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IDENTIFICATION OF CANDIDATE PELAGIC MARINE PROTECTED AREAS (MPAs) OFF WEST AFRICA: EVALUATING THEIR EFFECTIVENESS IN PROTECTING MARINE PREDATORS AND RISK OF FISHERY BYCATCH

VOLUME 1

Dissertação no âmbito do Mestrado Internacional em Ecologia Aplicada orientada pelo Doutor Vitor Hugo Paiva e pelo Professor Doutor Jaime Albino Ramos e apresentada ao Departamento de Ciências da Vida da Faculdade de Ciências e Tecnologia da Universidade de Coimbra.

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Identification of candidate pelagic marine protected areas (mpas) off west africa: evaluating their effectiveness in protecting marine predators and risk of fishery bycatch.

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I declare that this thesis was written and organized by me, and I confirm that it has not been previously submitted, in whole or in part, to obtain another academic degree. I confirm that the work described was mostly done by me, and other contributions are clearly acknowledged in the text with appropriate citations/references. Specifically, I acknowledge the contribution of colleagues of my working group ECOTOP, staff from Cabo Verde NGOs Biosfera and Projecto Vitó and colleagues from University of Barcelona who collected all seabird tracking data between 2013 – 2019. All data analysis and thesis writing was done by me.

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ABSTRACT

Cabo Verde is an archipelago off West Africa which is a hotspot of biodiversity, hosting numerous species of seabirds, turtles, whales, dolphins and fishes that are threatened by industrial fisheries and barely protected by a small network of Marine Protected Areas (MPAs). The implementation of protected areas in this region is essential to preserve its biodiversity and maintain the ecosystem services needed by the local population of the islands.

Seabirds possess many characteristics which turn them suitable to be used as sentinel species. They feed from the sea but breed on the land which makes them more accessible. These attributes make them easy to be observed and monitored, thus seabirds are often used in research to estimate the health status of ecosystems.

In order to determine Key Biodiversity Areas (KBAs) of Cabo Verde, we used two species of seabirds: the Cape Verde shearwater (*Calonectris edwardsii*) and the Bulwer's petrel (*Bulweria bulwerii*) from Cabo Verde. Two colonies of each species were tracked during 7 years, from 2013 to 2019 during the incubation and chick-rearing periods. Their core foraging areas were estimated using the '*track2KBA*' R package. Their distribution was then compared to the current KBAs and MPAs networks, other species distribution and fishery activities around the archipelago.

The Cape Verde shearwaters performed long trips to the coast of Senegal and Mauritania and short trips around the colonies. The Bulwer's petrels were more pelagic but their core foraging areas were focused around their colonies. These core foraging areas highly overlap with the current network of KBAs around the archipelago, but not with the MPAs (with the exception of Curral Velho's population of Cape Verde shearwaters). Moreover, the core foraging areas of the Cape Verde shearwater and the Bulwer's petrel overlap in total with 21 species out of the 24 selected for the analysis, and, overall, the fishing vessels off West Africa overlap with most of the core foraging areas of the Cape Verde shearwaters, especially trawlers. However, fishery activities barely overlapped with the core foraging areas of the Bulwer's petrels.

Therefore, the Cape Verde shearwaters and the Bulwer's petrels showed different Key Biodiversity Areas that are also used by other taxa and threatened by industrial fisheries. The next step is to implement protection regulations on these areas to preserve biodiversity and its ecosystem services.

RESUMO

Cabo Verde é um arquipélago ao largo da África Ocidental e é um hotspot de biodiversidade, albergando inúmeras espécies de aves marinhas, tartarugas, baleias, golfinhos e peixes que estão ameaçados pela pesca industrial e pouco protegidos por uma pequena rede de Áreas Marinhas Protegidas (AMPs). A implantação de áreas protegidas nesta região é essencial para preserver a sua biodiversidade e manter os serviços ecossistémicos necessários à população local das ilhas.

As aves marinhas possuem muitas características que as tornam adequadas para serem utilizadas como espécies sentinelas. Eles alimentam-se do mar, mas reproduzem-se em terra, o que as torna mais acessíveis. Esses atributos torna-as fáceis de serem observadas e monitorizadas, por isso as aves marinhas são frequentemente utilizadas em investigação para estimar o estado de saúde dos ecossistemas.

Para determinar as áreas-chave para a biodiversidade (*Key Biodiversity Areas*; KBAs) de Cabo Verde, foram utilizadas duas espécies de aves marinhas: a cagarra de Cabo Verde (*Calonectris edwardsii*) e o pedreiro (*Bulweria bulwerii*) de Cabo Verde. Duas colónias de cada espécie foram monitorizadas durante 7 anos, de 2013 a 2019, durante os períodos de incubação e alimentação dos filhotes. As suas principais áreas de procura de alimento foram estimadas usando o pacote R '*track2KBA*'. A sua distribuição foi então comparada com as atuais redes de KBAs e AMPs, distribuição de outras espécies e actividades de pesca em redor do arquipélago.

As cagarras de Cabo Verde realizaram longas viagens à costa do Senegal e Mauritânia e pequenas viagens em redor das colónias. Os pedreiros foram mais pelágicos, embora as suas principais áreas de procura de alimento se tenham concentrado nos arredores das colónias. Estas áreas de procura de aliemnto sobrepõem-se muito com a actual rede de KBAs em redor do arquipélago, mas menos com as AMP (com excepção da população de cagarra de Cabo Verde da colónia de Curral Velho). Além disso, as principais áreas de procura de aliemnto da cagarra de Cabo Verde e do pedreiro sobrepõem-se no total com 21 das 24 espécies seleccionadas para a análise e, globalmente, os navios de pesca ao largo da África Ocidental sobrepõem-se à maioria

das áreas de procura de alimento das cagarras de Cabo Verde, especialmente os arrastões. No entanto, as atividades piscatórias sobrepõem-se muito pouco com as principais áreas de procura de alimento dos pedreiros.

Assim, as cagarras de Cabo Verde e os pedreiros apresentaram diferentes KBAs que também são utilizadas por outros taxa e ameaçadas pela pesca industrial. O próximo passo será implementar regulamentações de proteção nessas áreas para preservar a biodiversidade e seus serviços ecossistémicos.

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INTRODUCTION

Marine Ecosystems

It is no secret today that human activities have a huge negative impact on biodiversity with 97.7% of the ocean's surface being affected by human-related stressors such as climate change, plastic pollution, fisheries, and others (Halpern et al., 2015; van Sebille et al., 2015; Game et al., 2009). Whilst humans started to harvest marine animals at least 42 000 years ago (O'Connor et al., 2011), overfishing only started a few centuries ago with big vertebrates and shellfish being intensively harvested by industrial fisheries. The consequences of overfishing were not immediate because the unfished species first took the trophic place of overfished ones until they were the target too, or died of other reasons (Jackson et al., 2012). This may cause an increase in the number of endangered species, which could destabilize the entire ecosystem. Moreover, Game et al., (2009) estimated that the threats' intensity will not only be more intense, but will also affect deeper strata of the ocean, with industrial fisheries targeting areas deeper than ever. Plastic pollution is omnipresent in the marine environment, with approximately 5.25 trillion plastic particles weighting 268 940 tons circulating (Eriksen et al., 2014). Plastic pollution affects marine animals because the size of microplastic particles is quite similar to the food they usually consume, but its effect does not stop on marine taxa as it climbs way up the food chain to humans (Thushari and Senevirathna, 2020). Plastic pollution also has socio-economic effects such as the decreasing tourism or human health, or less apparent effects like affecting the national economy by demanding an extra budget to remove the plastic waste (Thushari and Senevirathna, 2020).

This loss of biodiversity has an important impact on marine ecosystem services. With a huge amount of human population living by the coast and primarily depending on marine resources, marine ecosystems should be carefully watched because they provide a broad variety of services, not only provisioning for food and raw materials, but also supporting, regulating and cultural. A meta-analysis was published by Worm et al. (2006) showing the impacts of marine biodiversity loss on ecosystem services. They found a decreasing number of viable fisheries and nursery habitats, with the decreasing filtering and detoxification. Moreover, the risks increased too, with increased flooding events and species invasions.

Marine Protected Areas

Marine Protected Areas (MPAs) appeared as a holistic way to protect marine biodiversity and reduce negative impacts on ecosystem services. In 2008, the International Union for Conservation of Nature (IUCN) defined protected areas as "a clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values" (IUCN, 2022a). There are multiple types of MPAs, each with different intensity of regulations. In marine no-take areas, protection is fully implemented, and fishing is prohibited whilst in some other MPAs protection can be much less strict, allowing fisheries and implementing surveillance for illegal fishing or touristic practices (Dudley, 2008). In 2016, the IUCN World Conservation Congress set a target to reach at least 30% of MPAs by 2030, but currently only 7.7% of the ocean is protected and only 2.8% is fully protected (i.e. are marine protected areas; IUCN, 2016).

