreas de pesca e comparar com as principais áreas utilizadas pelas aves marinhas para se alimentar?

☐ Sim ☐ Não. Porquê?____

Para ser preenchido pelo entrevistador:

Como valoras a atitude do entrevistado?

☐ *Esconde muita informação* ☐ *Intermédio* ☐ *Parece totalmente sincero*

Table S2.2. Vessel power and length for artisanal and semi-industrial fisheries.

	Artisanal (209)			Semi-industrial (25)		
Motor power	< 30 HP	> 30 HP	Chi-square test	< 30 HP	> 30 HP	Chi-square test
	82	8	$\chi^2 = 226.66$, df = 2, $p < 0.001$	20	40	$\chi^2 = 2.24$, df = 2, $p = 0.326$
Vessel Length	< 10 m	> 10 m	Chi-square test	< 10 m	> 10 m	Chi-square test
	87	8	$\chi^2 = 267.00$, df = 2, $p < 0.001$	16	84	$\chi^2 = 29.84$, df = 2, $p < 0.001$

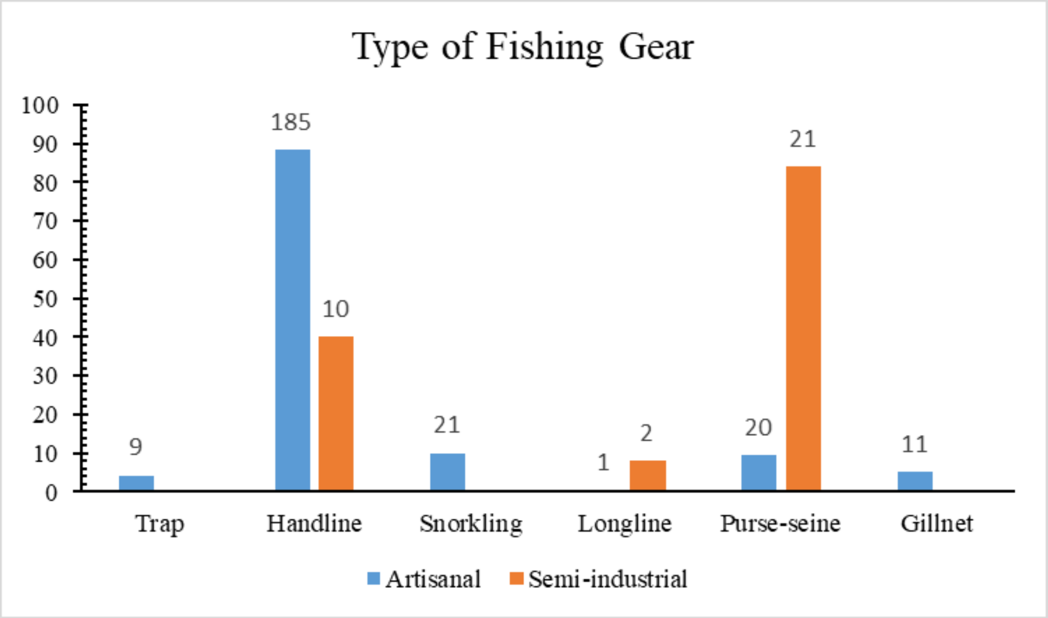


Figure S2.1. Frequency of occurrence of fishing arts identified by fishermen from artisanal and semi-industrial vessels.

Table S2.3. Fishing activity time for different fishing arts in artisanal and semi-industrial vessels. Frequency of occurrence (%) based on fishermen´s answers.

		Trip duration (days)			Time gear stay on the water			
Type	Art	≤1 day	2-5 days	> 5 days	<6H	6-12H	12-24H	>24H
Artisanal	Handline	55.5	13.4	14.4	9.6	35.9	27.3	8.6
	Snorkeling	6.7	1.0	0.5	2.4	4.8	1.0	-
	Purse-seine	0.5	2.9	5.3	-	1.9	0.5	5.7
	Gillnet	1.9	1.4	1.0	0.5	3.3	0.5	-
Semi-Industrial	Handline	4.0	12.0	20.0	4.0	24.0	4.0	4.0
	Longline	-	-	4.0	-	-	4.0	-
	Purse-seine	8.0	36.0	40.0	8.0	40.0	12.0	20.0

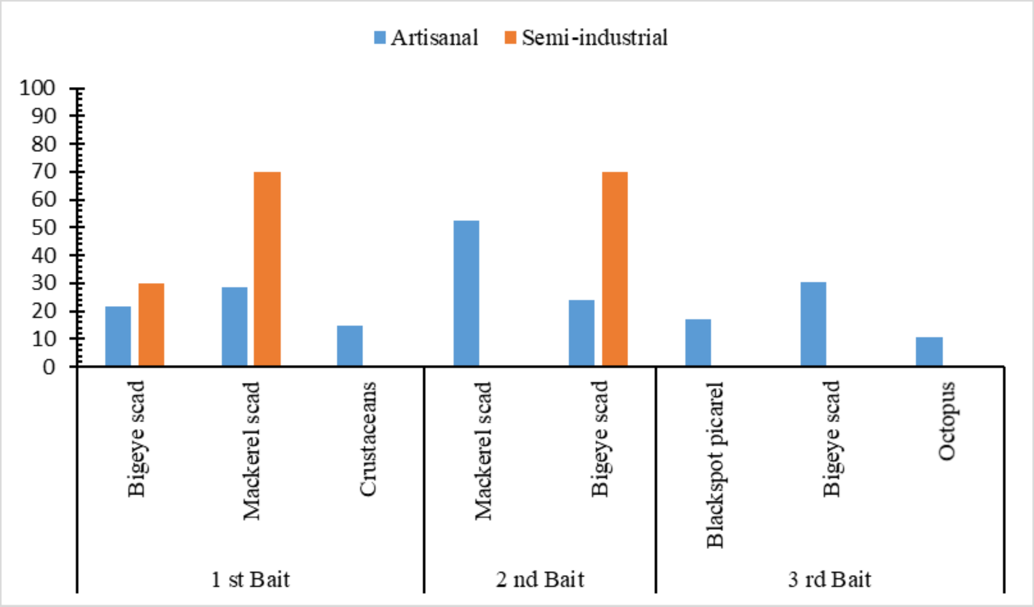


Figure S2.2. Frequency of occurrence of different bait species used in artisanal and semi-industrial vessels. Questions were related to the 3 most used bait during fishing operations. These results represent the species more frequently answered by fishermen in answering order.

Table S4.1. Monthly summary of the number of trips and individual (between brackets) brown (BRBO) and red-footed (RFBO) boobies tracked in the current study. Shaded area highlights the period when BRBO and RFBO co-occur in sympatry.

Year	Month	BRBO female	BRBO male	RFBO female	RFBO male
2018	September	38 (5)	42 (5)	17 (2)	22 (7)
2018	October	46 (4)	25 (3)	4 (2)	35 (7)
2018	November	50 (4)	72 (6)	—	—
2019	February	53 (9)	57 (11)	—	—
2019	March	5 (3)	20 (3)	—	—
2019	April	23 (3)	27 (5)	—	—
2019	May	5 (3)	13 (4)	—	—
2019	June	73 (9)	89 (13)	7 (2)	25 (4)
2019	July	13 (2)	45 (21)	4 (3)	14 (6)
2019	August	5 (3)	6 (6)	4 (2)	2 (2)

Table S4.2. Multi-collinearity among covariates selected for three Generalized Additive Mixed Models (GAMMs) assessed using variance inflation factors (GVIFs, *AEDForecasting* library in R. Highly colinear variables (VIF > 3) were removed prior to modeling. DEP – depth (m); CHLA – chlorophyll a concentration (mgm^{-3}); SST – sea surface temperature (°C); OMLT – ocean mixed layer thickness (cm); SSH – sea surface height (m); GDEP – depth gradient (%); GCHLA – CHLA gradient (%); GSST – SST gradient (%); GOMLT – OMLT gradient (%); GSSH – SSH gradient (%).

	(A) brown boobies during Nov.-May		(B) brown boobies during Jun.-Oct.		(C) red-footed boobies during Jun.-Oct.	
Env. variables	VIF value before selection	VIF value after selection	VIF value before selection	VIF value after selection	VIF value before selection	VIF value after selection
DEP	5.47	—	15.66	—	28.43	—
CHLA	2.14	2.06	5.47	—	2.55	2.19
SST	1.32	1.11	2.16	1.57	1.98	1.00
OMLT	1.05	1.00	2.00	1.24	1.34	1.06
SSH	2.00	1.78	1.84	1.22	2.39	2.22
GDEP	1.27	1.17	1.27	1.00	1.28	1.00
GCHLA	8.74	—	1.88	1.21	1.53	1.20
GSST	1.07	1.00	1.00	1.00	19.98	—
GOMLT	2.17	1.98	1.09	1.05	1.69	1.66
GSSH	9.69	—	2.47	2.31	2.47	2.40

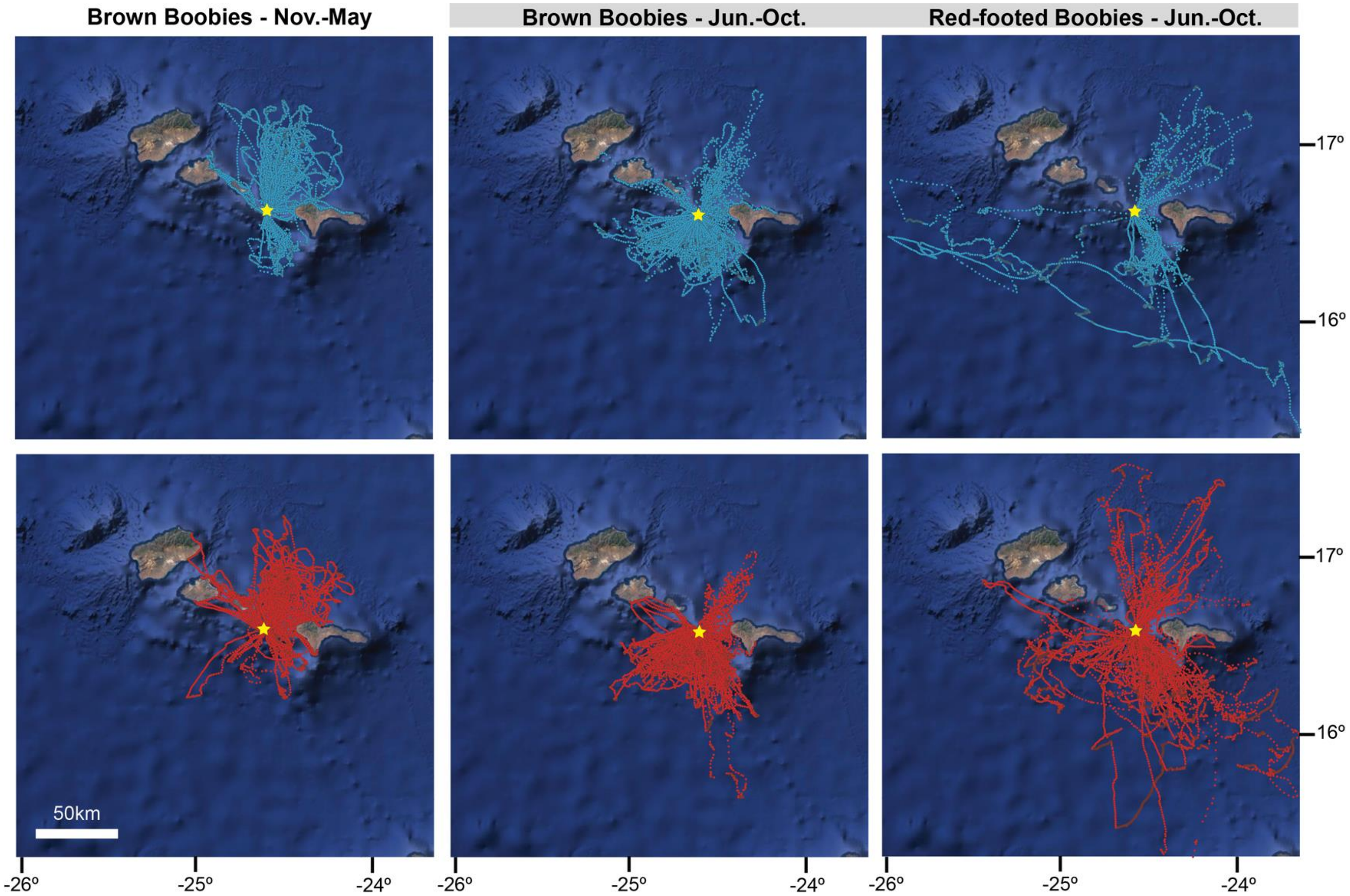


Figure S4.1. Foraging tracks female (blue) and male (red) brown (BRBO) and red-footed (RFBO) boobies, tracked between November 2018 – October 2019 at Raso Islet (star), Cabo Verde. Bathymetric relief in the background (max. 4012m). Shaded area highlights the period when BRBO and RFBO co-occur in sympatry.

Table S4.3. Comparison of isotopic niche metrics between study species, sexes, and seasons (Nov.-May vs. Jun.-Oct.). Carbon range, the distance between max. and min. δ^{13}C values; (2) nitrogen range, the distance between max. and min. δ^{15}N values; (3) total area (TA), as the convex hull area encompassed by all values in a δ^{13}C – δ^{15}N bi-plot space; (4) standard ellipse area (SEA); (5) standard ellipse corrected for sample size (SEA$_C$), depicting the area with 40% probability of containing a subsequently sampled datum; (6) mean distance to centroid (CD), as the average Euclidean distance of each isotopic value to the δ^{13}C - δ^{15}N centroid, where the centroid is the mean δ^{13}C – δ^{15}N value for all values in the food web; (7) mean nearest neighbour distance (NND), as the mean of the Euclidean distances to each value nearest neighbour in bi-plot space, and thus a measure of the overall density of 'values packing'; (8) SD nearest neighbour distance (SDNND), as a measure of the evenness of 'values packing' in bi-plot space that is less influenced than NND by sample size.

Species	Brown booby (BRBO)				Red-footed booby (RFBO)	
Study seasons	Nov. – May		Jun. – Oct.		Jun. – Oct.	
Sex	female	male	female	male	female	male
TA	2.72	3.69	3.50	3.68	2.65	5.94
SEA	1.09	1.11	1.76	1.53	3.28	2.28
SEA$_C$	1.17	1.16	1.89	1.60	4.91	2.42
Carbon Range	1.83	2.23	2.66	2.79	1.86	3.98
Nitrogen Range	2.29	2.20	2.21	1.80	2.70	2.46
Mean Distance to Centroid (CD)	0.71	0.74	0.96	1.03	1.29	1.16
Mean Nearest Neighbour Distance (NND)	0.33	0.31	0.36	0.24	1.32	0.43
SD Nearest Neighbour Distance	0.28	0.27	0.17	0.16	0.72	0.32

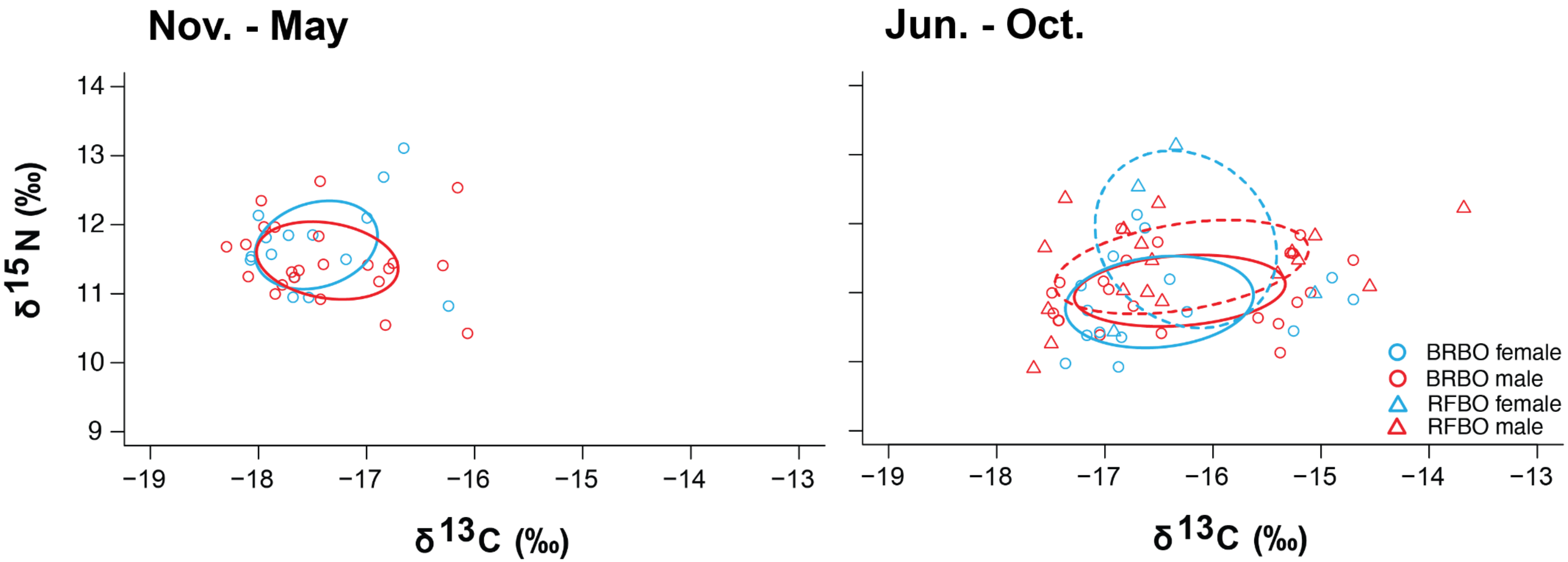


Figure S4.2. Isotopic bivariate niche space of female (blue; filled line) and male (red; filled line) brown boobies (BRBO; *Sula leucogaster*) and female (blue; dashed line) and male (red; dashed line) red-footed boobies (RFBO; *Sula sula*).

Table S4.4. Isotopic niche overlap (SEA_B) between study species (brown booby; BRBO and red-footed booby; RFBO), sex and seasons (Nov. – May and Jun. – Oct.).