To implement these protected areas, some criteria must be met. Indeed, not every zone of the ocean can be put under protection, because of social, economic, legal, and institutional factors. Indeed, potential MPAs can not only be seen as simple geographical zones, because they are used by local communities and international companies, they are subject to laws and regulations, and are connected to their surrounding areas. Moreover, these secondary dimensions will also help the development of MPAs. The human dimension, notably, was found to have a significant impact on the success of MPAs. Involving local communities has increased the benefits and effectiveness of the Great Barrier Reef Marine Park MPA, and even if this high level of participation cost time and other resources, it was proven to be cost-effective (Day, 2002). Using local people's knowledge can also show a great advantage in the implementation and management of MPAs. However, there is a distinction between coastal and pelagic areas, as people tend to care more about coastal zones that are closer to their home, culture and traditions than pelagic regions, which are far from their reach/perception. In 1999, IUCN listed and explained the criteria for implementing MPAs, and they are as followed. The biogeographic criterion is respected when there are rare biogeographic qualities or unique geological features in the selected area. There is the ecological criterion when there are important characteristics for the ecosystem such as endangered species, a variety of habitats or the presence of feeding, breeding or resting areas. The naturalness criterion demands that the area has not been subject to human-induced change. The economic criterion is respected if there is an economic contribution due to protection. There is the social importance when the area has a value to communities because of different qualities such as history, traditions, or aesthetic. There is the scientific importance when the site has a value for research and monitoring. There is the international or national significance when the site could be listed on a national or international system. The practicality or feasibility criterion asks for some protection against external destructive influences, and compatibility with other activities like education, tourism and existing uses. And finally, the duality or replication criterion which is important because MPAs can be affected by a destructive influence, so more than one sample of every major ecosystem type should be put under protection (Kelleher, 1999).

Less than 10% of the ocean has been put under protection, so much further protection is needed to determine wether the current network of MPAs have been effective or not in protecting and enhancing biodiversity indicators and to identify possible ways to turn this protection effective (Rodrigues et al. 2004). A meta-analysis done by Ferreira et al. (2022) on coastal MPAs of Brazil found that biodiversity metrics, like species diversity or density, are higher in protected sites than in non-protected areas. Yet, they noticed that fully protected areas are more effective than the partially protected ones. Indeed, partially protected MPAs have limited results unless they are 15 years old or more, and if they have a high level of connectivity, which are the most influential predictors (Halpern et al., 2014). However, the factors influencing the effectiveness of MPAs depends on the target of the protected area. Indeed, if the goal is to increase conservation, then there are five key features: "no take, well enforced, old (>10 years), large (>100 km2), and isolated by deep water or sand" (Edgar et al., 2014). But when the goal is to optimize catch the influence of the MPA's size varies as larger MPAs are more effective for species with a high value and/or low harvesting cost and smaller MPAs are more effective for species that are more lightly harvested for their low value and high harvesting cost (Cabral et al., 2019). Moreover, non-exploited species can also benefit from MPAs, which expands the positive impacts of these protected areas. No-take MPAs usually function as source of fish stocks to replenish contiguous unprotected areas, thus favouring commercial fisheries. This last point is an interesting dimension that brings a bigger picture of the MPA. Indeed, it is considered important, if not essential, to look at the overall picture before implementing and whilst managing an MPA. Focusing strictly on the defined areas could lead to "islands of protection" (Salm, Clark and Siirila, 2000). Whilst the high mobility of most of marine animals helps them, with some limitation, to respond to climate change stress, it poses a challenge for the implementation and the effectiveness of MPAs. So, another important point in the implementation of MPAs is taking into account the larvae, juvenile and adult's mobility. For instance, small marine reserves which only include the core distribution areas of targeted species are not so effective if the species forage in other area with potential threats. Considering dispersal, pelagic species might accentuate the difficulty of implementing the MPA as it demands a larger protected area or a network of MPAs with a high connectivity (Pittman et al., 2014). Furthermore, the activity that used to take place inside the MPA might be displaced in its surrounding, particularly for coastal MPAs and local fisheries as they usually happen near the fishers' home ports and thus can be moved too far away. The implementation of coastal MPAs can negatively affect the local fishers unless they keep fishing inside the MPA, even in a no-take zone, which is possible if their impact on the fish stock is less important than the that of outsiders (Charles and Wilson, 2009). And this agreement with local people, could also enhance the success of the MPAs, as seen previously. However, if the threat is by-catch of non-target species like birds, turtles, sharks or mammals, areas that are closed specifically to fishing gear such as industrial longliners, have been effective (Hall et al., 2000).

Seabirds

Seabirds possess many characteristics which turn them suitable to be used as sentinel species, for instance to estimate the health status of marine ecosystems. Among these characteristics are the fact that they are top predators, have a high longevity, are philopatric, often colonial, conspicuous, and large in size (Burger and Gochfeld, 2004).

Whilst most plant and animal marine species only live underwater, seabirds feed from the sea but breed on the land which makes them more accessible. These attributes make them easy to be observed and monitored, thus seabirds are often used in research to estimate the health status of ecosystems. Their diet, foraging effort, foraging success and efficiency are linked to environmental features, and population dynamics also have been related with climate changes (Grémillet and Charmantier, 2010). Besides being good indicators of marine environment health, seabirds are also interesting in conservation. Indeed, umbrella species are species whose requirements encapsulates the requirements of other less demanding species (Lambeck, 1997). And seabirds, being top predators and foraging over an often large area, fulfil this role. So, the conservation of seabirds can also impact the conservation of other co-occurring species. Hence, using foraging data of seabirds is an interesting method of determining Key Biodiversity Areas (KBAs) that would be potential MPAs. Key Biodiversity Areas are defined as "sites contributing significantly to the global persistence of biodiversity" in all ecosystems (IUCN, 2022c). A study made by Paleczny et al. (2015) between 1950 and 2010 showed that the monitored seabirds population declined by almost 70%. So, the conservation of seabirds is essential. Marine Important Bird Areas are sites that are essential for the conservation of marine birds, they cover about 2% of the sea (BirdLife International) and some of these areas are overlapping with MPAs like in Antarctica where marine IBAs overlap with 80.5% of key management areas, including MPAs (Handley et al., 2021). This emphasizes the utility of seabirds as umbrella species to determine MPAs. Some researchers used seabird sightings of 30 species during 8 years along the Portuguese coast to identify potential MPAs (Pereira et al., 2018). They found that the current IBAs already cover about one third of the areas prioritized for breeding species but less than 4% for the non-breeding species. So, by using the distribution of seabirds, they assessed the effectiveness of the current Portuguese coastal IBAs and determined new candidate areas for conservation.

However, one downside of using seabirds is the lack of data concerning pelagic species, which is problematic because wide-ranging pelagic species seem to be the group with the steepest decline in population numbers (Paleczny et al., 2015). This is the main reason why it is important to start focusing on pelagic seabirds, to collect more data on pelagic marine ecosystems. Using seabirds as indicators for Key Biodiversity Areas and the implementation of MPAs is new but increasing (Krüger et al., 2017; Paiva et al., 2015). A recent study was done in the South Atlantic Ocean, on the Tristan da Cunha Islands, where researchers tracked six globally threatened seabird species to identify areas of conservation interest (Dias et al., 2017). They concluded that for highly pelagic species, the conservation effort cannot only be focused on one country but requires a multi-national approach because they cover a wide area. Moreover, recently and for the first time, a MPA was implemented exclusively using seabird tracking information from 21 species, tagged at 56 colonies, and collected by dozens of researchers. It was in the North Atlantic Current and Evlanov Seamount, which is a hotspot for seabirds as up to 5 million individuals use this area (Davies et al., 2021).

Cabo Verde

Despite its arid climate conditions, the Cabo Verde archipelago possesses a wide marine biodiversity, including emblematic species of marine mammals, turtles, birds, and sharks (Benchimol et al., 2009). Over 17 whale and dolphin species have been reported in Cabo Verde islands and the neighbouring countries, such as the Common bottlenose dolphin (*Tursiops truncatus*) or the Humpback whale (*Megaptera novaeangliae*) (Reiner et al., 1996). The latter migrates thousands of kilometres every year from high latitudes where they find their feeding grounds to lower latitudes such as Cabo Verde where they breed (Duarte and Romeiras, 2009). In total, five species of marine turtles were reported for Cabo Verde: the leatherback (*Dermochelys coriacea*), the hawksbill (*Eretmochelys imbricata*), the olive ridley (*Leidochelys olivacea*), the green (*Chelonia mydas*), and the loggerhead (*Caretta caretta*) (Duarte and Romeiras, 2009). Boavista Island has recently been described as the third most important nesting site in the world for the loggerhead because more than 3000 individuals come to nest every year (Duarte and Romeiras, 2009). Moreover, the coral reefs of Cabo Verde have been identified as one of the world's top 10 threatened coral reef hotspots of biodiversity (Roberts et al., 2012). Semedo et al. (2020) listed the seabird species that have been reported on the archipelago, including six species of Procelariiformes, some of which are endemic, like the Cape Verde shearwater (*Calonectris edwardsii*), the Boyd's shearwater (*Puffinus lherminieri boydi*), the Cape Verde Petrel (*Pterodroma feae*), or the Cape Verde Storm-petrel (*Hydrobates jabejabe*), and others are only there for the breeding season, like the Bulwer's petrel (*Bulweria bulwerii*), the White-faced Storm-petrel (*Pelagodroma marina aedesorum*). There are also two species of Suliformes, the recently locally extinct Magnificent Frigatebird (*Fregata magnificens*) and the Brown Booby (*Sula leucogaster*), and one species of Phaethontiform, the Red-billed Tropicbird (*Phaethon aethereus*). Cabo Verde offers breeding habitats for 9 species of seabirds and about 130 bird species of migrants that mainly come from the Palearctic region to spend their winter months in the archipelago (Duarte and Romeiras, 2009). Seabirds are threatened by two main factors: climate change and anthropogenic-related stressors (Dias et al., 2019). In Cabo Verde, human activities have had a dramatic impact on the different seabird populations. Indeed, cats were introduced and observed predating on seabirds on several Islands such as like Santa Luzia (Oliveira et al., 2013) and Fogo (Militão et al., 2017), but other mammals like rats, dogs and goats also represent a threat, by predating or disrupting the potential seabirds' habitats. (Semedo et al. 2020). Seabirds of Cabo Verde face other predators like the ghost crab (*Ocypode cursor*) that feeds on their chick (Murphy, 1924; Semedo et al., 2020) or the giant gecko (*Tarentola gigas*) that feeds on the seabirds' eggs (Semedo et al., 2020). A quite recent menace for seabirds is the introduction of artificial light on the islands because it can disorient the birds, especially fledglings which could then be captured by introduced mammals or humans (Militão et al., 2017; Rodriguez et al., 2014). Cabo Verde archipelago has a MPA network, but it is small and coastal. In 2021, it had 27 MPAs which was the largest number of West Africa, but it covered only about 0.13% of the Cabo Verde sea jurisdiction, lower than any other country of the region except for