Comparisons	SEA_B	Overlap	Prop 95% overlap
Nov. – May			
BRBO male *vs.* BRBO female	0.51	0.85	0.58
Jun. – Oct.			
BRBO male *vs.* BRBO female	0.68	1.38	0.65
BRBO male *vs.* RFBO male	0.90	1.23	0.44
BRBO male *vs.* RFBO female	0.95	1.44	0.28
BRBO female *vs.* RFBO male	0.77	1.12	0.35
BRBO female *vs.* RFBO female	0.91	1.42	0.26
RFBO male *vs.* RFBO female	0.79	2.09	0.40

Table S4.5. Former studies reporting inter-sexual differences of brown (BB) and red-footed (RFB) boobies in their foraging distribution (foraging ≠), isotopic signatures ($\delta^{13}C$ / $\delta^{15}N$), dietary preferences [FF – Flying fish (Exocetidae); FS – Flying squid (Ommastrephidae); SP – Small pelagic - anchovy, herring, sardines (Clupeidae)] and body mass (M=male; F=female). Shown are also other population-specific characteristics, namely ocean basin (P-Pacific, A-Atlantic, I-Indian), population size, Chlorophyll *a* concentration (CHLA) in the colony surroundings, mean breeding period and breeding stage (I – Incubation; CR – Chick-rearing) when the study was conducted. (1) – Differences during two periods of the year; (2) - F>M $\delta^{13}C$ / F=M $\delta^{15}N$; (3) Females $\delta^{15}N$ values higher than males; (4) – Females consumed more flying fish and males consumed equal proportions of fish and squid; (5) - Consumed mostly flying squid; (6) – Unspecified prey with high pelagic signature; (7) – Unspecified breeding phase.

Sps	Ocean	Colony	Population size	CHLA (mg m-3)	Foraging ≠	Isotopic Sig.	Diet	Weight (g)	Breeding	Breeding stage	Publication
BB	P	Clipperton isl.	15000-25000 ind.	0.2	F>M	-	-	-	Nov	I&CR	(Gilardi 1992)
	P	Johnston Atoll	450 pairs	-	F<M	-	-	M = 1077 ± 78 F = 1491 ± 76	Mar	I	(Lewis et al. 2005)
	P	Sanildefonso Isl.	2000 pairs	High	F>M	F=M	SP	M = 1194 ± 85 F = 1448 ± 86	Mar	CR	(Weimerskirch et al. 2009b)
	P	Palmyra Atoll	~400 pairs	0.14	-	F>M	FF, SP, FS	-	Jul	I&CR	(Young et al. 2010a)
	A	Dog Isl.	2462 ind.	-	-	-	-	M = 1062 F = 1416	Mar-Apr	CR	(Soanes et al. 2015)
	I	Christmas Isl.	6000 pairs	-	-	F=M	-	-	Sep-Oct	I&CR	(Navarro et al. 2014)
	P	San Jorge Isl.	6000 ind.	High	F=M	-	SP	-	Nov-May	I&CR	(Castillo-Guerrero et al. 2016)
	P	Farallón Isl.	2400 ind.	High	F=M	-	SP	-	Jan-May	I&CR	(Castillo-Guerrero et al. 2016)
	P	Raine Isl.	2642 ind.	-	F>M	-	FF, FS[4]	M = 1197 ± 65 F = 1430 ± 147	Dec	CR	(Miller et al. 2018)
	A	Raso Islet	~289 ind.	0.15-0.38	F=M / F<M[1]	F=M	FF, FS	1246 ± 227	Feb-Nov	CR	This study
RFB	P	Johnston Atoll	1400 pairs	-	F=M	-	-	M = 1035 ± 70 F = 1182 ± 86	Mar	I	(Lewis et al. 2005)
	I	Europa Isl.	2800-3800 pairs	0.165	-	-	FF, FS	M = 780 F = 1050	Aug-Sep	I&CR	(Weimerskirch et al. 2005a)
	I	Europa Isl.	2800-3800 pairs	0.165	-	-	FF, FS	M = 780 F = 1050	Aug-Sep	I&CR	(Weimerskirch et al. 2005b)
	I	Europa Isl.	2800-3800 pairs	0.165	F(I) > M(I)	-	FF, FS[5]	M = 891 ± 64.4 F = 1020 ± 50.1	Aug-Sep	I&CR	(Weimerskirch et al. 2006b)
	I	Europa Isl.	9000 ind.	-	F>M	F>M/F=M[2]	FF, FS	-	Aug-Sep	B – U[7]	(Cherel et al. 2008)

P	Palmyra Atoll	~2500 pairs	-	-	F=M	FF, SP, FS	-	Jul	I&CR	(Young et al. 2010a)
P	Palmyra Atoll	1000-2500 pairs	0.1-0.2	F=M	F=M	U[6]	M = 839 ± 44 F = 954 ± 41	May-Nov	I&CR	(Young et al. 2010b)
I	Tromelin Isl	130-180 pairs	0.03-0.13	F=M	-	FF, FS[5]	M = 920 ± 71.6 F = 1054 ± 46.2	Dec-Jan	CR	(Kappes et al. 2011)
I	Europa Isl.	2800-3800 pairs	0.153-0.154	F=M	-	-	M = 800-900 F = 1000-1200	Sep-Nov	I&CR	(Mendez et al. 2016)
I	Europa Isl.	2800-3800 pairs	0.07	F=M	-	-	-	Sep-Oct	I	(Mendez et al. 2017a)
P	Walpole Isl.	1000 pairs	0.07	F=M	-	-	-	Sep	I	(Mendez et al. 2017a)
P	Chesterfiled Isl.	7200-7300 pairs	0.11	F=M	-	-	-	May-Jun	I	(Mendez et al. 2017a)
P	Genovesa Isl.	140000 pairs	> 0.15	F=M	-	-	-	Nov	I	(Mendez et al. 2017a)
I	Christmas Isl.	12000 pairs	> 0.15	F=M	-	-	-	Jul-Aug	I	(Mendez et al. 2017a)
A	Raso islet	~133 ind.	0.15-0.38	F=M	F>M[3]	FF, FS	1041±178	Jun-Oct	Non-breeding	This study

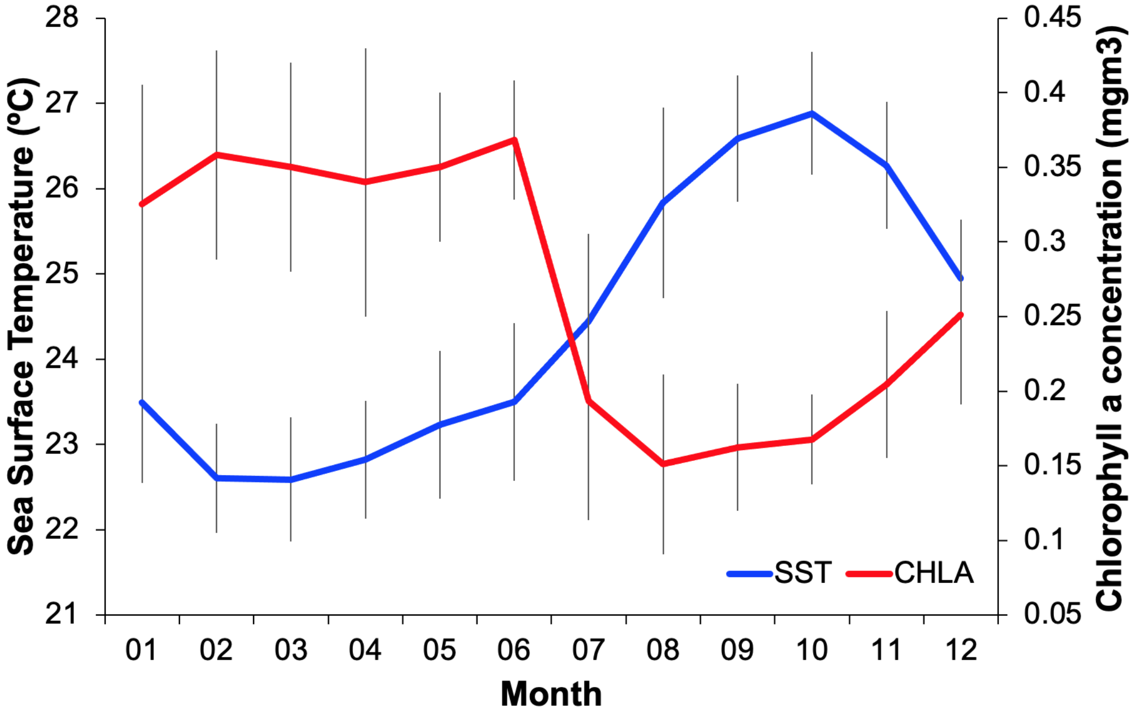


Figure S4.3. Monthly average (±SD) sea surface temperature and chlorophyll *a* concentration 250km around Raso Islet between September 2018 – August 2019 (study period).

Table S5.1. Average maximum distance, tracking duration and dates of 8 seabird species by year (2013 – 2019), colony (13 locations) and breeding phase (incubation *vs.* chick-rearing) in the Cabo Verde archipelago.

Species	Year	Main Island	Colony	Breeding phase	N birds	N trips	Max. dist. colony	Period (d)	Start tracking	End tracking
Bulwer's petrel	2017	Fogo	Ilhéu de Cima	chick-rearing	15	17	347.7 ± 120.6	6.9 ± 2.9	2017-06-22	2017-07-17
Bulwer's petrel	2018	Fogo	Ilhéu de Cima	incubation	16	16	471.5 ± 216.1	11.1 ± 4.4	2018-04-24	2018-05-21
Bulwer's petrel	2018	Fogo	Ilhéu de Cima	chick-rearing	24	27	442.1 ± 179.1	10.6± 7.0	2018-05-11	2018-07-19
Bulwer's petrel	2019	Fogo	Ilhéu de Cima	incubation	14	14	542.0 ± 144.6	10.5 ± 2.9	2019-04-28	2019-06-06
Bulwer's petrel	2019	Fogo	Ilhéu de Cima	chick-rearing	44	44	531.2 ± 183.3	10.6 ± 2.8	2019-04-20	2019-07-21
Bulwer's petrel	2017	São Nicolau	Ilhéu Raso	incubation	4	6	291.8 ± 147.9	3.3 ± 2.7	2017-06-12	2017-06-23
Bulwer's petrel	2017	São Nicolau	Ilhéu Raso	chick-rearing	13	32	321.7 ± 257.6	2.6 ± 1.8	2017-08-22	2017-08-31
Bulwer's petrel	2018	São Nicolau	Ilhéu Raso	incubation	7	12	362.9 ± 225.3	5.8 ± 4.2	2018-06-14	2018-07-01
Bulwer's petrel	2018	São Nicolau	Ilhéu Raso	chick-rearing	25	115	317.4 ± 269.3	2.1 ± 2.0	2018-07-28	2018-09-02
Bulwer's petrel	2019	São Nicolau	Ilhéu Raso	incubation	11	19	484.8 ± 284.0	4.5 ± 3.3	2019-06-12	2019-07-11
Bulwer's petrel	2019	São Nicolau	Ilhéu Raso	chick-rearing	14	39	351.7 ± 277.0	2.9 ± 2.6	2019-07-16	2019-08-29
Bulwer's petrel	2019	Sal	Ilhéu Rabo Junco	incubation	5	5	538.5 ± 129.8	8.3 ± 1.0	2019-06-23	2019-07-04
Cape Verde shearwater	2013	São Nicolau	Ilhéu Raso	incubation	12	13	618.7 ± 333.9	7.8 ± 4.0	2013-07-02	2013-07-17
Cape Verde shearwater	2013	São Nicolau	Ilhéu Raso	chick-rearing	10	58	176.5 ± 105.7	1.8 ± 2.7	2013-09-04	2013-09-26
Cape Verde shearwater	2014	São Nicolau	Ilhéu Raso	incubation	10	16	364.6 ± 257.0	3.7 ± 3.9	2014-06-17	2014-07-09
Cape Verde shearwater	2015	São Nicolau	Ilhéu Raso	incubation	13	41	222.6 ± 196.4	2.4 ± 3.0	2015-06-10	2015-07-01
Cape Verde shearwater	2015	São Nicolau	Ilhéu Raso	chick-rearing	12	107	94.2 ± 52.1	1.1 ± 1.2	2015-09-18	2015-10-02
Cape Verde shearwater	2016	São Nicolau	Ilhéu Raso	incubation	13	22	584.2 ± 354.1	5.3 ± 3.6	2016-06-14	2016-07-11
Cape Verde shearwater	2017	São Nicolau	Ilhéu Raso	incubation	16	40	382.4 ± 275.8	3.5 ± 3.6	2017-06-13	2017-07-09
Cape Verde shearwater	2017	São Nicolau	Ilhéu Raso	chick-rearing	27	203	229.1 ± 174.1	1.7 ± 2.0	2017-08-23	2017-09-15
Cape Verde shearwater	2018	São Nicolau	Ilhéu Raso	incubation	20	30	589.4 ± 336.8	4.6 ± 3.1	2018-06-15	2018-07-09
Cape Verde shearwater	2018	São Nicolau	Ilhéu Raso	chick-rearing	35	189	236.4 ± 174.0	1.7 ± 2.2	2018-08-18	2018-09-13
Cape Verde shearwater	2019	São Nicolau	Ilhéu Raso	incubation	10	15	606.1 ± 376.2	3.6 ± 2.7	2019-06-20	2019-07-04

Species	Year	Main Island	Colony	Breeding phase	N birds	N trips	Max. dist. colony	Period (d)	Start tracking	End tracking
Cape Verde shearwater	2019	São Nicolau	Ilhéu Raso	chick-rearing	29	160	210.8 ± 165.6	1.9 ± 2.5	2019-09-03	2019-09-23
Cape Verde shearwater	2017	Boavista	Curral Velho	incubation	35	37	387.7 ± 270.9	6.4 ± 3.5	2017-06-11	2017-07-10
Cape Verde shearwater	2018	Boavista	Curral Velho	incubation	32	35	562.0 ± 231.3	8.7 ± 4.3	2018-06-25	2018-07-31
Cape Verde shearwater	2018	Boavista	Curral Velho	chick-rearing	23	43	232.6 ± 170.0	5.9 ± 2.7	2018-06-26	2018-08-28
Cape Verde shearwater	2019	Boavista	Curral Velho	incubation	56	63	565.2 ± 263.2	9.3 ± 5.6	2019-06-23	2019-08-13
Cape Verde shearwater	2019	Boavista	Curral Velho	chick-rearing	27	58	391.5 ± 191.4	8.1 ± 5.7	2019-07-06	2019-08-30
Red-billed tropicbird	2017	Boavista	Ponta Roque	incubation	7	23	216.9 ± 126.9	6.6 ± 1.5	2017-08-07	2017-09-07
Red-billed tropicbird	2019	Boavista	Ponta Roque	incubation	2	16	94.2 ± 31.1	1.2 ± 0.9	2019-01-07	2019-04-28
Red-billed tropicbird	2017	Boavista	Ponta Rincon	incubation	24	49	125.2 ± 73.9	4.3 ± 2.8	2017-08-12	2017-12-03
Red-billed tropicbird	2017	Boavista	Ponta Rincon	chick-rearing	14	36	137.3 ± 69.7	5.8 ± 2.2	2017-08-21	2017-11-28
Red-billed tropicbird	2018	Boavista	Ponta Rincon	incubation	53	88	193.0 ± 72.3	5.1 ± 3.2	2018-01-03	2018-12-24
Red-billed tropicbird	2018	Boavista	Ponta Rincon	chick-rearing	41	79	144.1 ± 115.7	5.5 ± 2.2	2018-01-03	2018-12-24
Red-billed tropicbird	2019	Boavista	Ponta Rincon	incubation	10	32	156.3 ± 128.2	3.5 ± 2.7	2019-02-21	2019-09-05
Red-billed tropicbird	2019	Boavista	Ponta Rincon	chick-rearing	10	38	111.4 ± 76.0	3.5 ± 2.2	2019-01-31	2019-09-05
Red-billed tropicbird	2017	São Nicolau	Ilhéu Raso	incubation	5	27	107.5 ± 78.3	1.8 ± 1.6	2017-06-14	2017-06-19
Red-billed tropicbird	2017	São Nicolau	Ilhéu Raso	incubation	22	48	108.1 ± 69.9	2.9 ± 1.0	2017-01-06	2017-02-11
Red-billed tropicbird	2018	São Nicolau	Ilhéu Raso	incubation	15	36	312.5 ± 176.0	6.3 ± 3.3	2018-02-17	2018-06-21
Red-billed tropicbird	2018	São Nicolau	Ilhéu Raso	chick-rearing	20	45	257.3 ± 154.6	4.8 ± 2.4	2018-02-17	2018-03-31
Red-billed tropicbird	2019	São Nicolau	Ilhéu Raso	incubation	2	8	242.2 ± 189.8	3.2 ± 4.0	2019-06-11	2019-07-21
Red-billed tropicbird	2019	São Nicolau	Ilhéu Raso	chick-rearing	11	39	101.6 ± 68.0	0.7 ± 1.0	2019-02-13	2019-07-04
Red-billed tropicbird	2017	Sal	Serra Negra	incubation	10	20	118.7 ± 82.3	6.0 ± 2.9	2017-10-05	2017-12-31
Red-billed tropicbird	2017	Sal	Serra Negra	chick-rearing	11	27	86.3 ± 46.0	5.7 ± 1.3	2017-11-11	2017-12-28
Red-billed tropicbird	2018	Sal	Serra Negra	incubation	6	26	134.5 ± 109.9	4.1 ± 2.3	2018-01-01	2018-06-19
Red-billed tropicbird	2018	Sal	Serra Negra	chick-rearing	5	27	66.9 ± 51.7	4.1 ± 1.3	2018-01-15	2018-10-22
Red-billed tropicbird	2019	Sal	Serra Negra	incubation	3	10	146.4 ± 105.8	3.0 ± 4.3	2019-03-09	2019-12-01