Gambia and Western Sahara (Assis et al., 2021). Two MPAs were recently implemented: a large polygon close to Boa Vista Island which is now the largest marine protected area in this region, and a smaller polygon on the South-West coast of Santiago Island, called Parque Natural da Baia do Inferno e do Monte Angra. The lack of marine protected areas could be explained if there was no threat to the marine species around Cabo Verde, but this is not the case. Indeed, the industrial fishery activities around the archipelagos are quite intense, especially off West Africa (GFW | Map, 2021). The number of countries involved in fishing in the high seas, the landings, and the value of landed catch have been relatively stable between 1990 and 2006 whilst the fishing effort more than doubled, so countries are competing to catch limited resources, using increasingly larger fleets (Merrie et al., 2014), which increase the risk of by-catch. Drifting longlines were the most used fishing method in the high seas with 59% of the active vessels using longlines in 2016 (Sala et al., 2018), and thus they are one of the main threats to seabirds, which are caught by the hook of longlines when trying to grab the bait. It was estimated that between 160 000 and 320 000 seabirds are caught by longlines every year (Anderson et al., 2011). Bottom trawling was the fourth fishing gear operating in the high seas in 2016 and might be the most damaging fishing techniques because of its many impacts on the sediment, which reduces significantly organic matter and biodiversity (Pusceddu et al., 2014). Moreover, the purse-seine fishing method is also a potential threat to seabirds, especially due to the increasing use of Fish Aggregating Devices since the mid-1990s, on which diving seabird species such as shearwaters could get entangled (Baker and Hamilton, 2016). Between 2010 and 2015, on the Portuguese continental waters, Balearic shearwaters (*Puffinus mauretanicus*) highest annual mortality rate was obtained in purse seines (Araújo et al., 2022), and between 2005 and 2019 by the Chilean coast, the Sooty shearwater (*Ardenna grisea*) presented a high spatial overlap and time correlation with purse seine fishing effort (Simeone et al., 2021).

Study subject and purpose

The combination of the presence of important bird areas, the intense fishery activities, and the lack of protection in the region of Cabo Verde is a matter of strong concern for the marine biodiversity which is already declining. All these factors are the reason for this study, as we want to know which areas are important for marine species to protect them.

In this study, two seabird species, the Cape Verde shearwater (*Calonectris edwardsii*) and the Bulwer's petrel (*Bulweria bulwerii*) were tracked for 7 years (2013-2019) during their incubation and chick-rearing period in Cabo Verde. These seabirds are used as umbrella species for the rest of the marine biodiversity of the archipelago and their tracking data will help identify their core foraging areas and thus Key Biodiversity Areas off West Africa. The first step is to determine the overlap between the current MPA and KBA networks of Cabo Verde and the estimated core foraging areas (1). Furthermore, we will determine the environmental drivers of the interannual use of these core foraging areas (2). Then, to evaluate the effect of putting these core foraging areas under protection on the rest of the marine biodiversity around the archipelago, these sites will be compared to the distribution of other species including marine turtles, sharks, whales, dolphins, and other seabirds (3). Moreover, the estimated core foraging areas will also be compared to the fishery activities around Cabo Verde to estimate the potential threat of industrial fishing on the study species, and thus on the other species of the ecosystem (4).

We hypothesised that (1) the newfound KBAs will overlap with the current networks of MPAs and KBAs off West Africa especially during the chick-rearing period because the foraging distribution of the study species, particularly the Cape Verde Shearwater, is coastal during chick-rearing and pelagic during incubation (Paiva et al., 2015). (2) We expect the Cape Verde shearwaters and the Bulwer's petrels' foraging distribution to correlate with the distribution of their prey. (3) It is expected that the foraging distribution of the study species overlap with the distribution of other marine species due to the many observations around the archipelago and off West Africa (GBIF.org, 2022; movebank.org, 2022). (4) Fishing activities will likely overlap with the newfound KBAs because industrial fisheries currently operate in extensive regions off West Africa (Global Fishing Watch, 2021).

MATERIAL AND METHODS

Study area

Cabo Verde archipelago is located 570km off the coast of Senegal and is made of ten volcanic islands and several islets (Duarte and Romeiras, 2009). The islands can be classified in three groups: the Northern Islands that include Santo Antão, São Vicente, Santa Luzia and São Nicolau, the Eastern Islands that include Sal, Boavista and Maio and the Southern Islands that include Santiago, Fogo and Brava (Duarte and Romeiras, 2009). All islands expect for Santa Luzia are inhabited. Whilst the Eastern islands are quite flat with a maximum altitude of 436m on Maio island, the Northern and Southern islands have high mountains, including Pico do Fogo which is Cabo Verde's tallest mountain that rises to 2829m (Duarte and Romeiras, 2009). The climate of Cabo Verde is arid to semiarid (Martins and Rebelo 2009) and the annual precipitations ranges from 80-300 mm in the arid coastal zones to 1200-1600 mm in the highlands of the mountain islands (Duarte and Romeiras, 2009). A study made between 1865 and 2011 showed that the temperatures in the archipelago vary annually between 20.9°C for February and 26.4°C for September in average, but summer temperatures increased by at least 0.40°C per decade from 1981 to 2010 (Cropper and Hanna, 2014). Cabo Verde can be characterised by three oceanic-atmospheric phenomena: annual rainfall cycles, annual cycles of dust from the Sahara Desert and upwelling cycles from the West African coast like the Canary Current system which consists of a constant and nutrient-rich up-welling phenomena that gathers and sustains high abundance of small pelagic preys (Medina et al., 2015; Paiva et al., 2015).

Study species

Cape Verde shearwater

Cape Verde shearwater, *Calonectris edwardsii*, is an endemic species of Cabo Verde and is considered a near-threatened species by the IUCN red list (IUCN, 2022b). In Cabo Verde, the shearwaters are exposed to three main threats. On land, the introduction of invasive mammals like cats and rats is a menace to the populations of these shearwaters, as mentioned previously. Until 2009, the main threat on the archipelago was human capture as it was estimated that 10 000 juveniles were captured annually on the islands of Raso and Branco and sold on Santo Antão Island in order to cook the traditional dish called "caldo de Cagarra" (Monteiro, 2005; Hazevoet, 1997). However, their capture seemed to have decreased, if not ceased on Raso Island, due to the NGO Biosphere I which raised awareness on this practice and exposed the importance of the protection and conservation of this species (Alcyon team, 2019). Another risk is the accidental capture of the birds by fishing gear when they forage along the African West Coast during the breeding period.

The shearwaters reach the colony in March, they lay one egg in June that will hatch in July (Hazevoet 2015). Depending on the breeding period, the Cape Verde shearwaters display different foraging strategies. Indeed, during the incubation period, the birds perform longs trips of more than three days to the Northwest African coast where there is a nutrient-rich coastal upwelling (Paiva et al., 2015). However, during the chick-rearing period, the birds present a dual foraging strategy. They perform short trips close to the colony to provide for the chicks, and a few long trips to provision themselves (Paiva et al., 2015). Both parents feed the chick, they leave the nest before sunrise and return after sunset (Navarro and González-Solís, 2007). Then the fledging occurs around October and November (Rodrigues, 2014). The birds feed on the most abundant commercial fish species like the Madeiran sardinella (*Sardinella maderensis*) or the bigeye scad (*Selar crumenophthalmus*) and on non-commercial prey such as the keeltail needlefish (*Platybelone argalus lovii*) or the squid (*Loligo sp*) (Rodrigues, 2014).

Moreover, the Cape Verde Shearwater is considered as an ideal sentinel species of the health of the marine ecosystem of West Africa due to its top predator status, relative abundance, size, easy access to the colonies, low fecundity, and its high sensitivity to human-induced alterations to marine ecosystems (Paiva et al., 2015).

Bulwer's petrel

The second study species is the Bulwer's petrel, *Bulweria bulwerii*, which breeds on tropical and non-tropical islands in the Atlantic or Pacific oceans (del Hoyo, Elliot and Sargatal, 1992). They are probably the most nocturnal seabird species, as they forage about 90% of the night (Spear, Ainley and Walker, 2007). They predate on pelagic and mesopelagic fishes and cephalopods (Zonfrillo, 1986; Neves, Nolf and Clarke, 2011). Even if they are one of the most abundant species in the tropical and sub-tropical of the Atlantic Ocean (del Hoyo, Elliot and Sargatal, 1992), there is still little data on their distribution and foraging strategies during the breeding season (Dias et al., 2016).

Adults return to the breeding sites late April, they lay one egg in late May or early June, which hatches near the end of July after both parents incubate and the chicks fledge in September (Monteiro et al., 1996).

Tracking methods

Cape Verde shearwaters from Raso Islet (Lat, Long - 16.61, -24.6) and Curral Velho, Boavista Island (15.99, -22.79) were tracked with CatLog2 devices (Perthold Engineering; http://www.mrlee.com/science.html) while Bulwer's petrels from Cima (14.97, -24.64) and Raso (16.61, -24.6) Islets were tracked with nanoFix mini-GPS (Pathtrack Ltd; https://www.pathtrack.co.uk/products/productrange.html) (Figure 1). Both species were tracked during incubation and chick-rearing phases totalizing 1402 foraging excursions by 373 Cape Verde shearwaters and forays 682 by 187 Bulwer's petrels. The Cape Verde shearwaters from Curral Velho and the Bulwer's petrels from both colonies were tracked from 2017 to 2019, whilst the Cape Verde shearwaters from Raso were tracked from 2013 to 2019. 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.

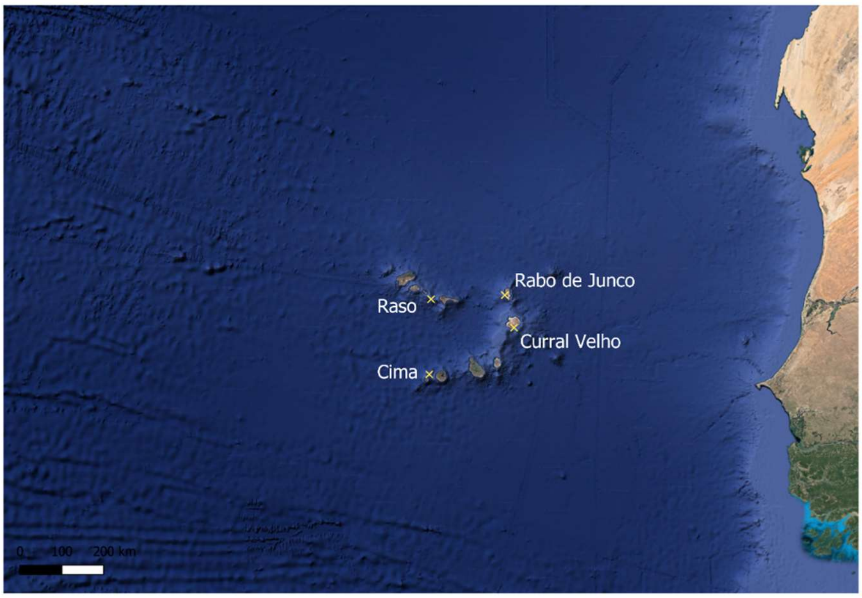
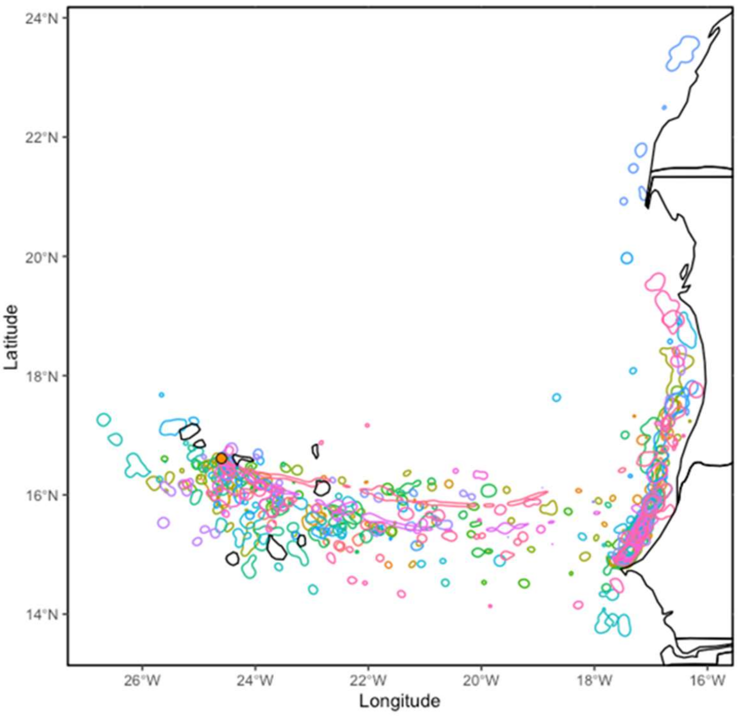


Figure 1. Study site locations were Cape Verde shearwaters (Raso Islet and Curral Velho-Boavista Island) and Bulwer's petrels (Raso, Cima and Rabo de Junco Islets) were tracked with GPS-loggers between 2013-2019.

Consistency in space use

In order to identify Key Biodiversity Areas using the foraging distribution of the Bulwer's petrel and the Cape Verde shearwater, the data was analysed for each species and each colony separately. A new trip was counted every time a bird returned to the colony. Then, all the trips were first divided between the chick-rearing and incubation phases, and in parallel they were divided between long and short trips from the colonies. The first subset is to visualize the potential change of behaviour from the birds between these two breeding phases. The second subset is to identify both coastal and pelagic important foraging areas. The analysis was done on R Studio using the '*Track2KBA'* R package (Beal et al., 2021). A trip was considered long distance if a bird went more than 180 km away from the colony, if not, it was considered a short trip. This distance was determined using the distance distribution of the birds. All trips were sorted to eliminate the incomplete ones using the ‘tripSplit’ function and a return buffer of 200 km. The buffer value was chosen by using the visual output of the function, decreasing the value until all incomplete trips were recognised as such by the algorithm. The smoothing parameter was estimated using the ‘findScale’ function with a ScaleARS of 1.5 km for chick-rearing breeding phase and short trips, and 5 km for the incubation phase and long trips. However, for the Curral Velho’s population of the Cape Verde shearwaters, too many birds were tracked for the ‘sumTrips’ function to process the data needed for the ‘findScale’ function. So, a smoothing parameter of h=10 was used for the incubation phase and long trips, and h=3 for chick-rearing and short trips. The utilisation distribution (UD) of the birds was estimated using the ‘estSpaceUse’ function with a kernel of 50% (Figure 2), and the accuracy of this distribution was calculated with the ‘repAssess’ function. Finally, the important foraging areas were estimated using the ‘findSite’ function, with a level UD of 50% and estimated sizes of the populations (10000 Bulwer’s petrel on each island, 13000 Cape Verde shearwaters for Raso and 7000 for Curral Velho) (Figure 2).



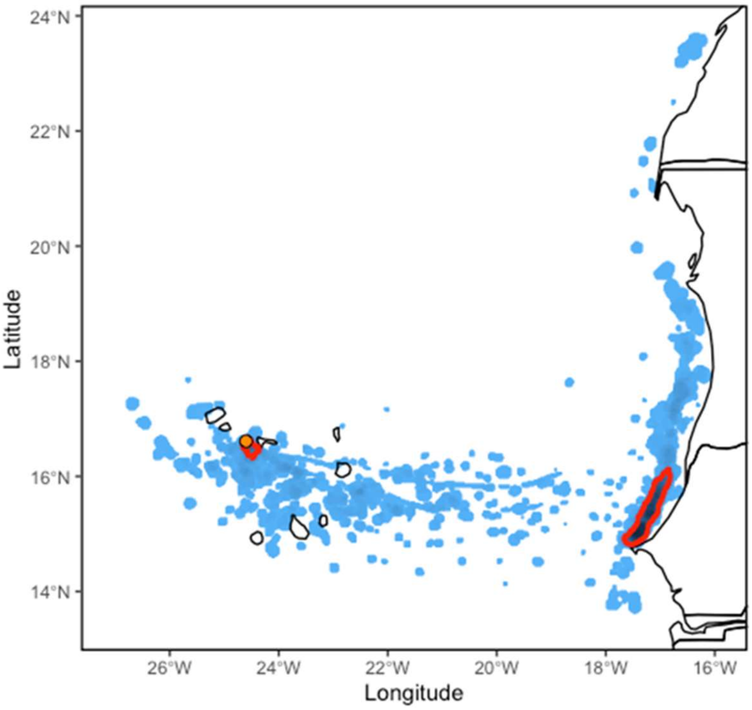


Figure 2. 50% Kernel Utilization distributions (UD) (top) and Key Biodiversity Area (KBA) (bottom) of Cape Verde shearwaters from Ilhéu Raso (S. Nicolau, Cabo Verde) during the incubation phase. Different colours are different individuals (top) and red polygon represents proposed KBA at 93.4 % representativeness (bottom). Central dot represents the breeding colony.