Species	Year	Main Island	Colony	Breeding phase	N birds	N trips	Max. dist. colony	Period (d)	Start tracking	End tracking
Red-billed tropicbird	2019	Sal	Serra Negra	chick-rearing	5	12	47.4 ± 28.3	1.3 ± 1.2	2019-03-09	2019-12-10
Red-billed tropicbird	2018	Sal	Cadjetinha e Furna	incubation	15	38	224.3 ± 133.0	5.6 ± 3.2	2018-02-11	2018-12-05
Red-billed tropicbird	2018	Sal	Cadjetinha e Furna	chick-rearing	15	39	116.4 ± 93.6	4.2 ± 3.4	2018-01-27	2018-12-20
Red-billed tropicbird	2019	Sal	Cadjetinha e Furna	chick-rearing	39	47	67.5 ± 36.8	1.7 ± 1.7	2019-01-02	2019-04-03
Red-billed tropicbird	2018	Sal	Monte Leão	incubation	3	8	171.5 ± 106.0	4.8 ± 0.5	2018-04-11	2018-05-30
Red-billed tropicbird	2018	Sal	Monte Leão	chick-rearing	4	17	75.6 ± 22.5	4.5 ± 1.2	2018-04-14	2018-05-22
Red-billed tropicbird	2019	Sal	Monte Leão	incubation	3	12	128.2 ± 87.5	1.0 ± 0.9	2019-02-13	2019-04-05
Red-billed tropicbird	2019	Sal	Monte Leão	chick-rearing	5	18	46.3 ± 24.0	1.0 ± 0.6	2019-02-23	2019-04-05
Red-billed tropicbird	2019	Brava	Ilhéu Cima	incubation	12	32	193.7 ± 106.3	4.5 ± 2.3	2019-06-16	2019-11-18
Red-billed tropicbird	2019	Brava	Ilhéu Cima	chick-rearing	10	31	61.6 ± 36.9	3.0 ± 1.3	2019-11-09	2019-12-18
Cape Verde petrel	2018	Fogo	Fogo	incubation	6	10	577.4 ± 325.4	8.0 ± 4.0	2018-02-06	2018-04-26
Cape Verde petrel	2018	Fogo	Fogo	chick-rearing	5	15	477.4 ± 201.7	8.2 ± 2.4	2018-03-04	2018-04-24
Cape Verde petrel	2019	Fogo	Fogo	incubation	5	9	914.4 ± 156.8	11.8 ± 3.1	2019-01-30	2019-02-25
Cape Verde petrel	2018	Santo Antão	Santo Antão	chick-rearing	2	5	497.5 ± 291.9	3.7 ± 2.0	2018-02-13	2018-03-17
Cape Verde petrel	2019	Santo Antão	Santo Antão	chick-rearing	2	8	420.2 ± 273.3	5.3 ± 4.8	2019-03-03	2019-04-02
Cape Verde storm petrel	2018	Fogo	Ilhéu de Cima	incubation	11	16	360.2 ± 143.5	7.9 ± 8.6	2018-11-11	2018-12-23
Cape Verde storm petrel	2018	Fogo	Ilhéu de Cima	chick-rearing	13	29	267.2 ± 127.8	11.6 ± 7.7	2018-11-11	2018-12-31
Cape Verde storm petrel	2019	Fogo	Ilhéu de Cima	incubation	24	29	380.2 ± 160.2	6.1 ± 1.9	2019-03-20	2019-11-21
Cape Verde storm petrel	2019	Fogo	Ilhéu de Cima	chick-rearing	8	22	376.5 ± 82.2	8.7 ± 2.5	2019-01-01	2019-06-04
Cape Verde little shearwater	2018	Fogo	Ilhéu de Cima	incubation	22	28	243.2 ± 73.3	8.1 ± 4.0	2018-02-23	2018-03-20
Cape Verde little shearwater	2019	Fogo	Ilhéu de Cima	chick-rearing	27	48	155.4 ± 74.9	6.1 ± 2.4	2019-03-08	2019-04-25
Cape Verde little shearwater	2018	São Nicolau	Ilhéu Raso	incubation	4	13	68.6 ± 32.5	2.7 ± 2.8	2018-03-08	2018-03-19
Cape Verde little shearwater	2019	São Nicolau	Ilhéu Raso	incubation	3	6	128.2 ± 95.1	4.8 ± 3.5	2019-02-16	2019-03-13

Species	Year	Main Island	Colony	Breeding phase	N birds	N trips	Max. dist. colony	Period (d)	Start tracking	End tracking
Cape Verde little shearwater	2019	São Nicolau	Ilhéu Raso	chick-rearing	23	99	97.0 ± 53.6	1.2 ± 0.9	2019-03-29	2019-05-04
Brown booby	2017	Boavista	Curral Velho	chick-rearing	9	58	24.0 ± 15.3	0.1 ± 0.1	2017-06-13	2017-06-25
Brown booby	2018	São Nicolau	Ilhéu Raso	chick-rearing	38	370	29.1 ± 15.1	0.8 ± 2.8	2018-03-11	2018-11-30
Brown booby	2019	São Nicolau	Ilhéu Raso	chick-rearing	54	412	28.6 ± 17.6	0.1 ± 0.1	2019-02-13	2019-09-03
Red-footed booby	2018	São Nicolau	Ilhéu Raso	non-breeding	11	78	60.5 ± 31.7	1.0 ± 2.6	2018-09-01	2018-10-27
Red-footed booby	2019	São Nicolau	Ilhéu Raso	non-breeding	26	56	73.0 ± 35.5	0.8 ± 1.1	2019-06-16	2019-09-05
White-faced storm petrel	2019	Boavista	Ilhéu dos Passaros	incubation	14	15	244.7 ± 59.1	7.2 ± 5.8	2019-03-08	2019-04-16

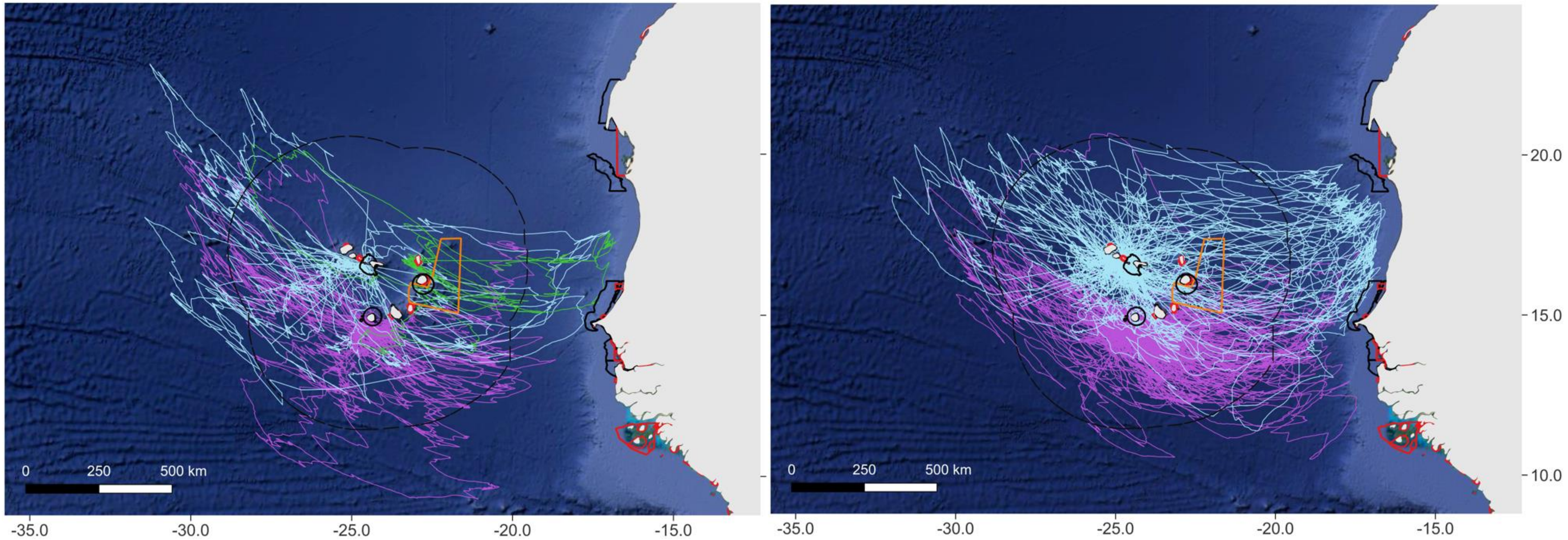


Figure S5.1. Foraging distribution of Bulwer's petrels *Bulweria bulwerii* from Ilhéus Raso (light blue), Cima (pink) and Rabo de Junco (green), during the incubation (left) and chick-rearing (right) phases (see Table S1 for further details). Dashed black contour represents the Cabo Verde EEZ, black polygons are current network of Key Biodiversity Areas (https://www.keybiodiversityareas.org), red contours are Marine Protected Areas of Cabo Verde and off West Africa and the orange polygon sets a potential pelagic MPA (Oceania) under designation. Bathymetry in the background.

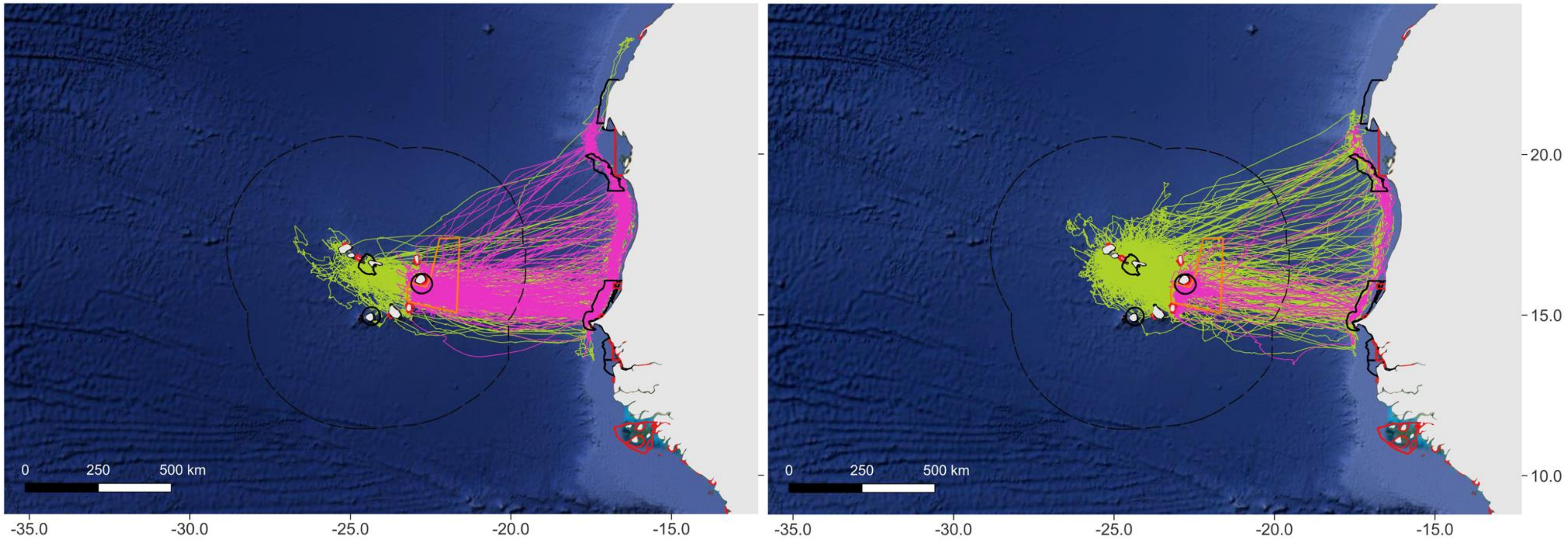


Figure S5.2. Foraging distribution of Cape Verde shearwaters *Calonectris edwardsii* from Ilhéus Raso (green), Cima (pink) and Rabo de Junco (green), during the incubation (left) and chick-rearing (right) phases (see Table S1 for further details). Dashed black contour represents the Cabo Verde EEZ, black polygons are current network of Key Biodiversity Areas (https://www.keybiodiversityareas.org), red contours are Marine Protected Areas of Cabo Verde and off West Africa and the orange polygon sets a potential pelagic MPA (Oceania) under designation. Bathymetry in the background.

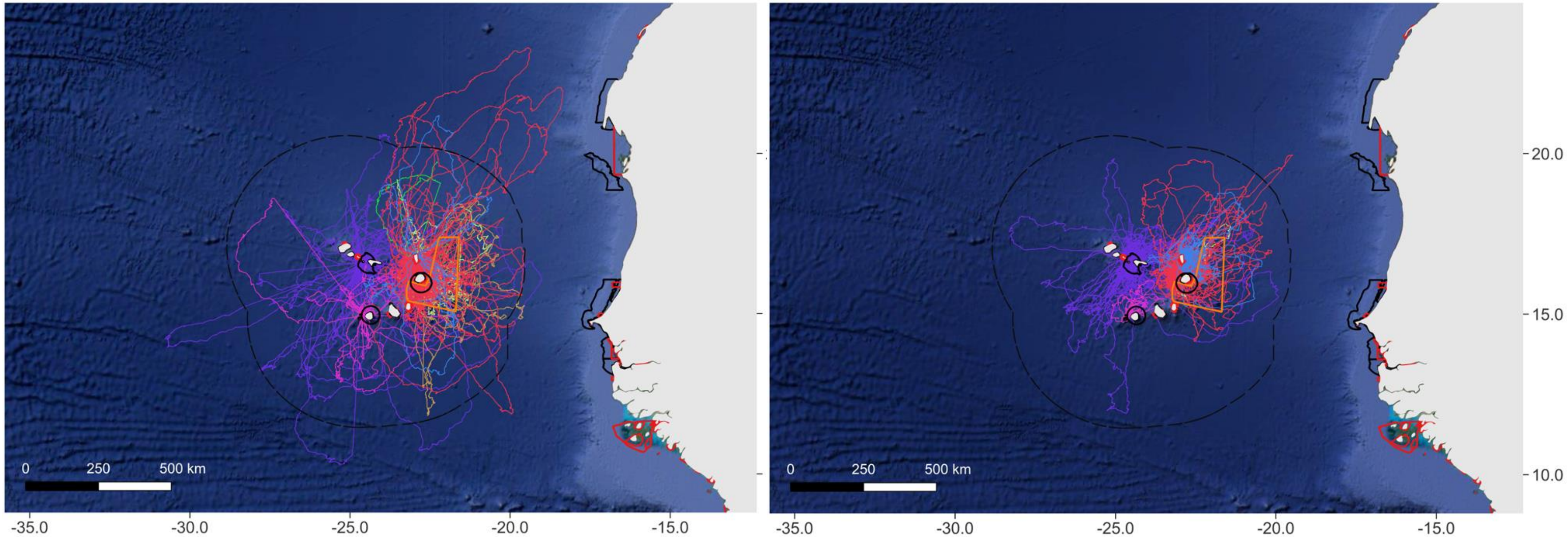


Figure S5.3. Foraging distribution of Red-billed tropicbird *Phaethon aethereus* from Cadjetinha and Furna (royal blue), Ilhéu de Cima (pink), Monte Leão (green), Ponta Roque (gold), Ponta do Sol and Ponta Rincón (coral), Ilhéu Raso (light blue) and Serra Negra (dark yellow) during incubation (left) and chick-rearing (right) phases (see Table S1 for further details). Dashed black contour represents the Cabo Verde EEZ, black polygons are current network of Key Biodiversity Areas (https://www.keybiodiversityareas.org), red contours are Marine Protected Areas of Cabo Verde and off West Africa and the orange polygon sets a potential pelagic MPA (Oceania) under designation. Bathymetry in the background.

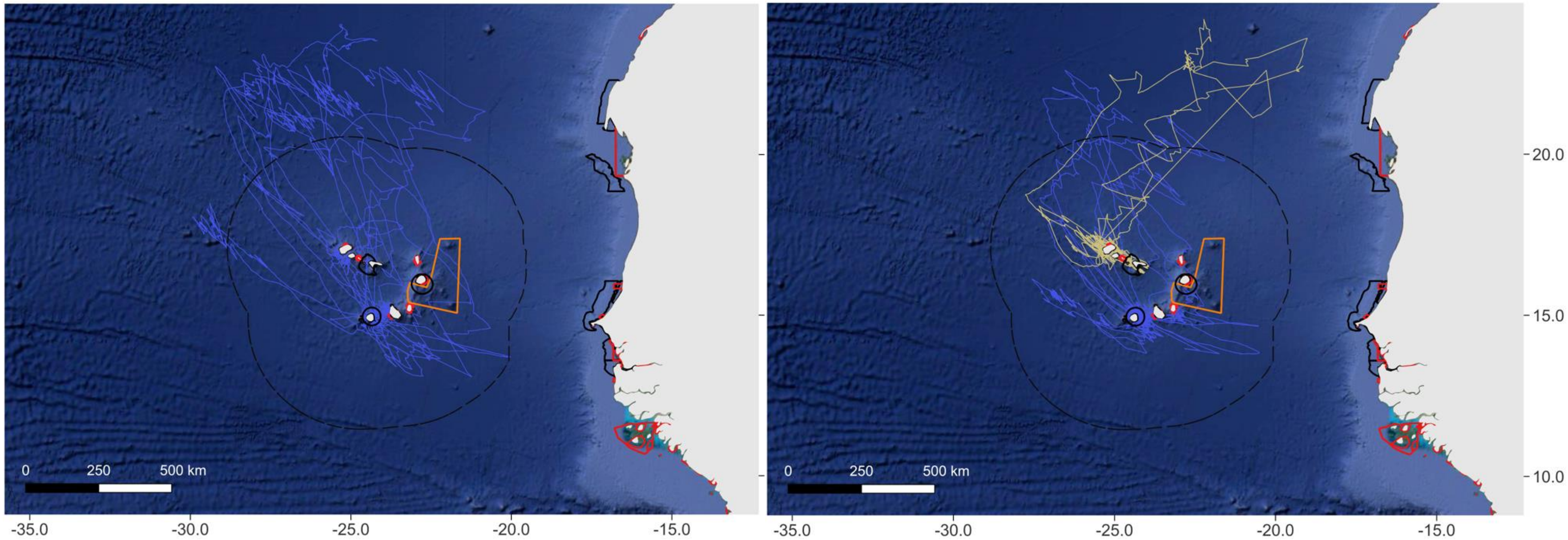


Figure S5.4. Foraging distribution of Cape Verde petrel *Pterodroma feae* from Fogo (royal blue) and Santo Antão (green) during incubation (left) and chick-rearing (right) phases (see Table S1 for further details). Dashed black contour represents the Cabo Verde EEZ, black polygons are current network of Key Biodiversity Areas (https://www.keybiodiversityareas.org), red contours are Marine Protected Areas of Cabo Verde and off West Africa and the orange polygon sets a potential pelagic MPA (Oceania) under designation. Bathymetry in the background.

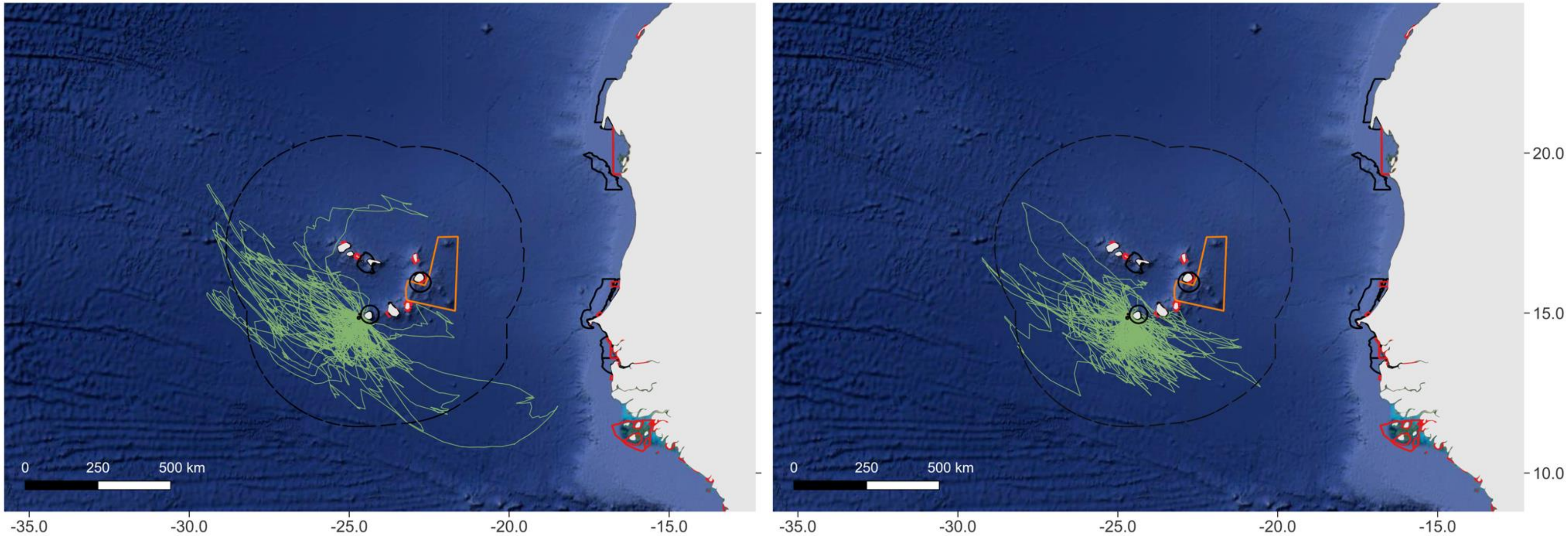


Figure S5.5. Foraging distribution of Cape Verde storm petrel *Hydrobates jabejabe* from Ilhéu de Cima during incubation (left) and chick-rearing (right) phases (see Table S1 for further details). Dashed black contour represents the Cabo Verde EEZ, black polygons are current network of Key Biodiversity Areas (https://www.keybiodiversityareas.org), red contours are Marine Protected Areas of Cabo Verde and off West Africa and the orange polygon sets a potential pelagic MPA (Oceania) under designation. Bathymetry in the background.

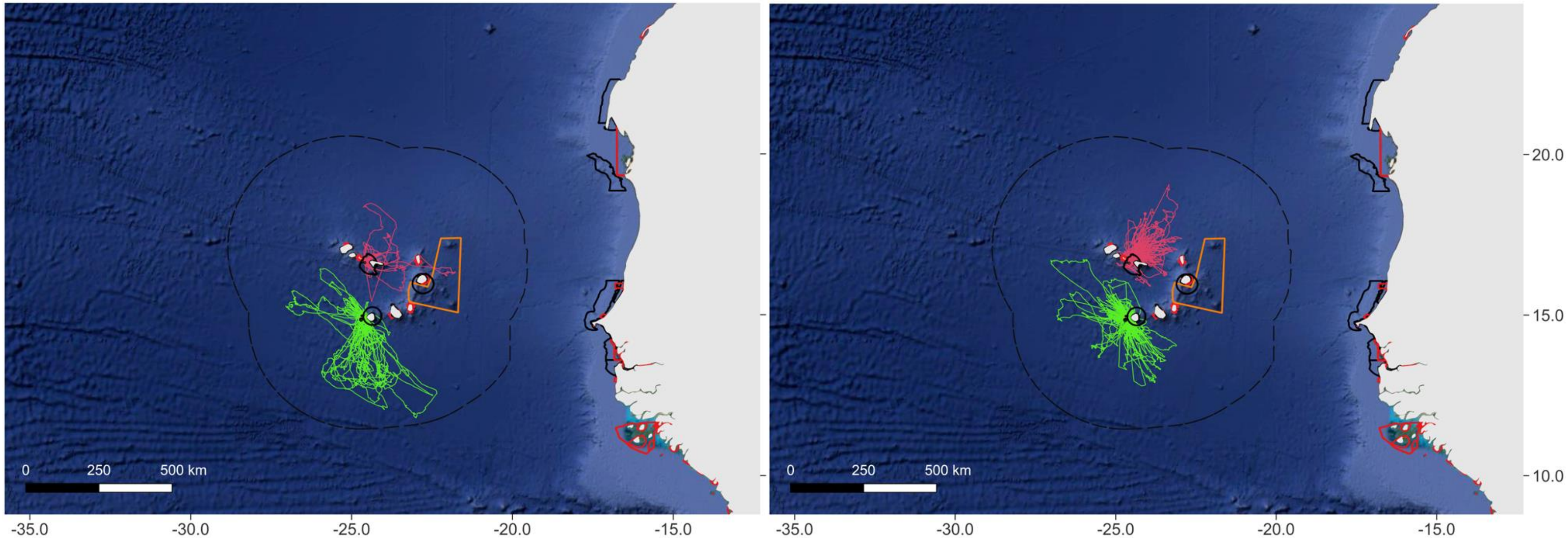


Figure S5.6. Foraging distribution of Cape Verde Little shearwater *Puffinus boydii* from Ilhéus Raso (coral) and Cima (green) during incubation (left) and chick-rearing (right) phases (see Table S1 for further details). Dashed black contour represents the Cabo Verde EEZ, black polygons are current network of Key Biodiversity Areas (https://www.keybiodiversityareas.org), red contours are Marine Protected Areas of Cabo Verde and off West Africa and the orange polygon sets a potential pelagic MPA (Oceania) under designation. Bathymetry in the background.

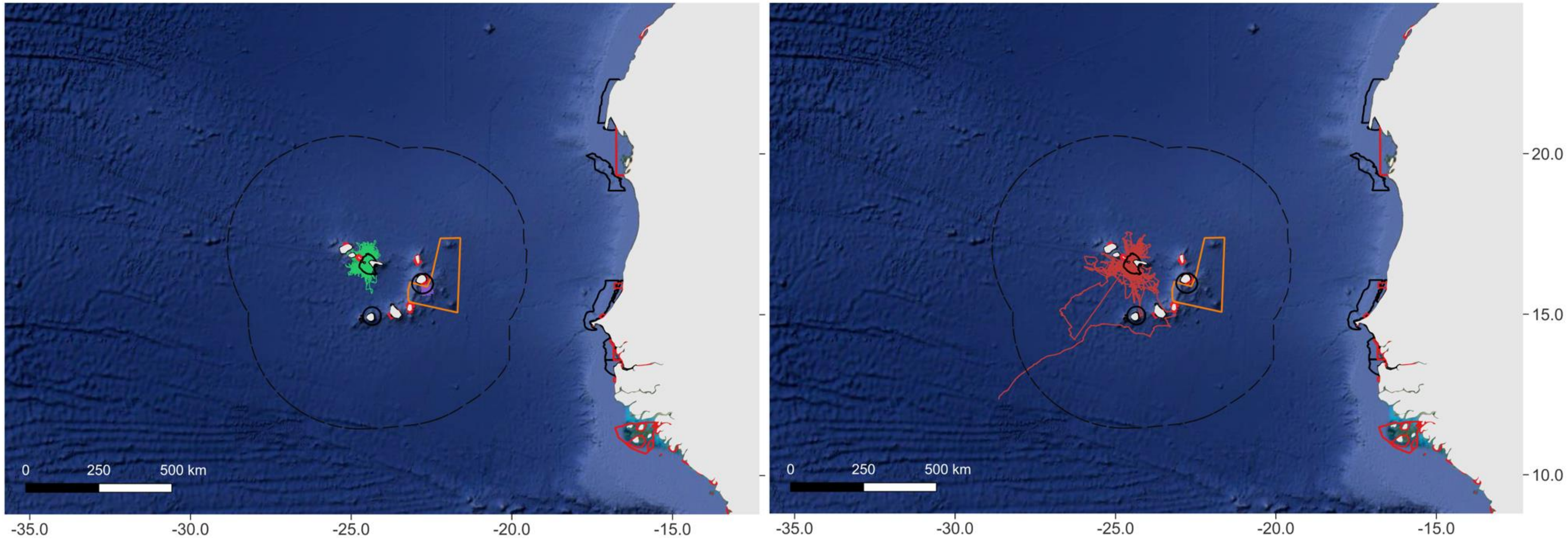


Figure S5.7. Foraging distributions of brown boobies *Sula leucogaster* from Ilhéu Raso (green) and Curral Velho (light blue) during the incubation phase (left) and non-breeding red-footed boobies *Sula sula* from Ilhéu Raso (right) (see Table S1 for further details). Dashed black contour represents the Cabo Verde EEZ, black polygons are current network of Key Biodiversity Areas (https://www.keybiodiversityareas.org), red contours are Marine Protected Areas of Cabo Verde and off West Africa and the orange polygon sets a potential pelagic MPA (Oceania) under designation. Bathymetry in the background.

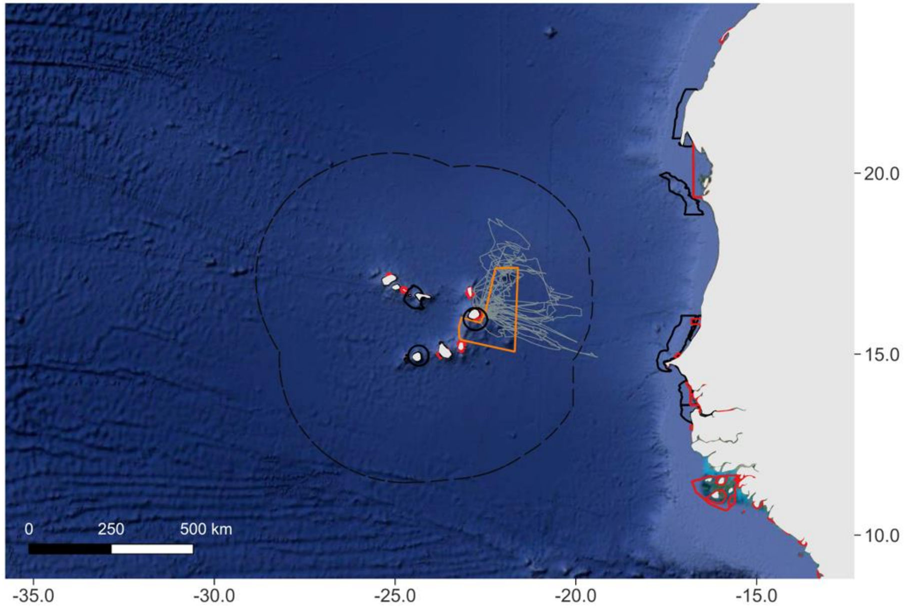


Figure S5.8. Foraging distribution of white-faced storm petrel *Pelagodroma marina* from Ilhéu dos Pássaros during the incubation phase (see Table S1 for further details). Dashed black contour represents the Cabo Verde EEZ, black polygons are current network of Key Biodiversity Areas (https://www.keybiodiversityareas.org), red contours are Marine Protected Areas of Cabo Verde and off West Africa and the orange polygon sets a potential pelagic MPA (Oceania) under designation. Bathymetry in the background.

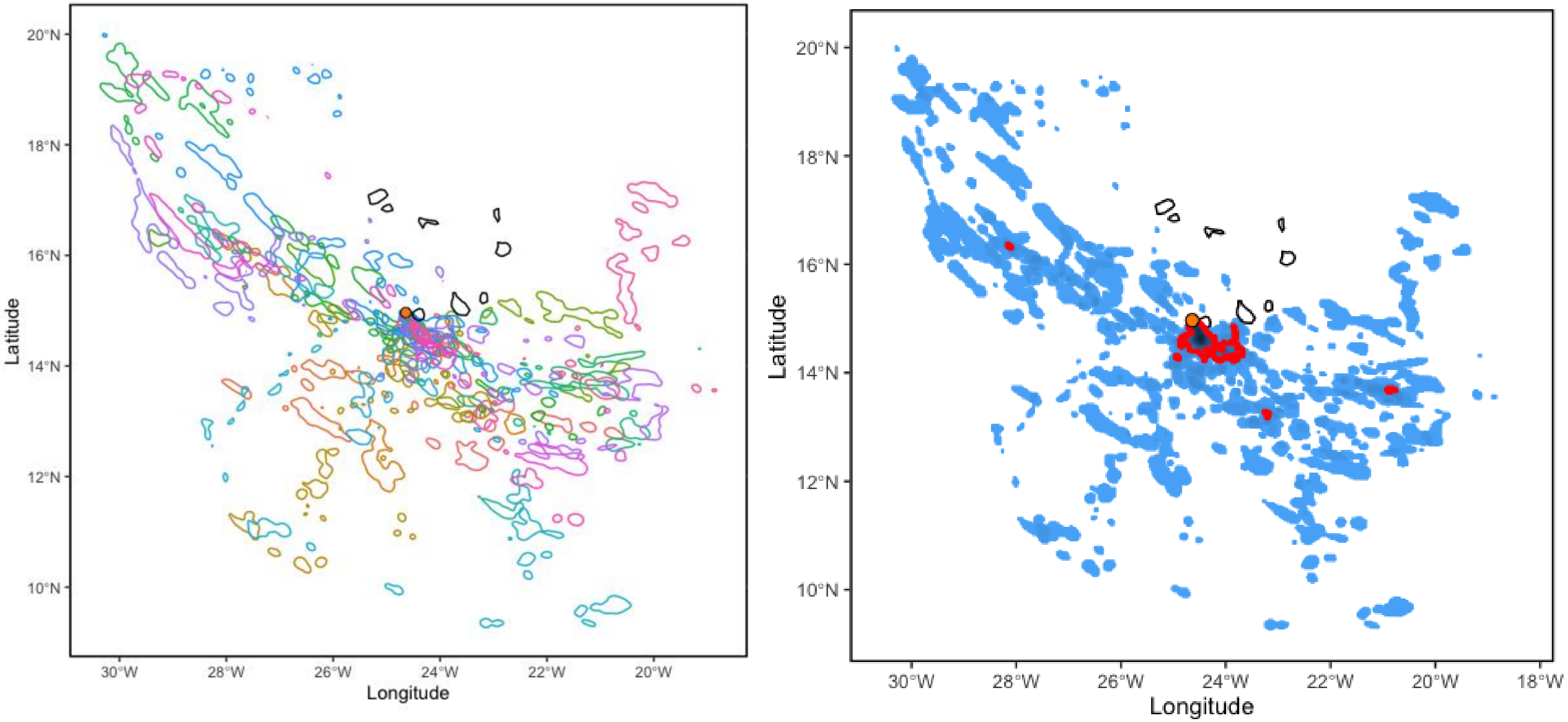


Figure S5.9. 50% Kernel Utilization distributions (UD) (left) and Key Biodiversity Area (KBA) (right) of Bulwer's petrels from Ilhéu de Cima (Fogo, Cabo Verde) during the incubation phase. Different colours are different individuals (left) and red polygon represents proposed KBA at 88.5% representativeness (right). Central dot represents the breeding colony.

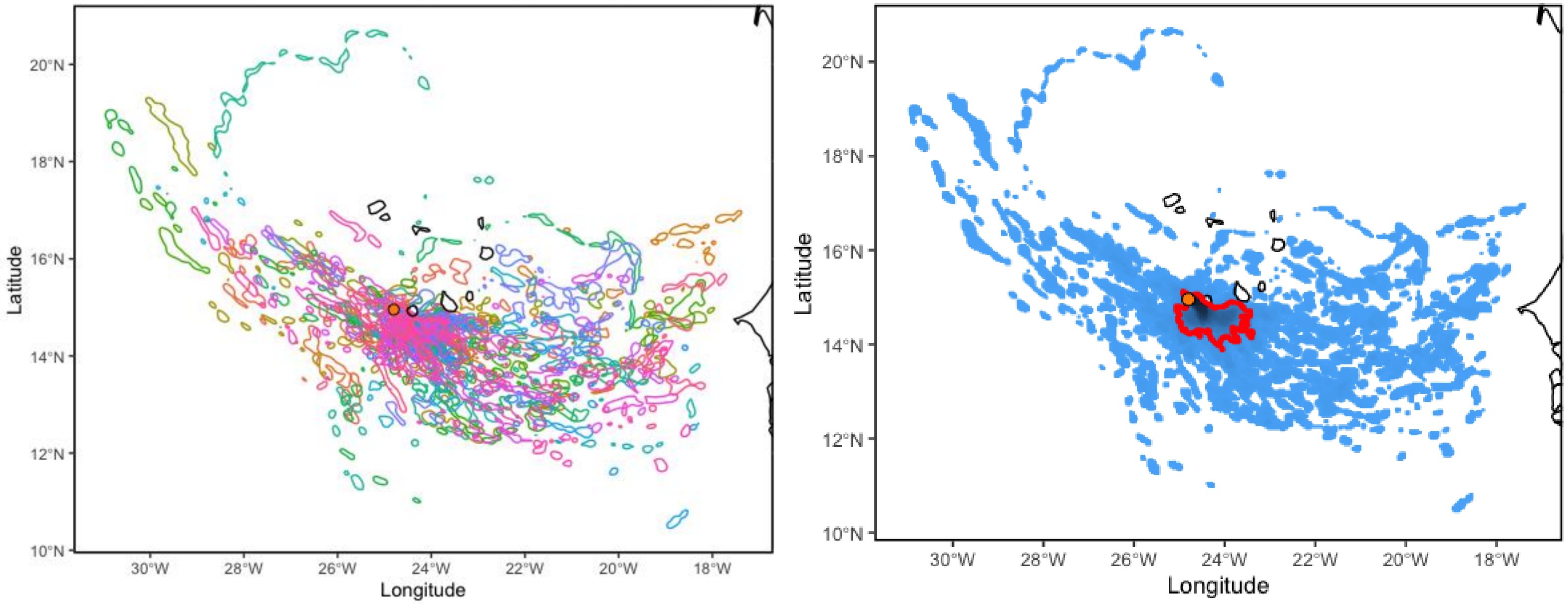


Figure S5.10. 50% Kernel Utilization distributions (UD) (left) and Key Biodiversity Area (KBA) (right) of Bulwer's petrels from Ilhéu de Cima (Fogo, Cabo Verde) during the chick-rearing phase. Different colours are different individuals (left) and red polygon represents proposed KBA at 97.2% representativeness (right). Central dot represents the breeding colony.