Overlap of the core foraging areas with the current network of protected areas.

To know if the estimated important foraging areas are already covered by the current network of KBAs and MPAs off West Africa (Figure 3) or if they need further protection, an overlap analysis was performed on QGIS using the current MPAs' network from Western Africa imported from (UNEP-WCMC and IUCN, 2022) and the current network of KBAs obtained from the Key Biodiversity Areas database (https://www.keybiodiversityareas.org). The total area and the percentage of the area of each estimated core foraging area covered by implemented MPAs and KBAs was then calculated.

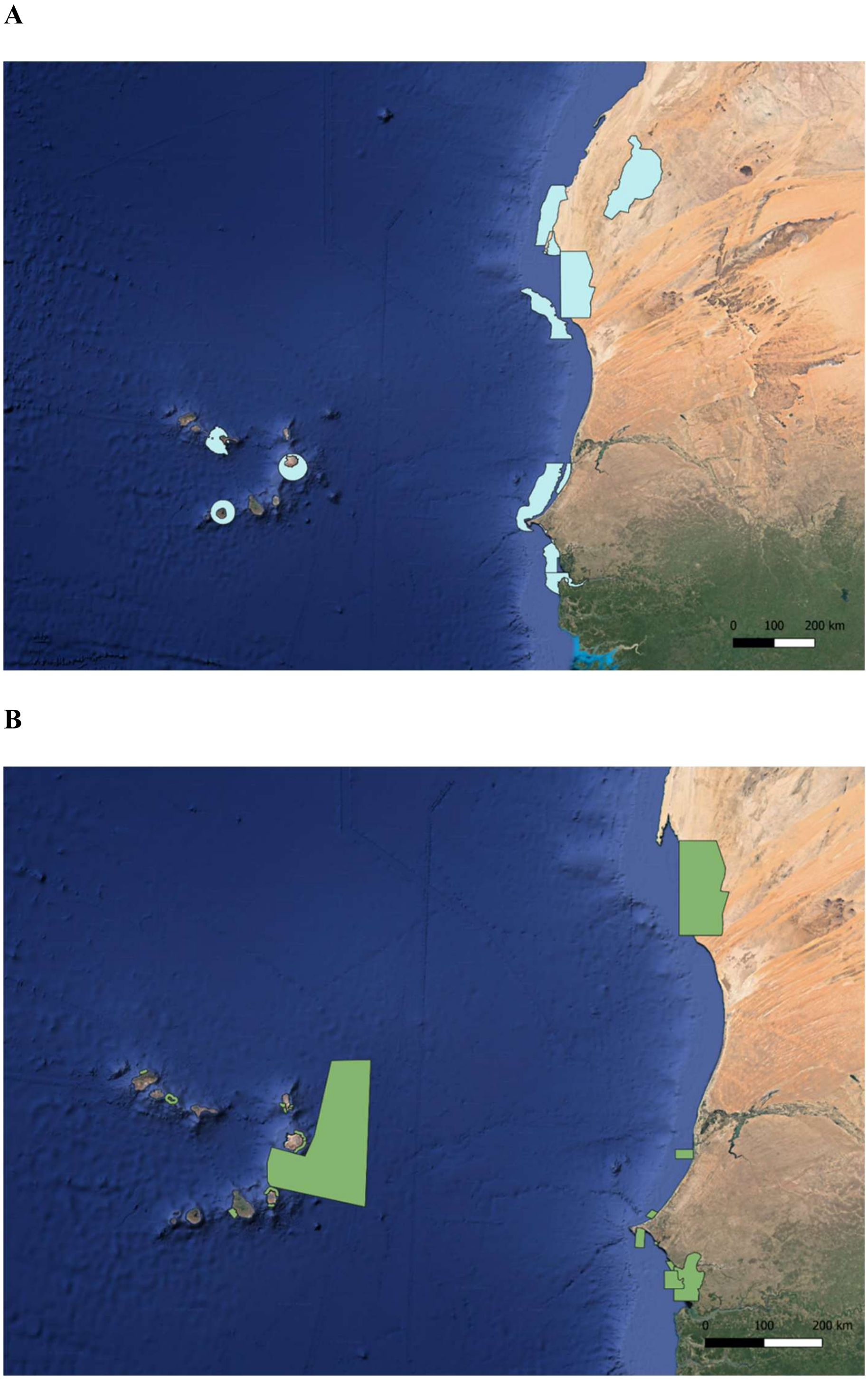


Figure 3. Map of current (A) Key Biodiversity Areas (blue polygons) and (B) Marine Protected Areas (green polygons) off West Africa. Only the coastal areas of the green terrestrial polygons are considered as MPAs.

Environmental drivers of the interannual use of core foraging areas

To determine the environmental drivers of the interannual use of the estimated KBAs by the two studied species, we extracted Spatial Ecosystem and Population Dynamics Model – SEAPODYM data (http://www.seapodym.eu) from Copernicus database (https://myocean.marine.copernicus.eu), at spatio-temporal resolutions of 0.1º and monthly, respectively. Environmental predictors included (1) net primary productivity (mg m^{-2} day^{-1}), (2) mass content of zooplankton (g m^{-2}), (3) mass content of epipelagic fish (g m^{-2}) and (4) mass content of mesopelagic fish (g m^{-2}). Downloaded rasters were then processed through several functions of *raster* R package (Hijmans 2022) to aggregate the monthly values to the different tracking periods, using the average and extracting the raw values from inside the estimated KBAs each study year (2013-2019) for each combination of study species – population – phase.

Overlap of the core foraging areas with the distribution of other marine predators

To know if the estimated KBAs can also protect other marine species, former studies from Cabo Verde and its neighbouring countries where other species were tracked were used. Polygons were drawn on QGIS (QGIS Desktop *v.* 3.18.2) using maps of the tracking data of two species of turtles, fifteen species of birds, two species of sharks, three species of whales, one species of dolphin and one species of ray (Table 1)

The polygons were drawn by doing the following steps: (1) Layer – Create Layer – New Shapefile Layer – Geometry type: Polygon – Toggle Editing – Add Polygon Feature. Then, (2) the Overlap analysis tool for QGIS was used to calculate the area and percentage of the area of the estimated KBAs covered by the distribution of each selected taxa.

Table 1. List of the species used to calculate the overlap with the estimated core foraging areas of the Cape Verde shearwaters and the Bulwer's petrels.

Common English name	**Scientific name**	**IUCN red list category (ICUN, 2022b)**	**Reference**
Audouin's gull	*Ichthyaetus audouinii*	Vulnerable	Bécares et al., 2016.
Audubon's shearwater	*Puffinus lherminieri*	Least concern	Gonzalez-Solis, 2007-2021; Paiva, 2018-2019.
Blue shark	*Prionace glauca*	Near threatened	Queiroz et al., 2016 ; Vedor et al., 2021.
Brown booby	*Sula leucogaster*	Least concern	Gonzalez-Solis, 2007-2021; Paiva, 2018-2019.
Cape Verde petrel	*Pterodroma feae*	Near threatened	Gonzalez-Solis, 2007-2021.
Cape Verde storm petrel	*Hydrobates jabejabe*	Least concern	Gonzales-Solis, 2019-2021.
Caspian tern	*Hydroprogne caspia*	Least concern	Veen et al., 2014-2015.
Chilean devil ray	*Mobula tarapacana*	Endangered	Thorrold et al., 2014.
Common bottlenose dolphin	*Tursiops truncatus*	Least concern	Correia et al., 2022 ; de Vries, 2022 ; Happywhale, 2021; iNaturalist, 2022; Lanfredi and Notarbartolo di Sciara, 2014; Maughan and Arnold, 2010.
Cory's shearwater	*Calonectris borealis*	Least concern	Dias et al., 2012 ; Missagia et al., 2015.
Humpback whale	*Megaptera novaeangliae*	Least concern	Correia et al., 2022 ; de Vries and Lemmens, 2022. Happywhale, 2021 ; iNaturalist, 2022 ; Woolmer, 2013.
Leatherback sea turtle	*Dermochelys coriacea*	Vulnerable	Cooper, 2021; Correia et al., 2022; Dondorp and Creuwels, 2022; United States Geological Survey.
Lesser black-backed gul	*Larus fuscus*	Least concern	Stienen et al., 2017.
Loggerhead sea turtle	*Caretta caretta*	Vulnerable	ADS Biodiversidad, 2020; Cruz, 2021.
Northern gannet	*Morus bassanus*	Least concern	Gremillet et al., 2015.
Red-billed tropicbird	*Phaethon aethereus*	Least concern	Gonzalez-Solis, 2009-2021; Paiva, 2017-2019.
Red footed booby	*Sula sula*	Least concern	Paiva, 2018-2019.
Royal tern	*Thalasseus maximus*	Least concern	Veen et al., 2014-2015.
Scopoli's shearwater	*Calonectris diomedea*	Least concern	Gremillet et al., 2015.
Shortfin mako shark	*Isurus oxyrinchus*	Endangered	Queiroz et al., 2019.
Short-finned pilot whale	*Globicephala macrorhynchus*	Least concern	de Vries and Lemmens, 2022; Happywhale, 2021; iNaturalist, 2022; Maughan and Arnold, 2010.
Slender-billed gull	*Larus genei*	Least concern	Veen et al., 2014.
Sperm whale	*Physeter macrocephalus*	Vulnerable	Correia et al., 2022
White faced storm petrel	*Pelagodroma marina*	Least concern	Gonzales-Solis, 2019-2021.

Overlap of the core foraging areas with fishery activities

Fisheries are one of the main threats for seabirds in Cabo Verde, so it is important to study the intensity of fishing activities at the important foraging areas for our two study species. The data was collected through the *fishRmen* dashboard (Buonomo, 2021; https://shyentist.shinyapps.io/fish-r-man/) using specific parameters to match fishery data to our tracking data in terms of range, study period and fisheries with which seabirds (and other marine taxa) might interact and be by-caught (Table 2).

Table 2. Parameters used to download fisheries data.

Query table	AIS data at 100th degree
Date	Bulwer's petrel: 12 June 2017 – 31 August 2017 24 April 2018 – 02 September 2018 20 April 2019 – 29 August 2019 Cape Verde shearwater: 2 July 2013 – 26 September 2013 17 June 2014 – 09 July 2014 10 June 2015 – 02 October 2015 14 June 2016 – 11 July 2016 11 June 2017 – 15 September 2017 15 June 2018 – 13 September 2018 20 June 2019 – 23 September 2019
Latitude	Min = 8 ; Max = 25
Longitude	Min = -33 ; Max = -15
Geartype	Drifting longlines and Set longlines ; Trawlers ; Pole and line ; Purse seines, tuna purse seines, other purse seines, other seines, seiners

Then, the fishing areas were delimited with a 95% kernel on R using the '*adehabitatHR'* package (Calenge, 2006). We chose to use this high kernel value to be consistent with the overlap analysis of the other marine predators, which available data was their entire distribution, and not their core foraging areas. To only keep the data on vessels actually fishing and not only passing by, only the data of the vessels fishing more than 0.01 hours was computed. A map of the core fishing areas was exported as a shapefile and added on QGIS where the overlap between the estimated KBAs and the yearly fishing activities was calculated. The overlap is calculated for every year of the study to potentially observe a variation in the impact of fisheries on seabirds' distribution.

Data analysis

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. 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.

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 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.

General Linear Models (GLMs) were used to test the effect of study year (2013-2019) on the (1) Net primary productivity (NPP; mg m^{-2} day^{-1}), mass content of (2) zooplankton (ZOO; g m^{-2}), (3) epipelagic fish (EPI; g m^{-2}) and (4) mesopelagic fish (MES; g m^{-2}).

RESULTS

Foraging patterns

The tracks of the two colonies of the Cape Verde shearwaters from Raso Islet and Curral Velho exhibited high similarity in their foraging patterns and distribution. Indeed, both colonies foraged around the nest and travelled as far as off West Africa (Figure 4). Cape Verde shearwaters showed different foraging strategies depending on the breeding phase, performing a lower number of trips per bird during incubation (2.1 ± 0.6 trips per bird) than chick-rearing (6.4 ± 2.2 trips per bird), yet incubation trips were usually longer in duration and distance from the breeding colony. Cape Verde shearwaters from Raso performed 29% of short trips during chick-rearing, against 7% during incubation. Curral Velho's population performed 5% of short trip during chick-rearing against 27% during incubation (Table 3).

Unlike Cape Verde shearwaters, Bulwer's petrels from Raso and Cima Islets did not overlap/ exhibited spatial segregation in their foraging distribution. Indeed, the population of Cima Islet foraged more to the South whilst the population of Raso Islet foraged mostly towards Northern latitudes. However, both colonies were comparably more pelagic than the Cape Verde shearwaters, foraging West of their respective colonies, towards the middle of the Atlantic (Figure 4). Moreover, the Bulwer's petrels also performed less trips during the incubation (1.6 ± 0.4 trips per bird) than during the chick-rearing period (4.0 ± 1.2 trips per bird), and the birds also foraged during a longer period of time and at longer distance from their colony during incubation (Table 4).

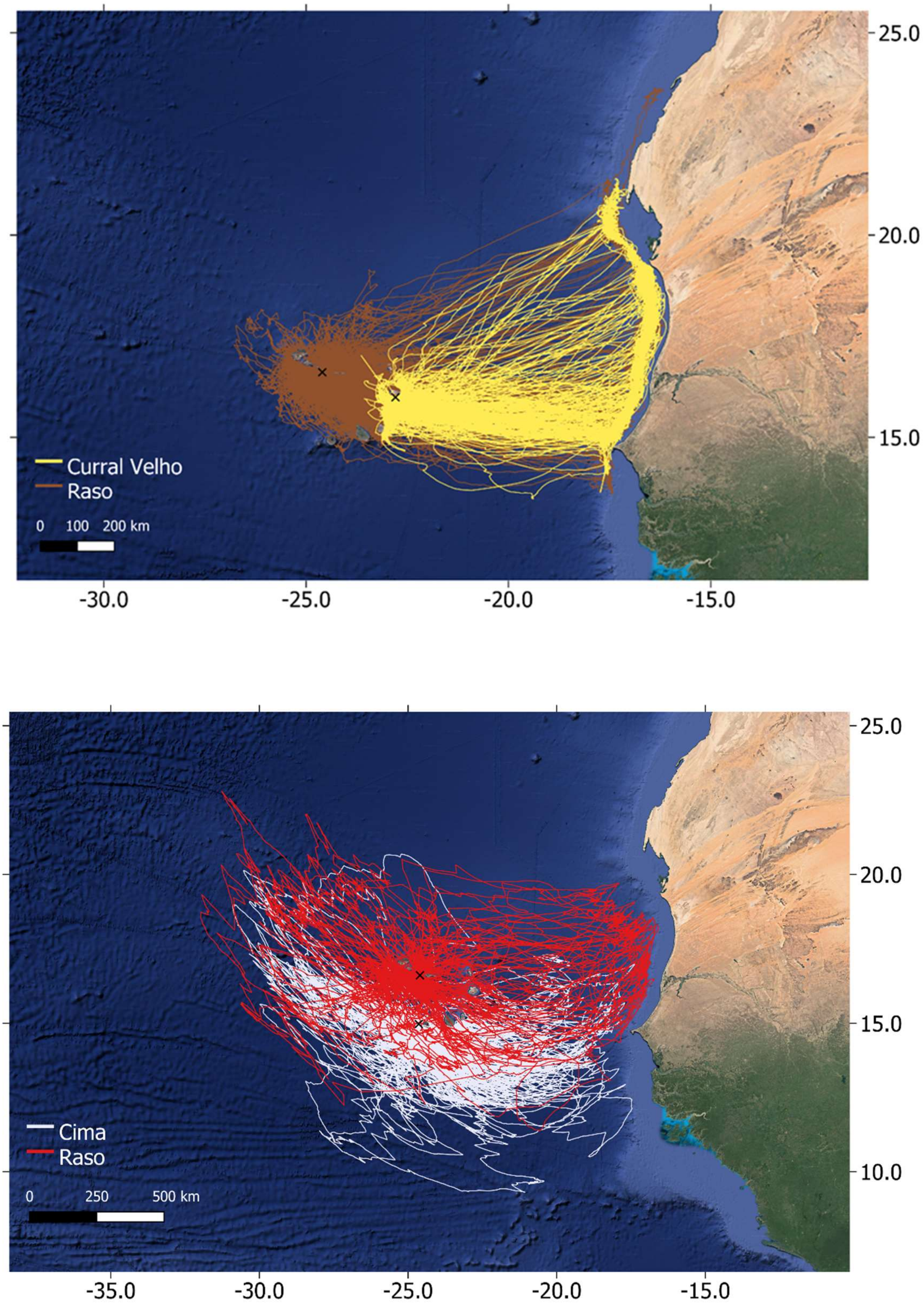


Figure 4. Foraging distribution of Bulwer's petrel (upper panel) tracked from Raso (red) and Cima (light blue) Islets and Cape Verde Shearwater (down panel) from Raso Islet (brown) and Curral Velho (yellow; Boavista Island), between 2013 – 2019.

Table 3. Summary statistics for the Cape Verde Shearwater (*Calonectris edwardsii*). Also shown are mean trip duration (Trip. Dur.) and mean maximum distance from colony (Max. Dist.).

Colony	Year	Phase	N birds	N trips	Trip. Dur. ± SD (days)	Max. Dist. ± SD (km)
Curral Velho	2017	Chick-rearing	—	—	—	—
		Incubation	34	62	3.80 ± 3.35	292.56 ± 272.36
	2018	Chick-rearing	23	84	1.61 ± 1.99	90.13 ± 164.88
		Incubation	32	66	4.51 ± 4.77	329.41 ± 311.62
	2019	Chick-rearing	27	109	2.04 ± 3.04	148.25 ± 221.70
		Incubation	56	137	4.57 ± 5.33	349.00 ± 319.11
Raso	2013	Chick-rearing	7	58	1.83 ± 2.76	176.49 ± 205.72
		Incubation	11	13	7.83 ± 4.04	618.70 ± 333.92
	2014	Incubation	7	19	3.78 ± 3.97	364.64 ± 357.00
	2015	Chick-rearing	12	109	1.18 ± 1.27	94.22 ± 92.12
		Incubation	13	42	2.50 ± 3.06	222.66 ± 296.42
	2016	Incubation	13	24	5.35 ± 3.63	584.17 ± 354.09
	2017	Chick-rearing	27	229	1.77 ± 2.02	229.13 ± 274.13
		Incubation	16	44	3.60 ± 3.65	382.44 ± 375.81
	2018	Chick-rearing	36	195	1.79 ± 2.27	236.37 ± 274.05
		Incubation	20	36	4.64 ± 3.13	589.37 ± 336.84
	2019	Chick-rearing	29	160	1.99 ± 2.54	210.84 ± 265.61
		Incubation	10	15	3.68 ± 2.80	606.09 ± 376.27

Table 4. Summary statistics for the Bulwer's petrel (*Bulweria bulwerii*). Also shown are mean trip duration (Trip. Dur.) and mean maximum distance from colony (Max. Dist.).