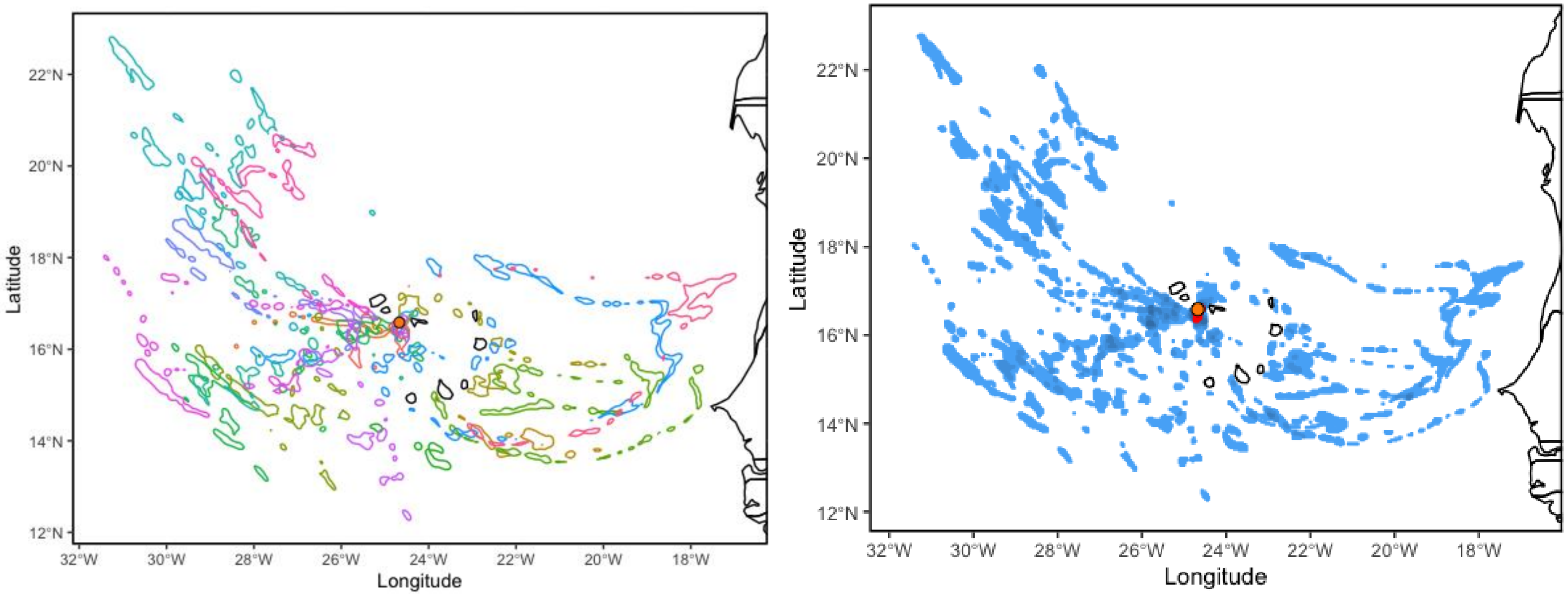


Figure S5.11. 50% Kernel Utilization distributions (UD) (left) and Key Biodiversity Area (KBA) (right) of Bulwer's petrels from Ilhéu Raso (S. Nicolau, Cabo Verde) during the incubation phase. Different colours are different individuals (left) and red polygon represents proposed KBA at 74 % representativeness (right). Central dot represents the breeding colony.

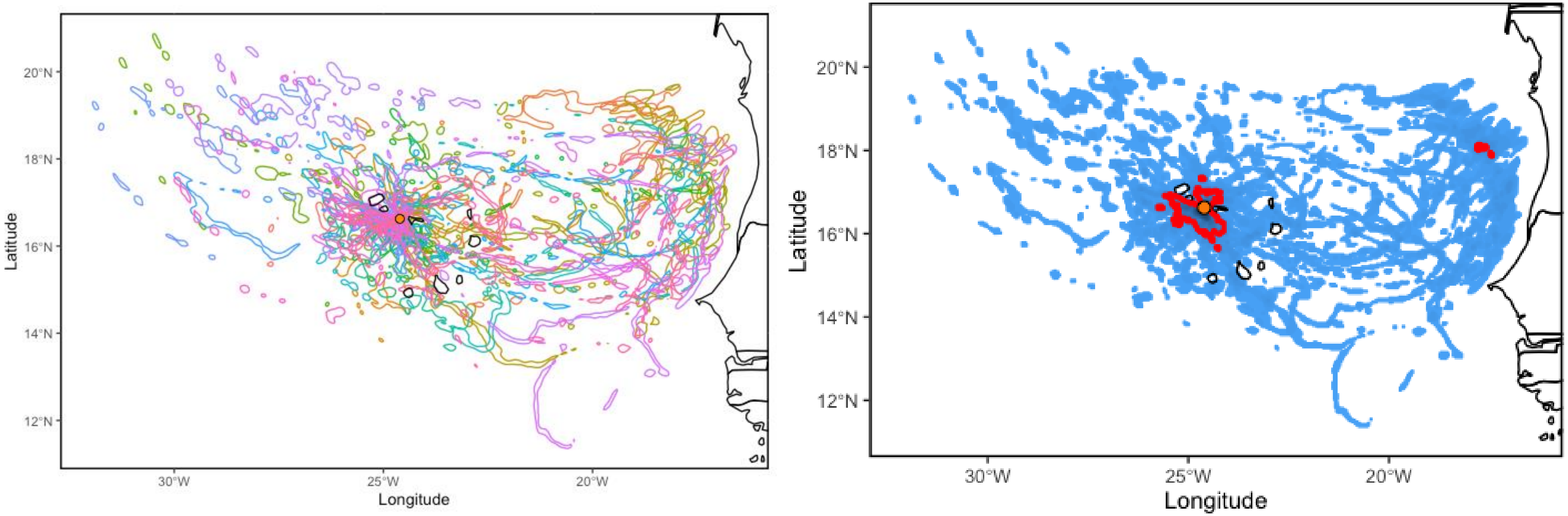


Figure S5.12. 50% Kernel Utilization distributions (UD) (left) and Key Biodiversity Area (KBA) (right) of Bulwer's petrels from Ilhéu Raso (S. Nicolau, Cabo Verde) during the chick-rearing phase. Different colours are different individuals (left) and red polygon represents proposed KBA at 91.2 % representativeness (right). Central dot represents the breeding colony.

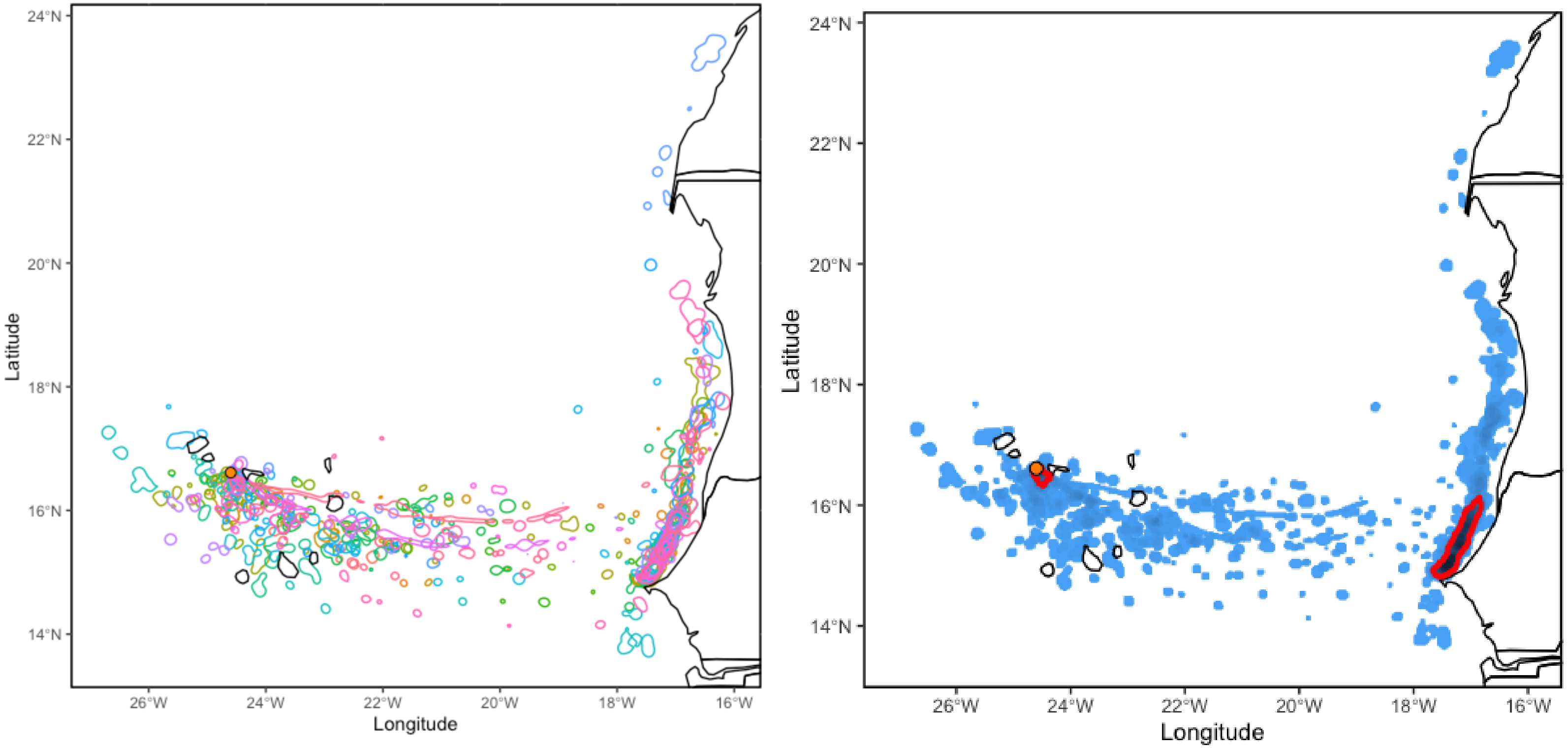


Figure S5.13. 50% Kernel Utilization distributions (UD) (left) and Key Biodiversity Area (KBA) (right) of Cape Verde shearwaters from Ilhéu Raso (S. Nicolau, Cabo Verde) during the incubation phase. Different colours are different individuals (left) and red polygon represents proposed KBA at 93.4 % representativeness (right). Central dot represents the breeding colony.

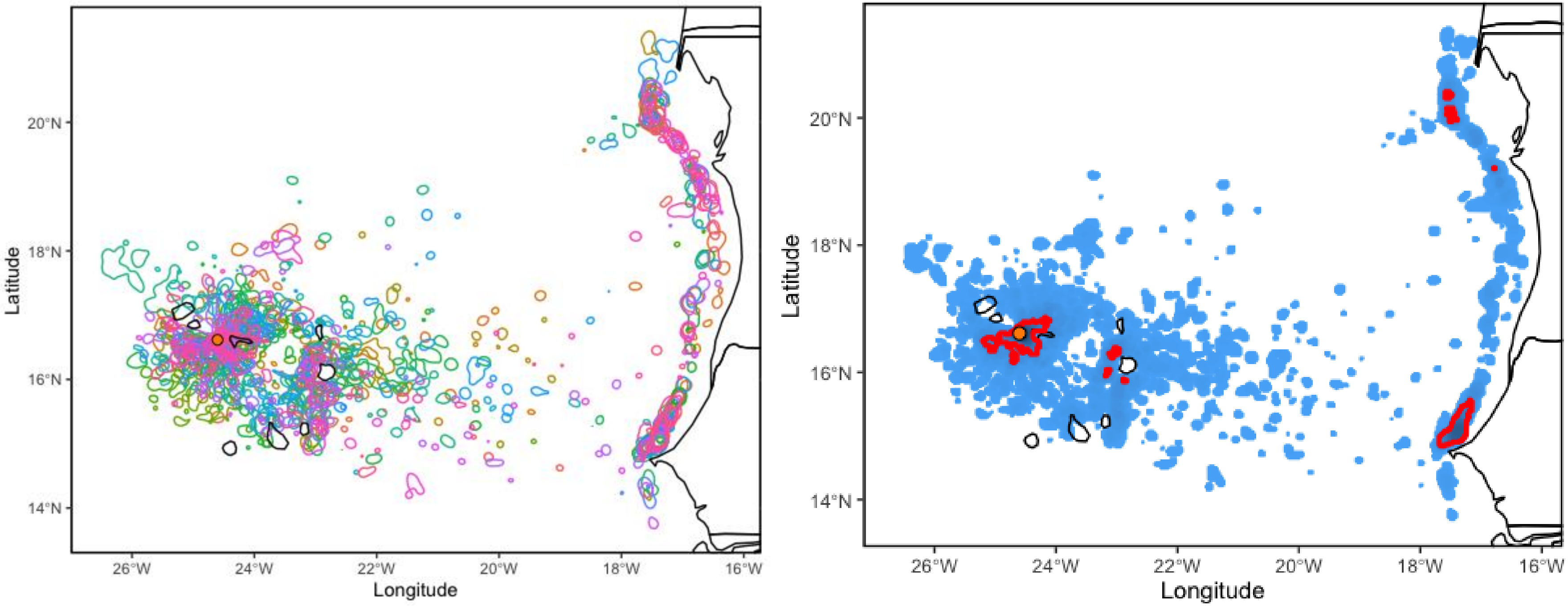


Figure S5.14. 50% Kernel Utilization distributions (UD) (left) and Key Biodiversity Area (KBA) (right) of Cape Verde shearwaters from Ilhéu Raso (S. Nicolau, Cabo Verde) during the chick-rearing phase. Different colours are different individuals (left) and red polygon represents proposed KBA at 94.3 % representativeness (right). Central dot represents the breeding colony.

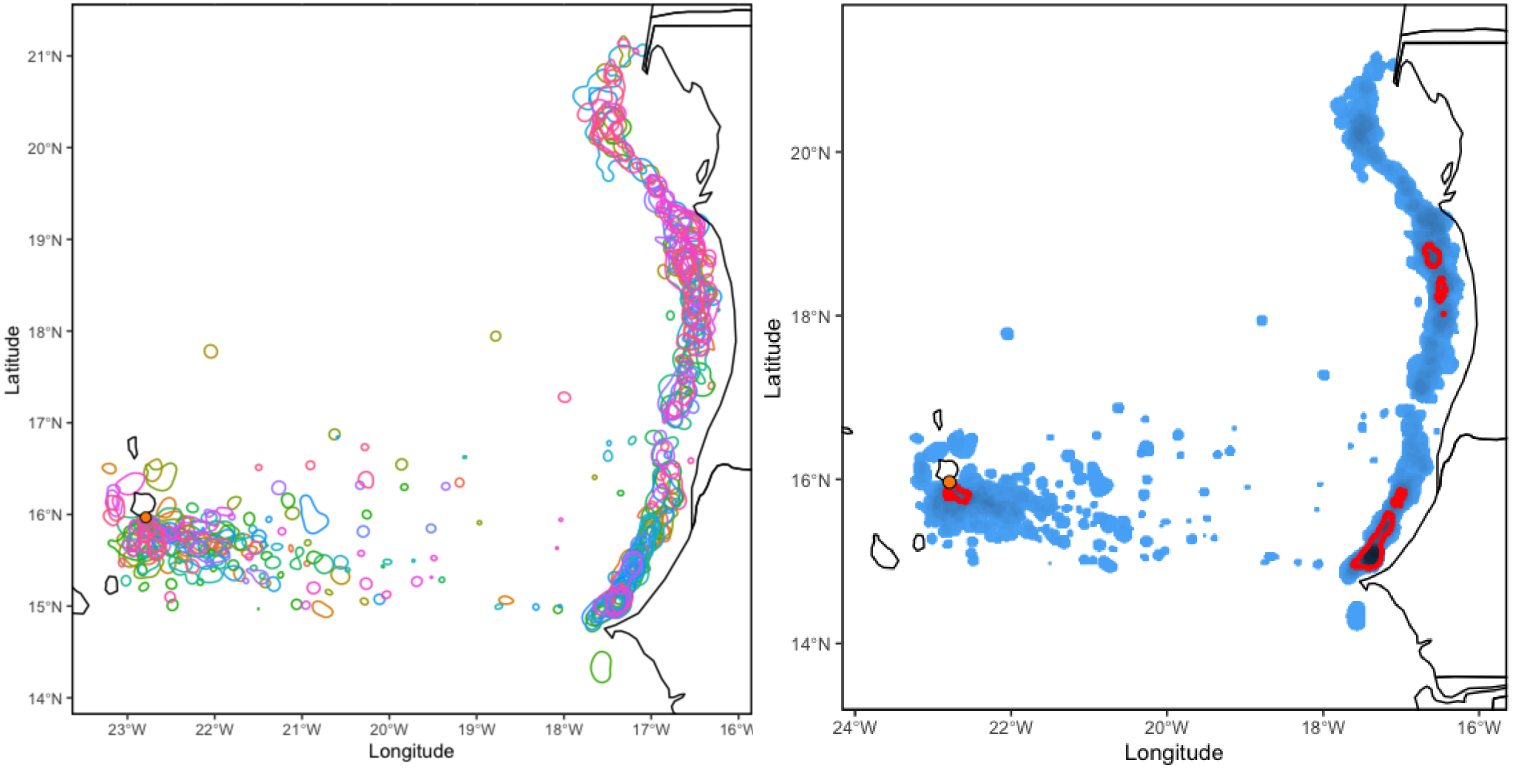


Figure S5.15. 50% Kernel Utilization distributions (UD) (left) and Key Biodiversity Area (KBA) (right) of Cape Verde shearwaters from Curral Velho (Boavista, Cabo Verde) during the incubation phase. Different colours are different individuals (left) and red polygon represents proposed KBA at 94.5 % representativeness (right). Central dot represents the breeding colony.

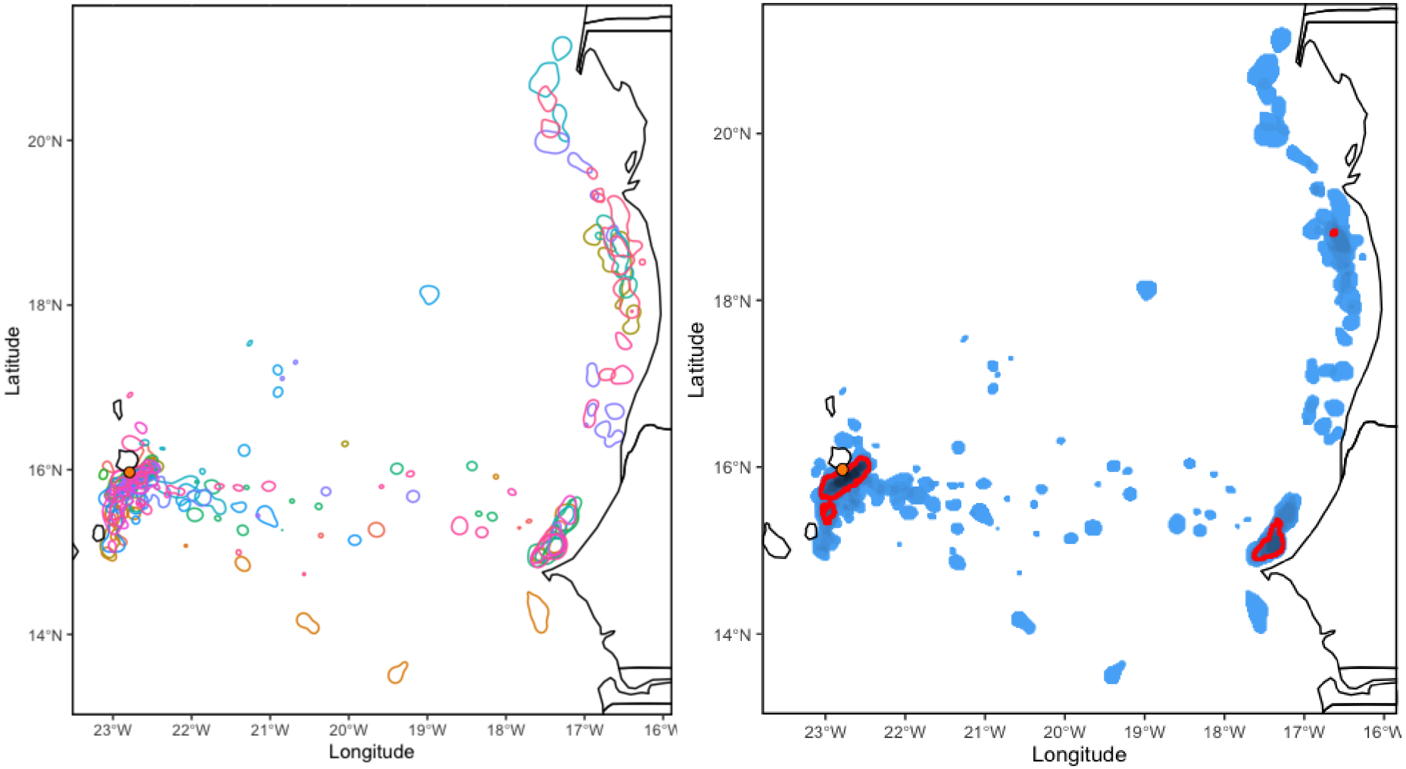


Figure S5.16. 50% Kernel Utilization distributions (UD) (left) and Key Biodiversity Area (KBA) (right) of Cape Verde shearwaters from Curral Velho (Boavista, Cabo Verde) during the chick-rearing phase. Different colours are different individuals (left) and red polygon represents proposed KBA at 91.1 % representativeness (right). Central dot represents the breeding colony.

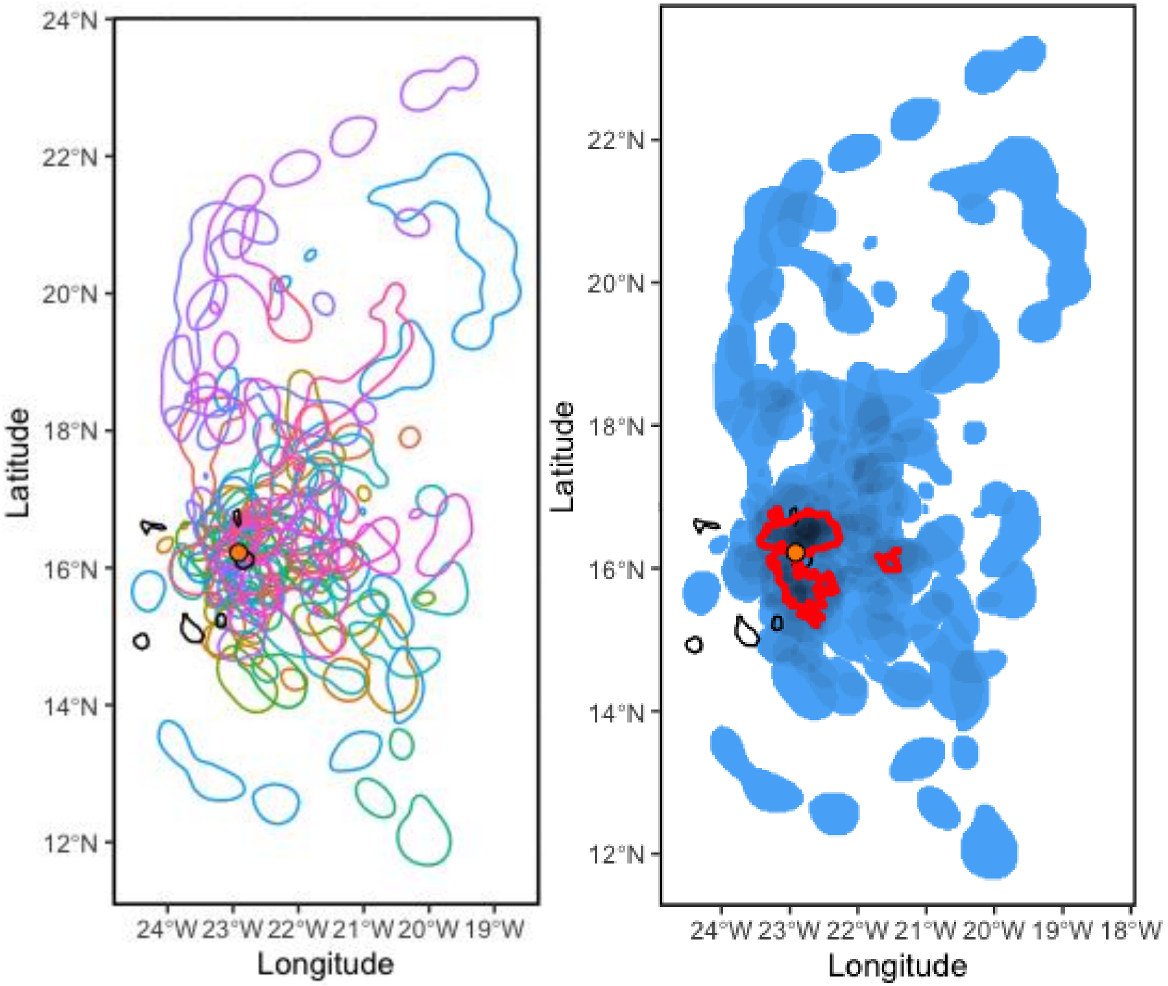


Figure S5.17. 50% Kernel Utilization distributions (UD) (left) and Key Biodiversity Area (KBA) (right) of red-billed tropicbird from Ponta Rincon (Boavista, Cabo Verde) during the incubation phase. Different colours are different individuals (left) and red polygon represents proposed KBA at 82.9% representativeness (right). Central dot represents the breeding colony.

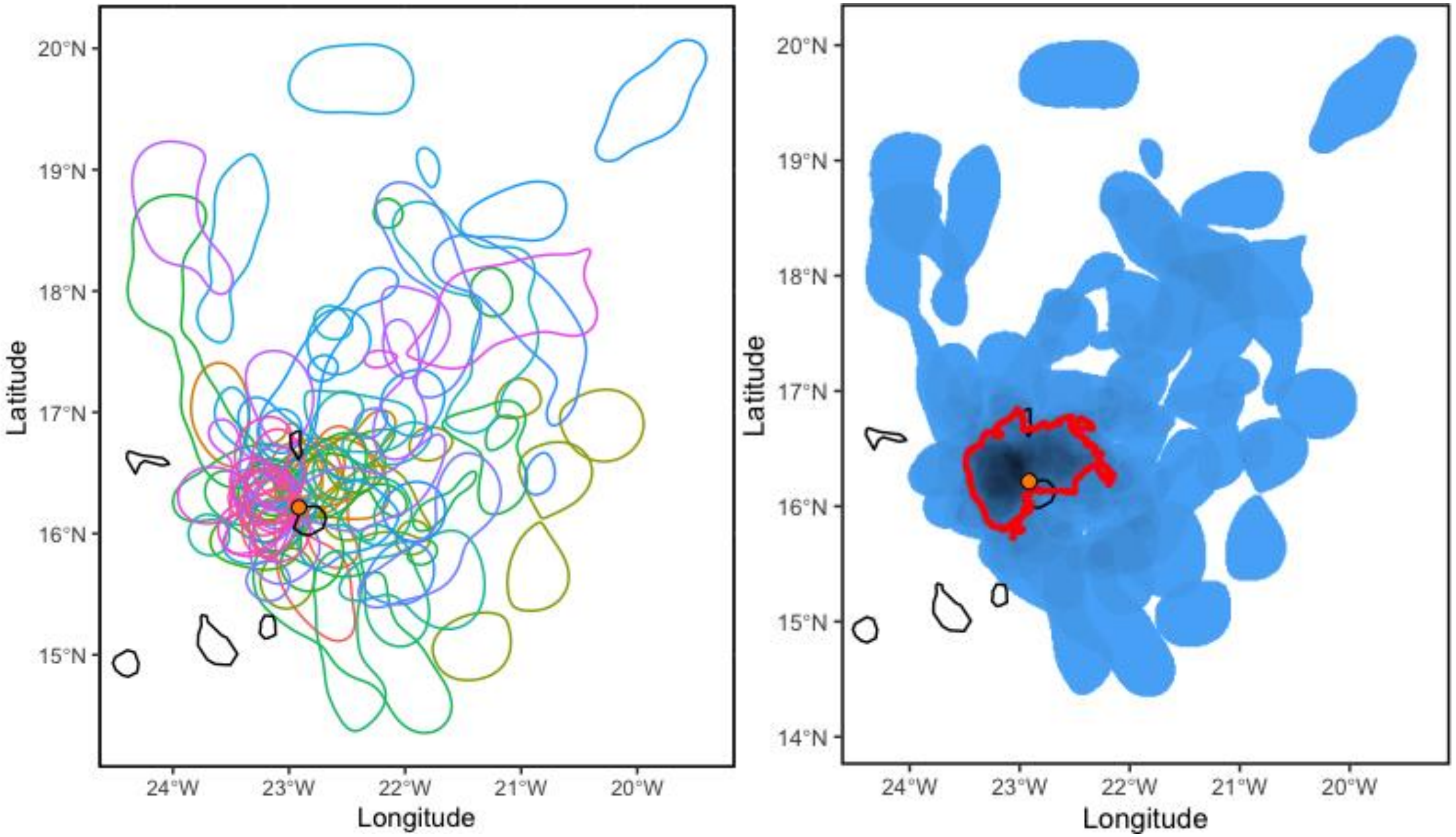


Figure S5.18. 50% Kernel Utilization distributions (UD) (left) and Key Biodiversity Area (KBA) (right) of red-billed tropicbird from Ponta Rincon (Boavista, Cabo Verde) during the chick-rearing phase. Different colours are different individuals (left) and red polygon represents proposed KBA at 95.8% representativeness (right). Central dot represents the breeding colony.

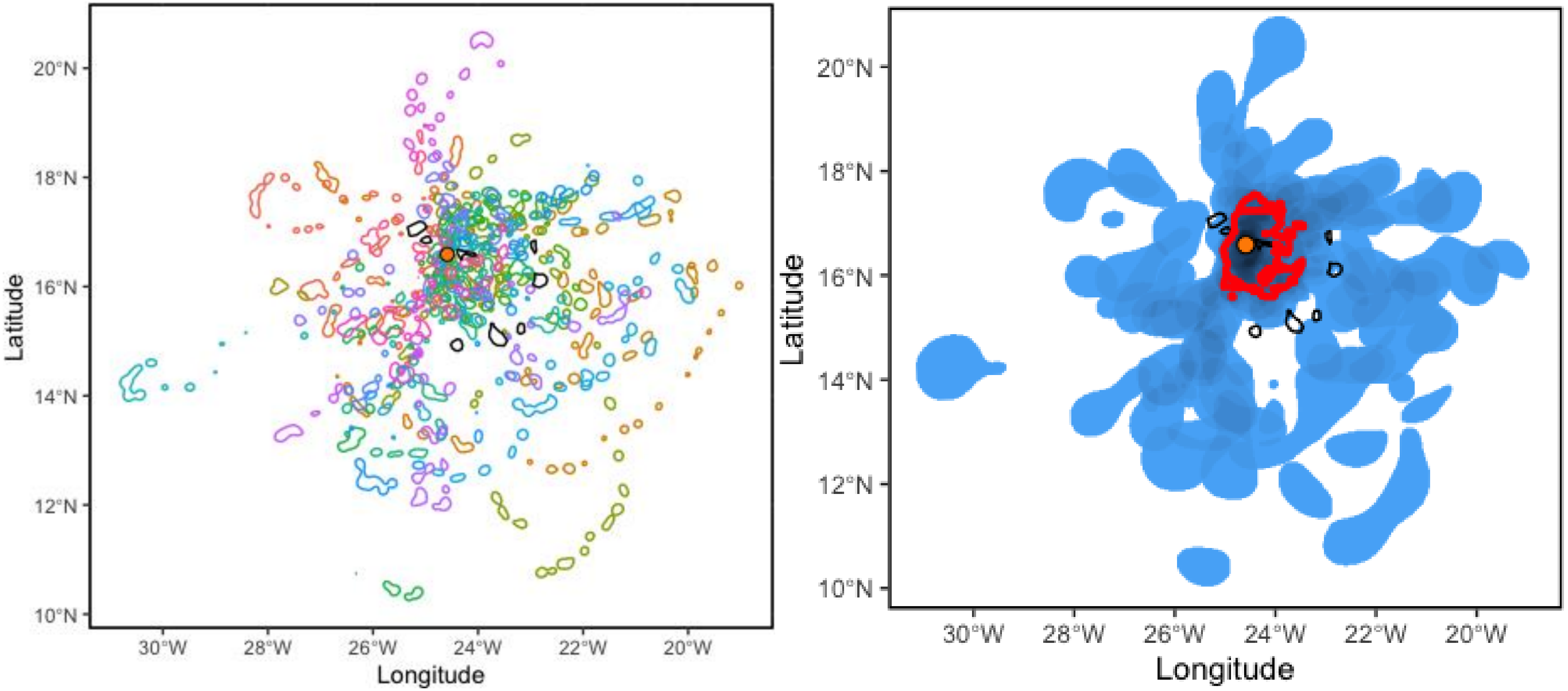


Figure S5.19. 50% Kernel Utilization distributions (UD) (left) and Key Biodiversity Area (KBA) (right) of red-billed tropicbird from Ilhéu Raso (São Nicolau, Cabo Verde). Different colours are different individuals (left) and red polygon represents proposed KBA at 87.7% representativeness (right). Central dot represents the breeding colony.

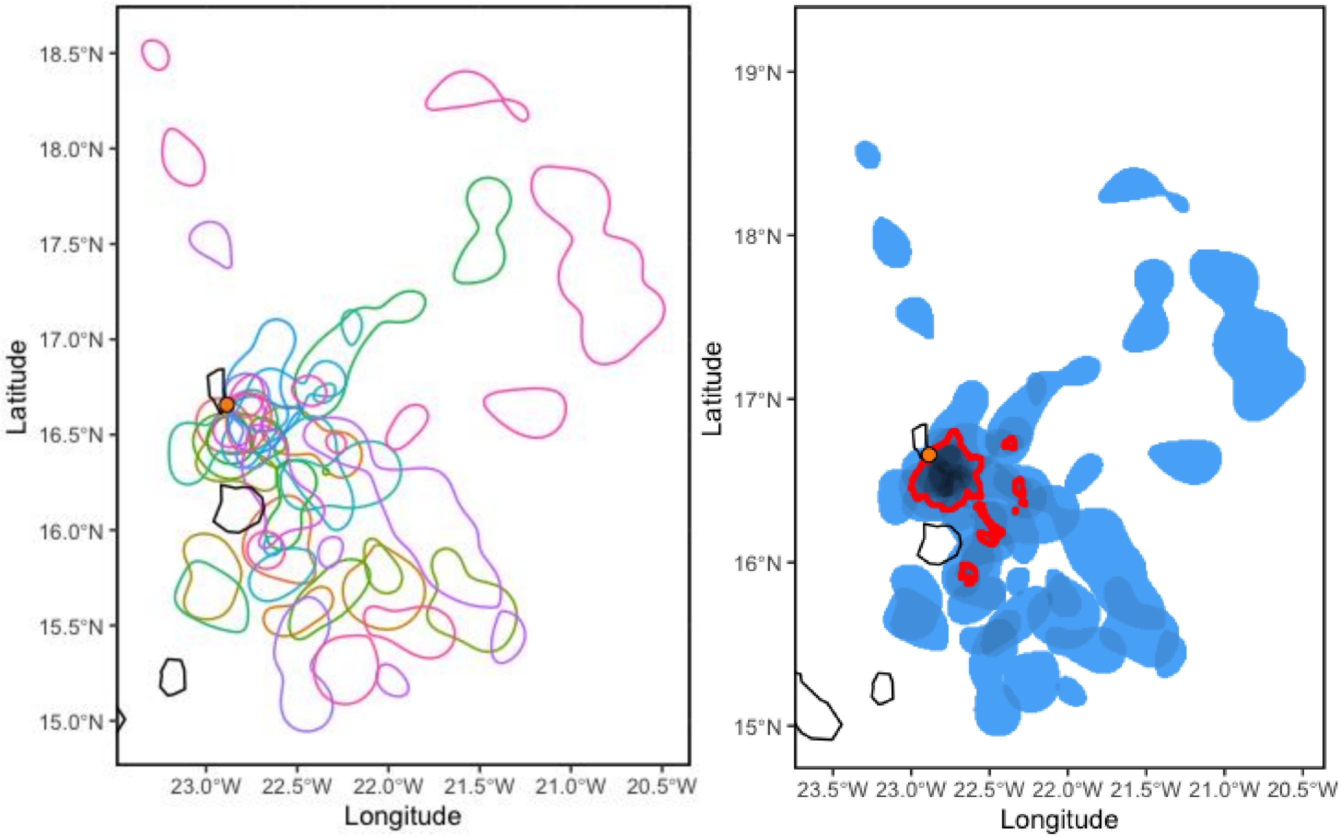


Figure S5.20. 50% Kernel Utilization distributions (UD) (left) and Key Biodiversity Area (KBA) (right) of red-billed tropicbird from Serra Negra (Sal, Cabo Verde). Different colours are different individuals (left) and red polygon represents proposed KBA at 83.8% representativeness (right). Central dot represents the breeding colony.