Colony	Year	Breeding phase	N birds	N trips	Trip. Dur. ± SD (days)	Max. Dist. ± SD (km)
Cima	2017	Chick-rearing	15	63	1.91± 1.63	196.24 ± 140.20
		Incubation	—	—	—	—
	2018	Chick-rearing	24	133	2.10 ± 1.94	201.51 ± 174.55
		Incubation	16	37	4.80 ± 5.47	235.30 ± 253.50
	2019	Chick-rearing	44	230	1.97 ± 1.94	206.46 ± 198.48
		Incubation	14	21	6.84 ± 4.81	393.16 ± 252.90
Raso	2017	Chick-rearing	13	34	2.50 ± 1.86	304.78 ± 259.02
		Incubation	4	6	3.36 ± 2.76	291.80 ± 247.92
	2018	Chick-rearing	25	91	2.75 ± 2.31	333.92 ± 271.00
		Incubation	7	11	6.36 ± 4.01	393.35 ± 208.86
	2019	Chick-rearing	14	41	2.81 ± 2.50	337.03 ± 276.10
		Incubation	11	15	5.88 ± 3.99	475.88 ± 299.29

Consistency in space use

During incubation and long trips, Cape Verde shearwaters from Curral Velho foraged both in the colony surroundings and off West Africa, between the middle coast of Mauritania and the northern coast of Senegal, with core foraging areas of 7923.23 km² and 6932.14 km² respectively (Figure 5). During the chick-rearing phase, the shearwaters also foraged near the nest and off West Africa, but only by the northern coast of Senegal, and their core foraging area was smaller, with 1460.85 km². The foraging strategy of the shearwaters during short trips differed, as the birds focused their foraging effort near the nest, on a smaller area of 665.025 km², so 10 times smaller than the core area used during long trips. Cape Verde shearwaters from Raso also relied on areas surrounding their colony to forage during their short trips, using a core area of 2095.12 km². Cape Verde shearwaters had similar core foraging areas during the chick-rearing period and short trips, with similar site locations and sizes of respectively 4169.01 km² and 3698.91 km². During incubation, Cape Verde shearwaters mainly foraged close to the northern coast of Senegal and on a small site at close distance from their colony, using a total area of 1489.051 km². The R-value of the ANOSIM analysis varied between -0.10 and 0.10, showing spatial consistency in their core foraging sites (50% Kernel UDs) both within and between the years, for both colonies during the two breeding phases and for the two trip durations (Figure 6).

Bulwer's petrels from Cima Islet used a core foraging area of 12179.2 km² during chick-rearing in their colony surroundings, which was 3.4 times larger than during incubation, although the sites overlapped. The core foraging area used during the long trips was 11168.2 km², which was very similar to the area of the chick-rearing phase. A similar pattern was observed on the population of Raso Islet, with a core foraging area during chick-rearing of 8122.44 km² which was 51 times larger than the one used during incubation (158.588 km²). The size of the core area covered by Bulwer's petrels during long trips was 2008.71 km², which was 1.7 times larger than the one covered during short trips (1199.09 km²) (Figure 7). The R-value from the ANOSIM analysis is around 0.2 for the two breeding periods and trip durations of both colonies meaning that the core foraging areas are quite consistent within the year but with considerable variation between years (i.e. positive R-values; Figure 6).

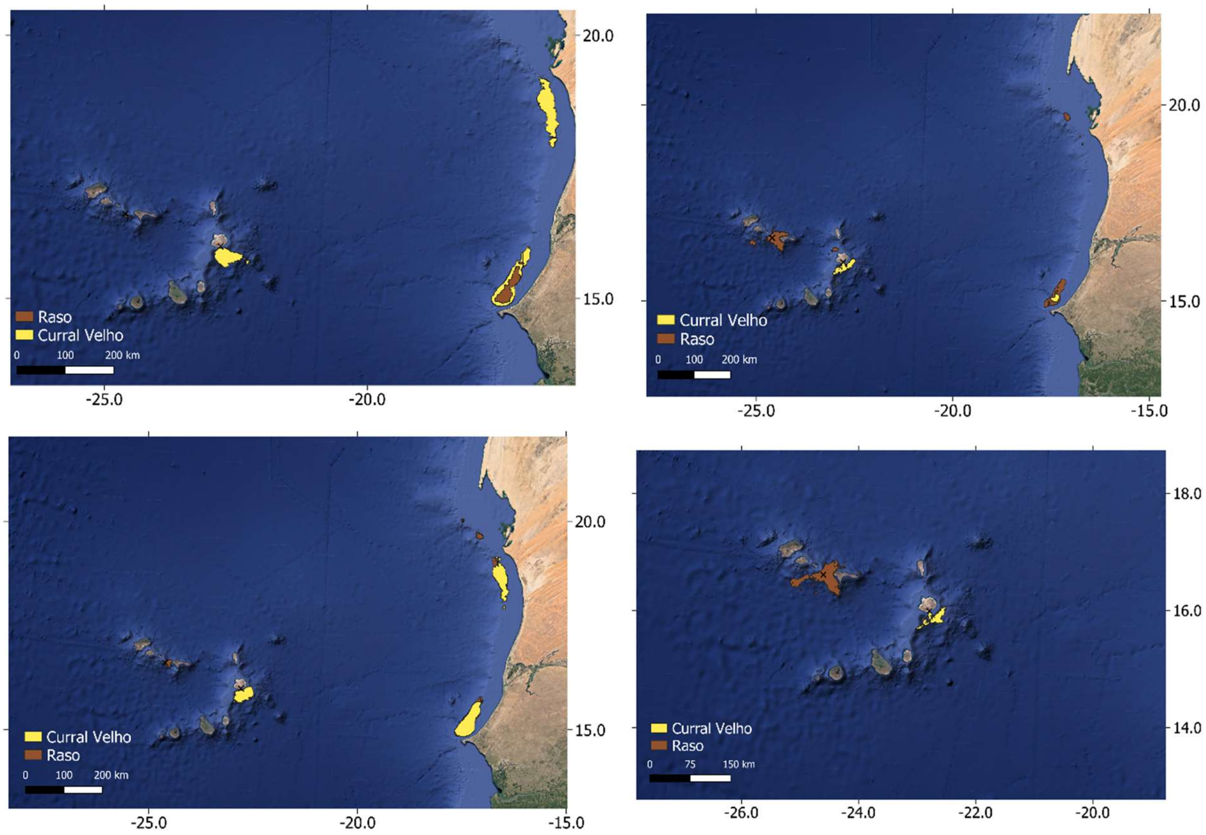


Figure 5. Important foraging areas for the Cape Verde shearwater. Incubation phase (top left), Chick-rearing phase (top right), long trip (bottom left), short trip (bottom right).

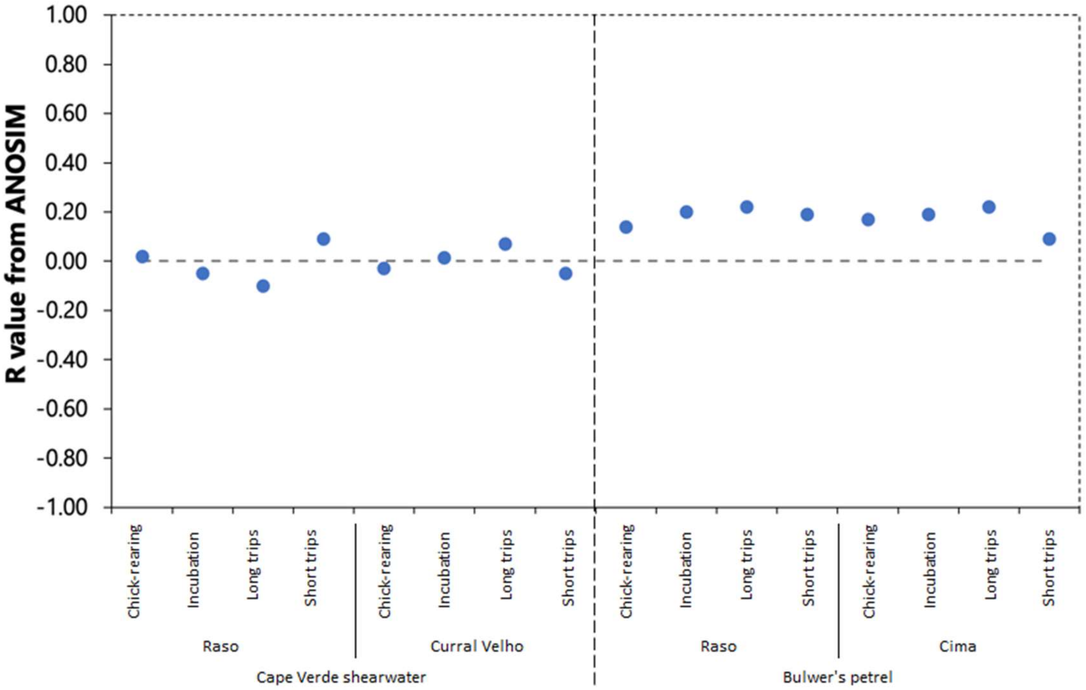


Figure 6. Results of the ANOSIM analysis, showing the variability in R values in the datasets analysed for the Bhattacharyya's affinity index. ANOSIM R values can potentially vary between -1 (within-year variability > between-years variability) and 1 (between-years variability > within year-variability).