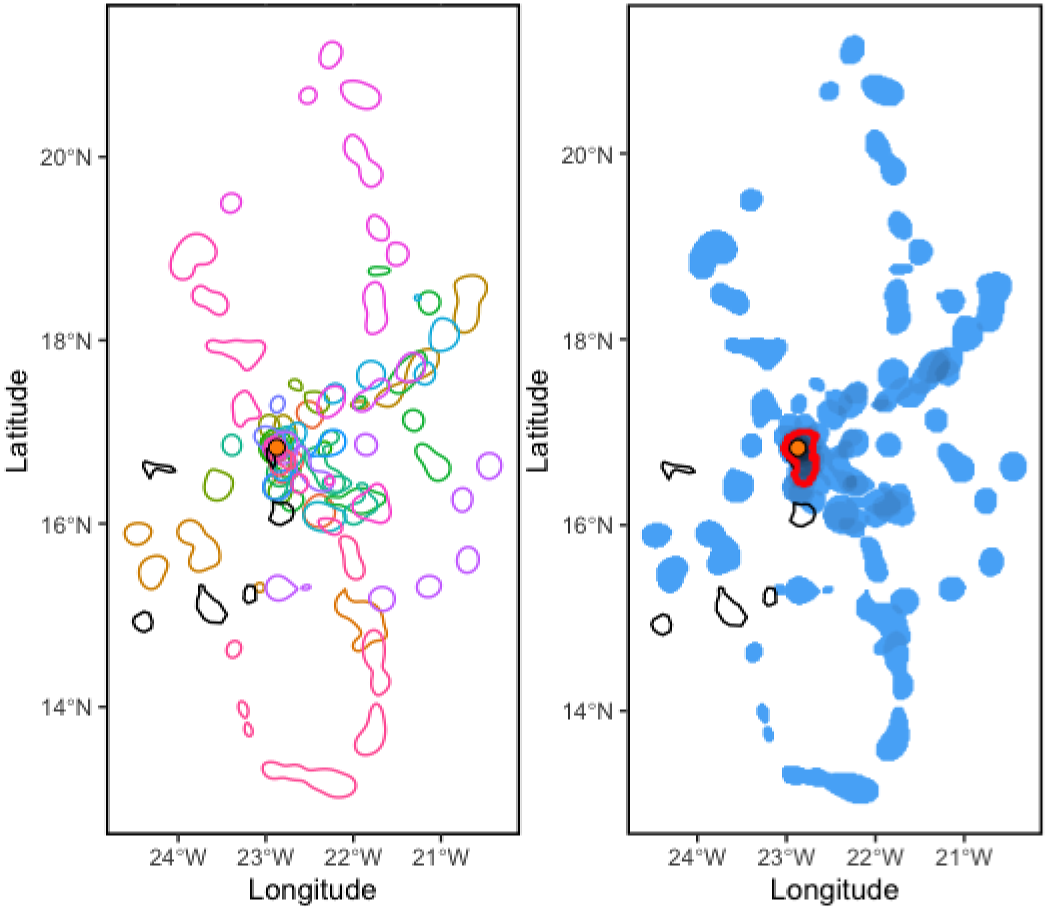


Figure S5.21. 50% Kernel Utilization distributions (UD) (left) and Key Biodiversity Area (KBA) (right) of red-billed tropicbird from Cadjetinha e Furna (Sal, Cabo Verde). Different colours are different individuals (left) and red polygon represents proposed KBA at 89.7% representativeness (right). Central dot represents the breeding colony.

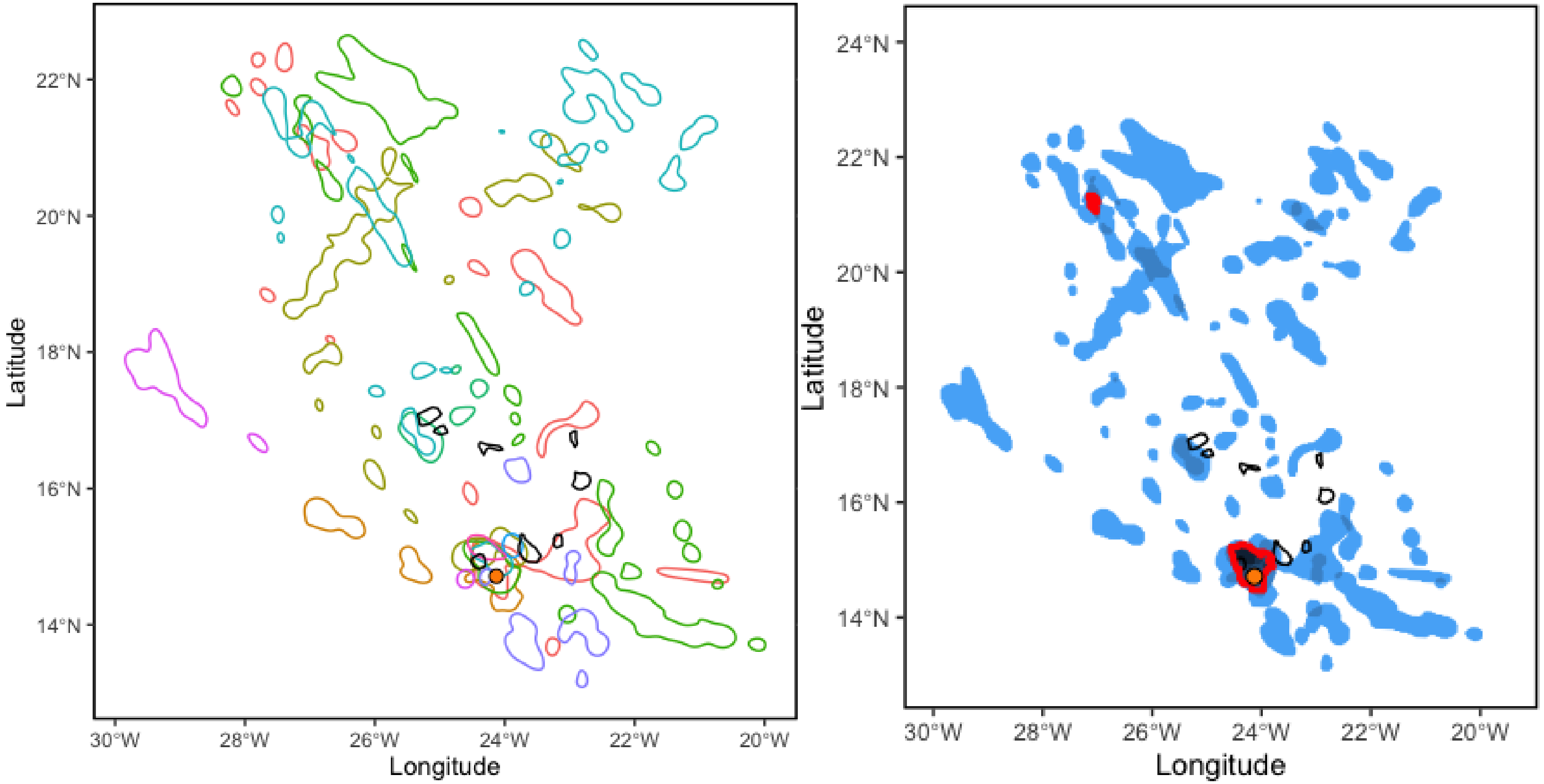


Figure S5.22. 50% Kernel Utilization distributions (UD) (left) and Key Biodiversity Area (KBA) (right) of Cape Verde Petrel from Fogo (Fogo, Cabo Verde). Different colours are different individuals (left) and red polygon represents proposed KBA at 70.9% representativeness (right). Central dot represents the breeding colony.

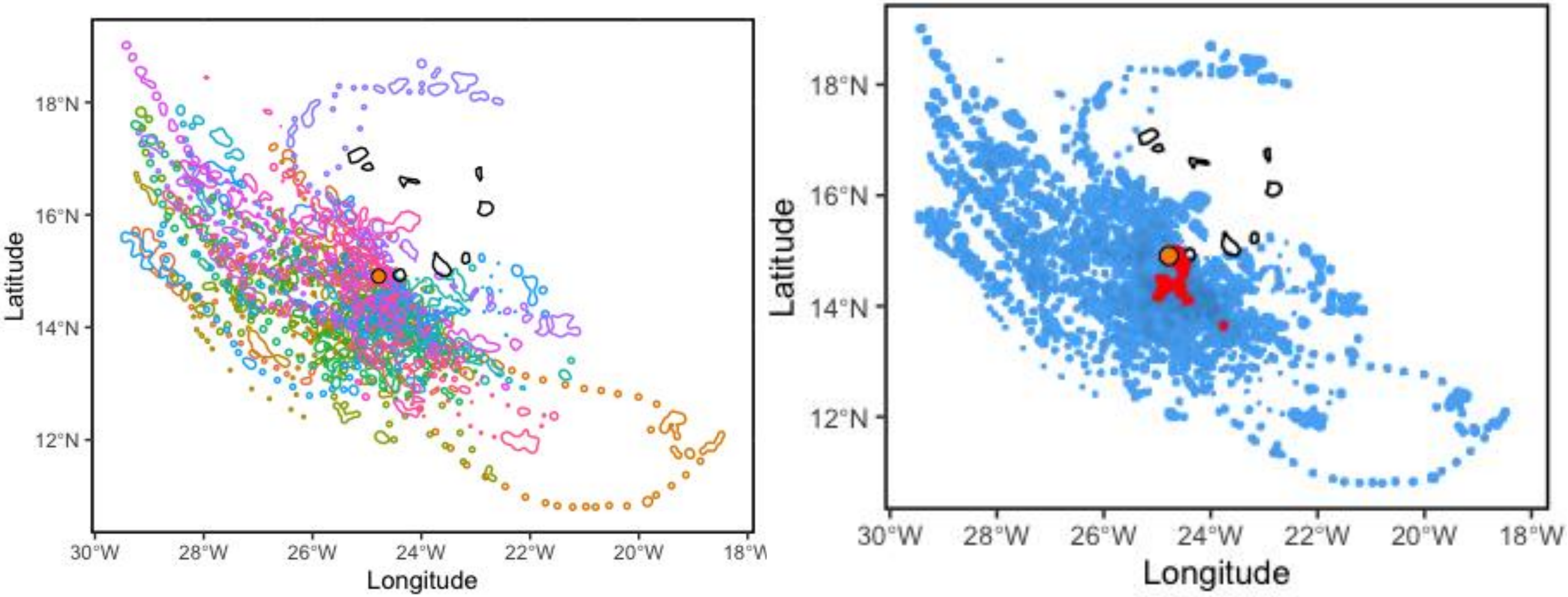


Figure S5.23. 50% Kernel Utilization distributions (UD) (left) and Key Biodiversity Area (KBA) (right) of Cape Verde storm petrel from Ilhéu de Cima (Fogo, Cabo Verde). Different colours are different individuals (left) and red polygon represents proposed KBA at 85.9 % representativeness (right). Central dot represents the breeding colony.

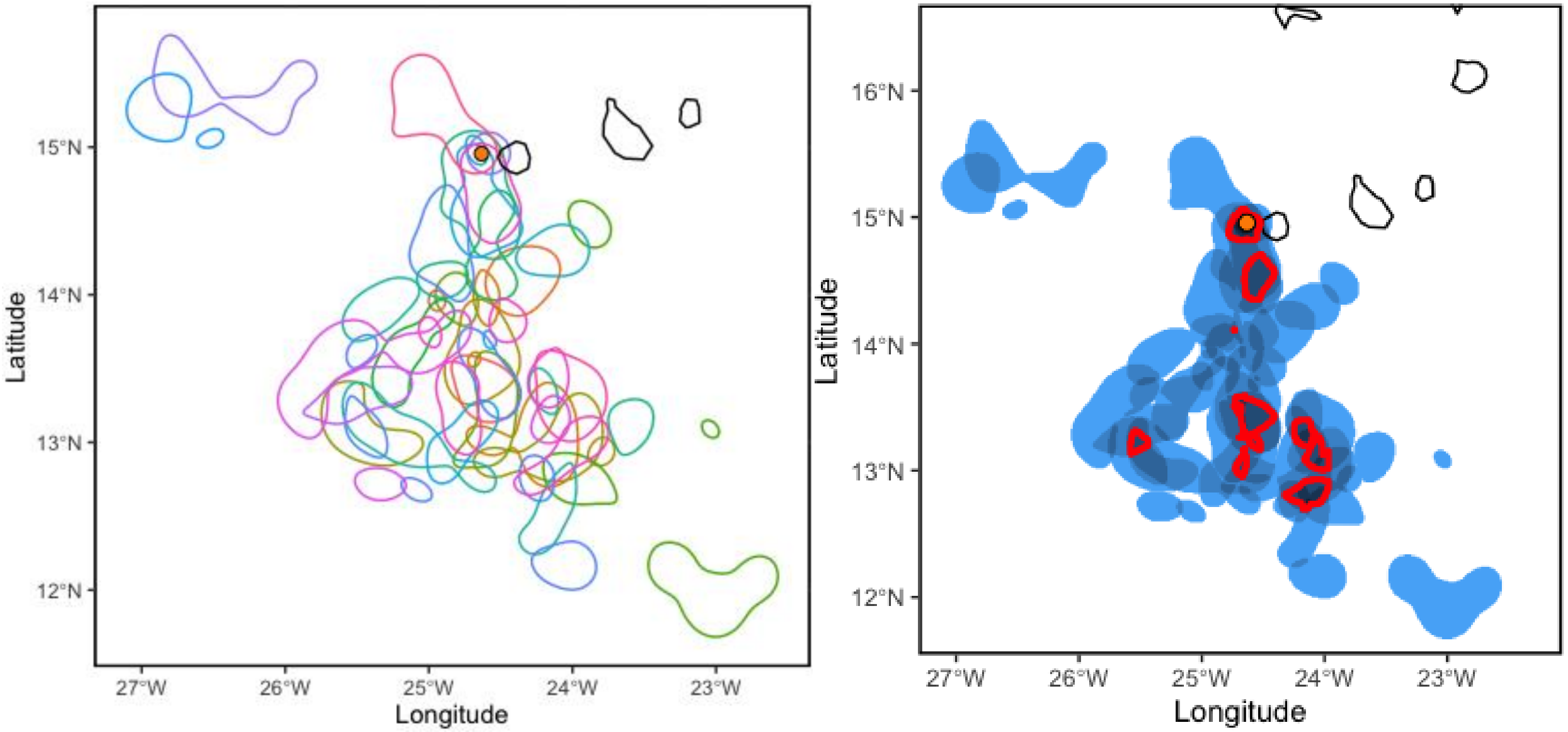


Figure S5.24. 50% Kernel Utilization distributions (UD) (left) and Key Biodiversity Area (KBA) (right) of Cape Verde little shearwater from Ilhéu de Cima (Fogo, Cabo Verde) during the incubation phase. Different colours are different individuals (left) and red polygon represents proposed KBA at 78.3 % representativeness (right). Central dot represents the breeding colony.

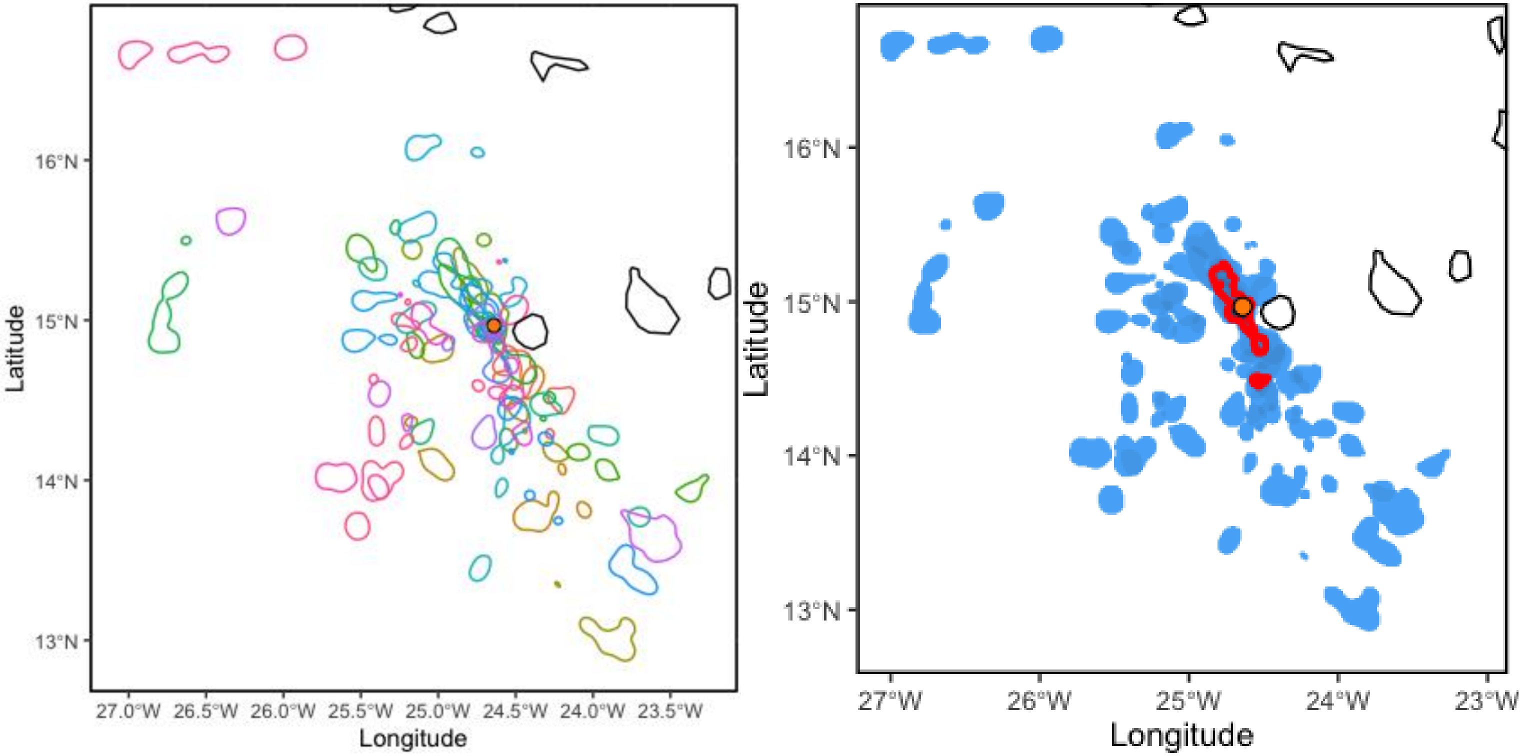


Figure S5.25. 50% Kernel Utilization distributions (UD) (left) and Key Biodiversity Area (KBA) (right) of Cape Verde little shearwater from Ilhéu de Cima (Fogo, Cabo Verde) during the chick-rearing phase. Different colours are different individuals (left) and red polygon represents proposed KBA at 86.9 % representativeness (right). Central dot represents the breeding colony.

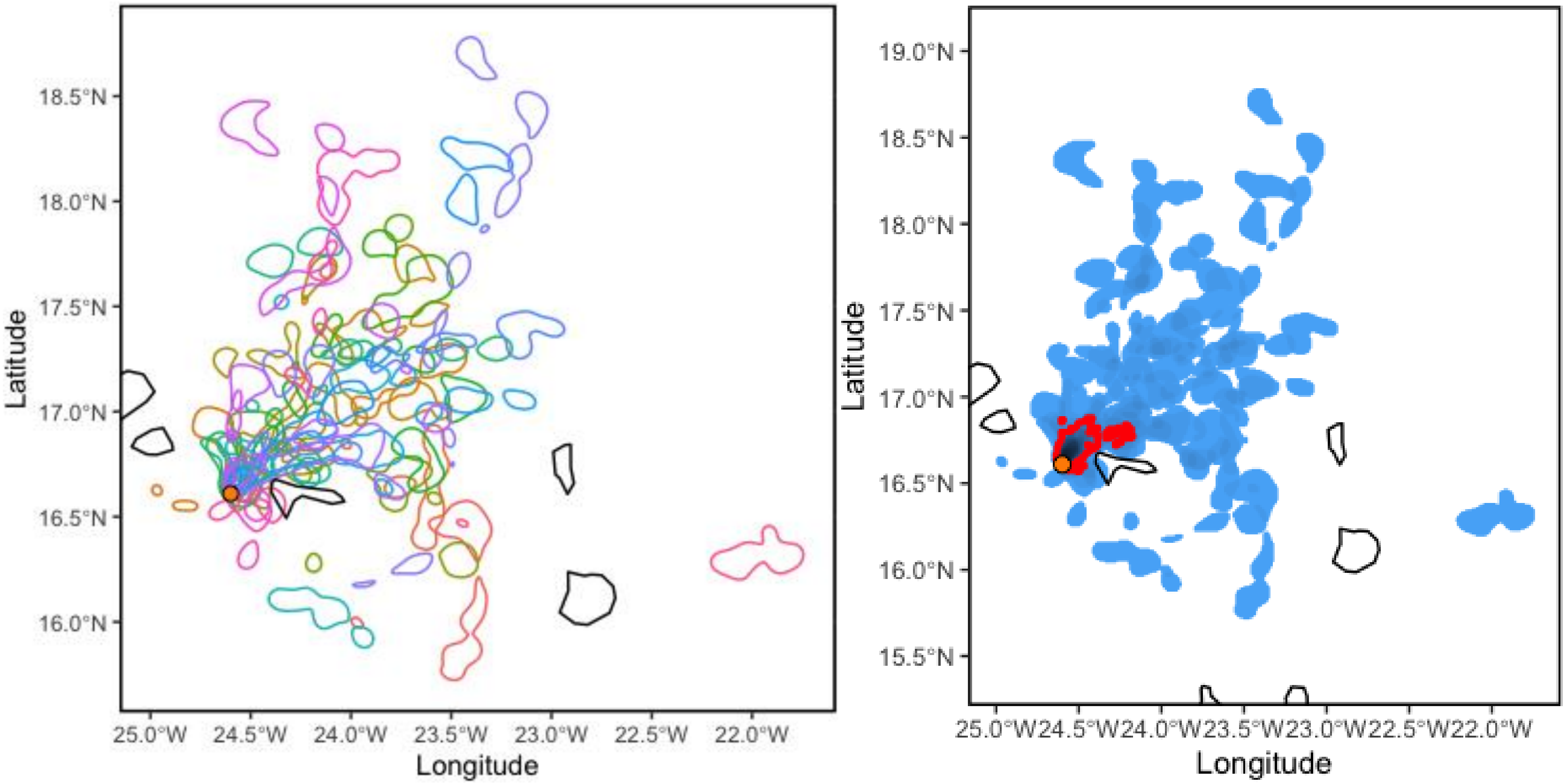


Figure S5.26. 50% Kernel Utilization distributions (UD) (left) and Key Biodiversity Area (KBA) (right) of Cape Verde little shearwater from Ilhéu Raso (São Nicolau, Cabo Verde). Different colours are different individuals (left) and red polygon represents proposed KBA at 86.5 % representativeness (right). Central dot represents the breeding colony.

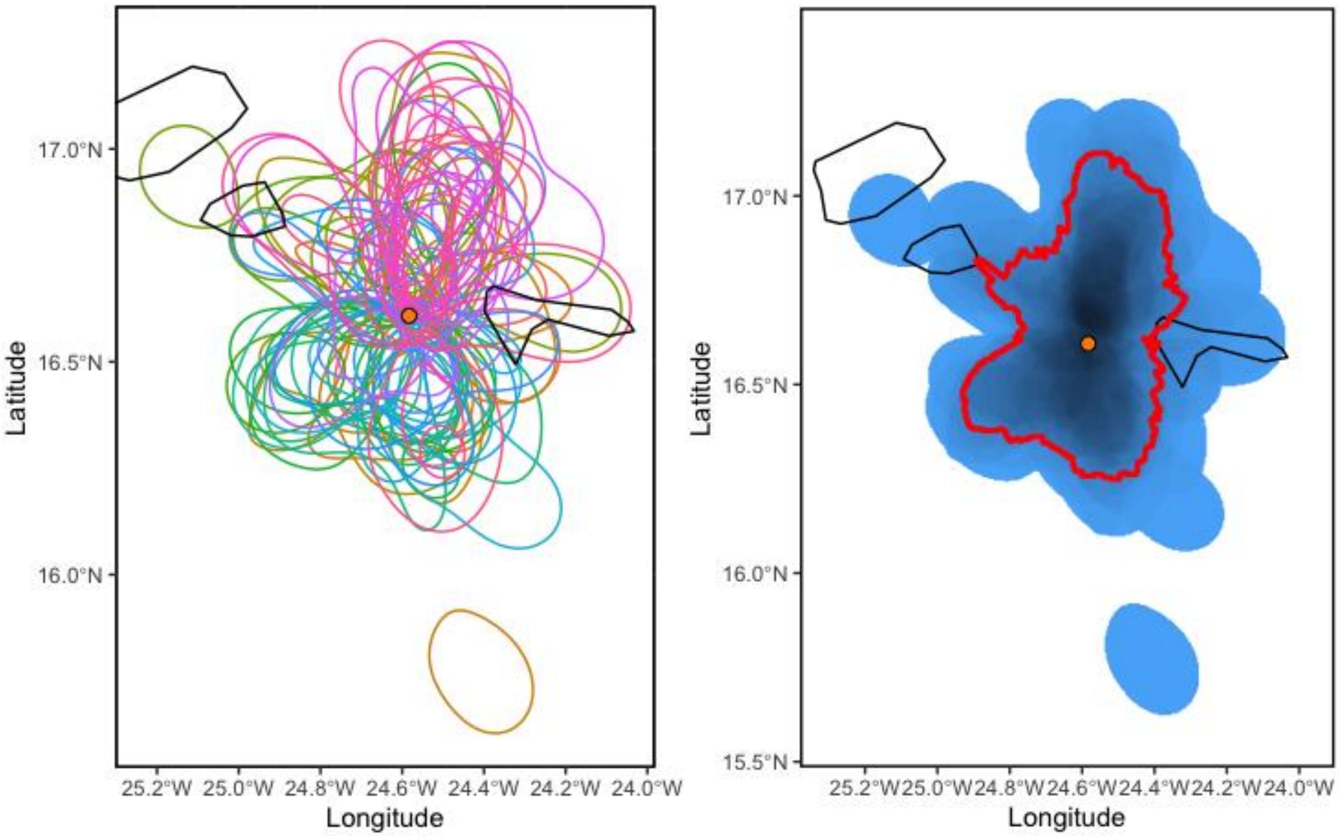


Figure S5.27. 50% Kernel Utilization distributions (UD) (left) and Key Biodiversity Area (KBA) (right) of Brown boobies from Ilhéu Raso (São Nicolau, Cabo Verde). Different colours are different individuals (left) and red polygon represents proposed KBA at 97.6 % representativeness (right). Central dot represents the breeding colony.

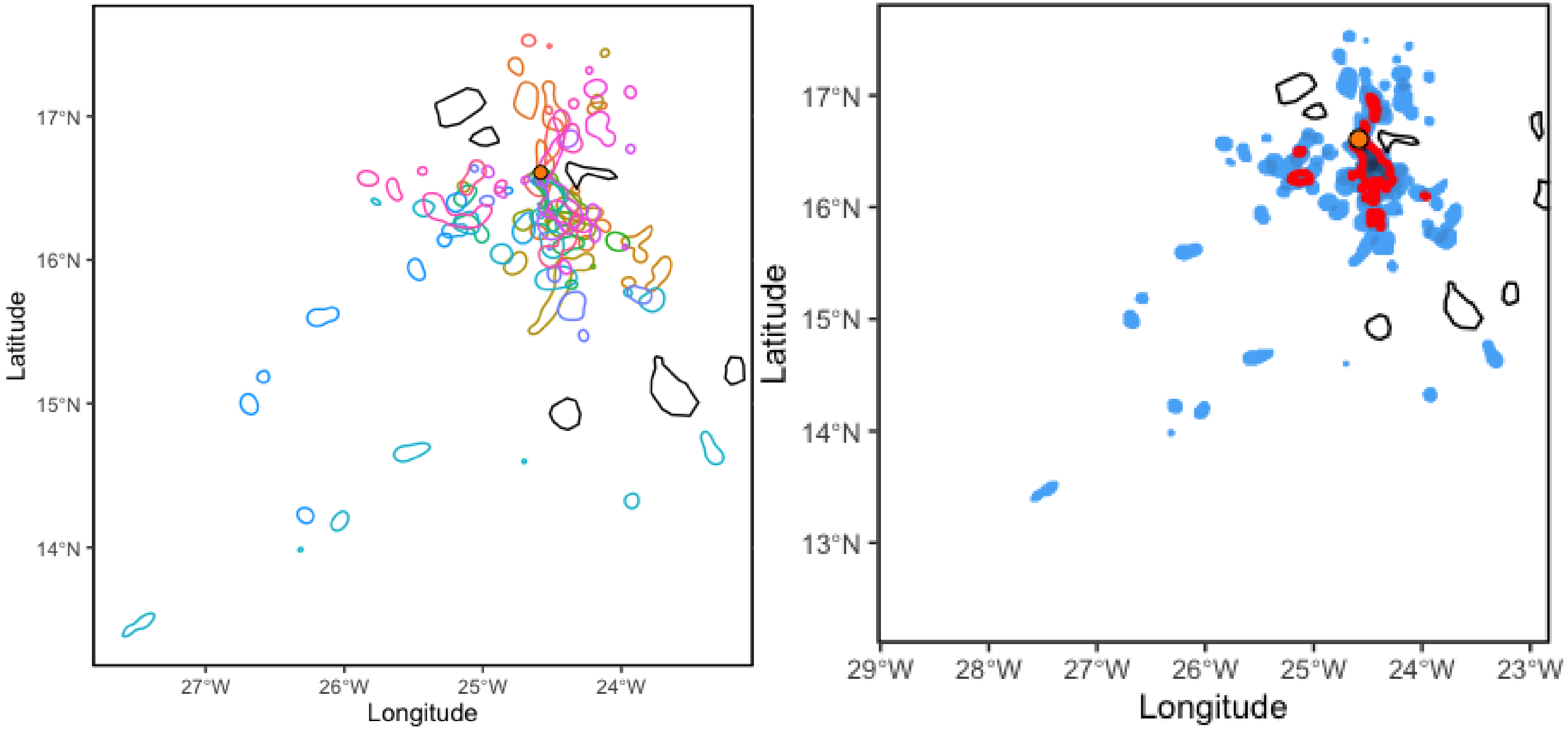


Figure S5.28. 50% Kernel Utilization distributions (UD) (left) and Key Biodiversity Area (KBA) (right) of red-footed boobies from Ilhéu Raso (São Nicolau, Cabo Verde). Different colours are different individuals (left) and red polygon represents proposed KBA at 82.5 % representativeness (right). Central dot represents the breeding colony.

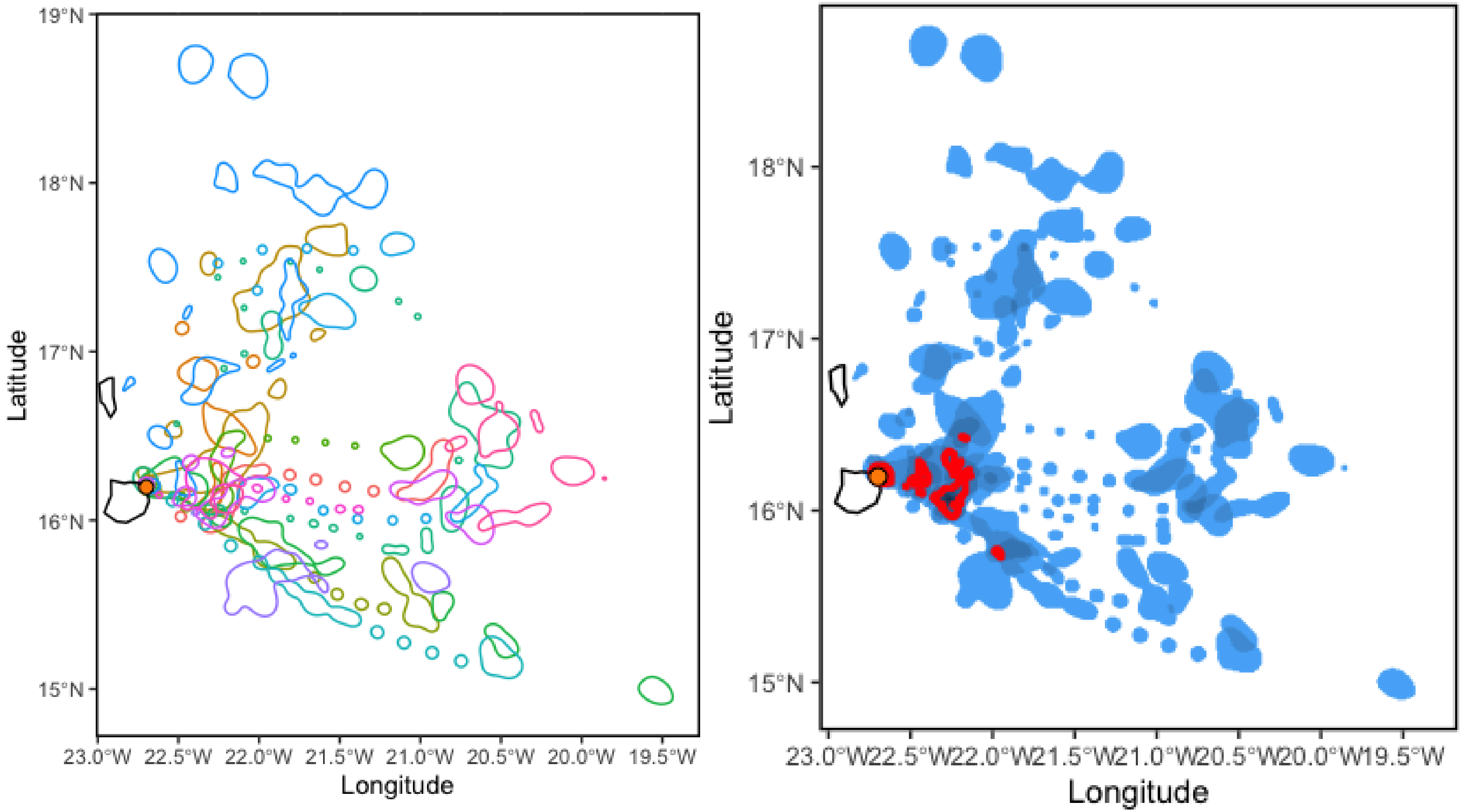


Figure S5.29. 50% Kernel Utilization distributions (UD) (left) and Key Biodiversity Area (KBA) (right) of white-faced storm petrel from Ilhéu dos Pássaros (Boavista, Cabo Verde). Different colours are different individuals (left) and red polygon represents proposed KBA at 76.9 % representativeness (right). Central dot represents the breeding colony