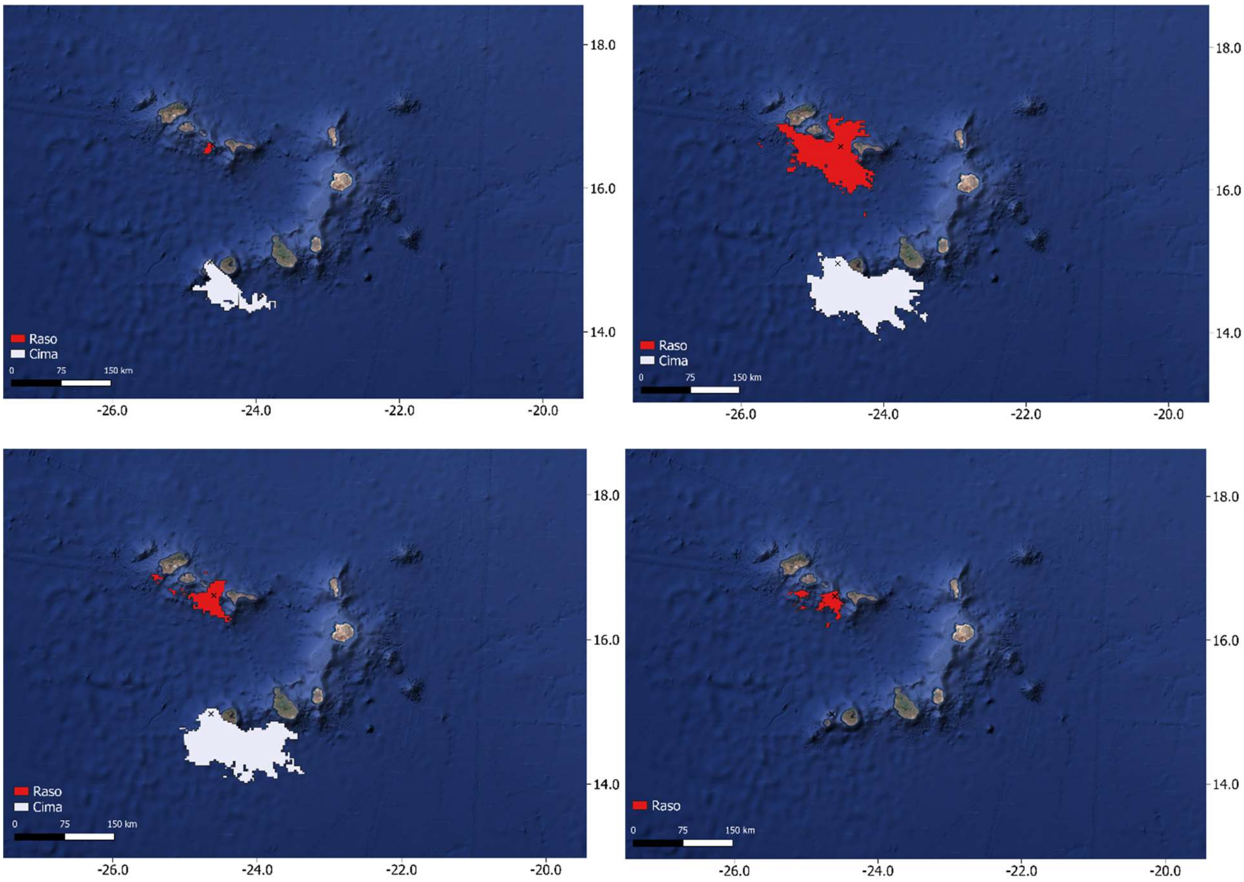


Figure 7. Important foraging areas for the Bulwer's petrel. Incubation phase (top left), Chick-rearing phase (top right), long trip (bottom left), short trip (bottom right).

Overlap of the core foraging areas with the current network of Key Biodiversity Areas (KBAs) and Marine Protected Areas (MPAs)

For the two study species, the estimated core foraging areas were much less covered by the MPAs than by the KBAs. Indeed, Cape Verde shearwaters from Raso Islet had their core foraging areas highly covered by KBAs with an overlap varying between 99.68% and 73.73%, with overlaps higher than expected by change (i.e. permuted overlaps) (Table 5). Yet MPAs covered less than 1% of the four core foraging areas (Incubation, Chick-rearing, Long trips and Short trips) of this population. This pattern was also noticeable for the population from Curral Velho, but with less drastic results, the short trips area still being covered by 83.33% (Table 6).

The current network of KBAs showed a maximum coverage of only 7.38% of the estimated core foraging area of Bulwer's petrels from Cima Islet during the chick-rearing period (Table 5). As for the population of Raso, the overlap varied greatly with a coverage of 80.0% for the incubation period whilst only a quarter of the chick-rearing core foraging area overlapped with the KBAs. However, foraging Bulwer's petrels from both study colonies exhibited a generally low overlap with the current network of MPAs. Indeed, less than 1% of the core foraging areas of birds from Cima Islet are protected, and the maximum protecting reached for birds from Raso was 1.94% for the long trips category (Table 6). The greatest difference occurred during the incubation period which had a coverage of 80% by KBAs, but 0.1% by MPAs.

Table 5. Metrics of Bhattacharyya's affinity (BA) overlap (in %) between core foraging distribution (50% kernel Utilization Distribution, UD) of Cape Verde shearwaters and Bulwer's petrels and the current network of Key Biodiversity Areas (KBAs) off the west Africa marine region. *P* represents the proportion of randomized overlaps that were smaller than the observed overlap. Significant differences are shown in **bold**.

	Observed overlap	**Permuted overlap (mean±SD)**	***P***
Cape Verde shearwater			
Raso			
Chick-rearing	86.5	80.1 ± 16.4	0.21
Incubation	99.7	56.2 ± 18.9	**0.01**
Long trip	96.4	65.3 ± 11.1	**0.02**
Short trip	73.7	82.2 ± 17.4	**0.03**
Curral Velho			
Chick-rearing	91.8	81.3 ± 22.2	0.09
Incubation	60.8	58.2 ± 16.7	0.21
Long trip	67.5	69.9 ± 18.9	0.17
Short trip	96.6	75.4 ± 19.9	**0.01**
Bulwer's petrel			
Raso			
Chick-rearing	25.5	71.3 ± 18.4	**0.01**
Incubation	80.0	56.3 ± 21.1	**0.03**
Long trip	63.4	53.9 ± 23.2	0.10
Short trip	56.4	76.2 ± 19.0	**0.02**
Cima			
Chick-rearing	7.4	76.3 ± 11.6	**0.001**
Incubation	12.7	61.3 ± 15.3	**0.01**
Long trip	7.5	56.2 ± 11.9	**0.001**
Short trip	—	—	—

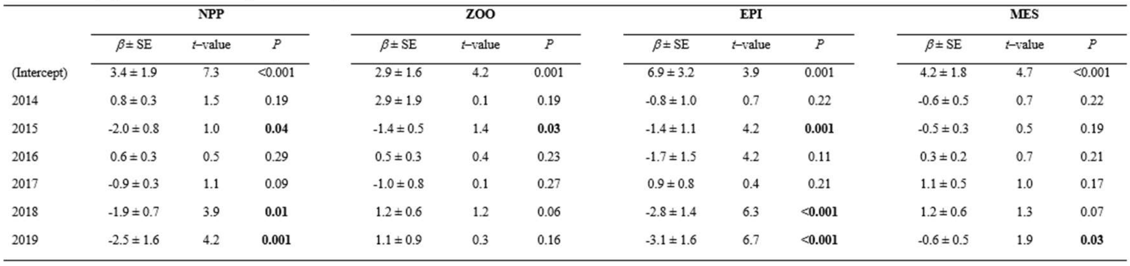
Table 6. Metrics of Bhattacharyya's affinity (BA) overlap (in %) between core foraging distribution (50% kernel Utilization Distribution, UD) of Cape Verde shearwaters and Bulwer's petrels and the current network of Marine Protected Areas (MPAs) off the west Africa marine region. *P* represents the proportion of randomized overlaps that were smaller than the observed overlap. Significant differences are shown in **bold**.

	Observed overlap	Permuted overlap (mean±SD)	*P*
Cape Verde shearwater			
Raso			
Chick-rearing	0.1	11.4 ± 13.8	**0.02**
Incubation	0.1	5.3 ± 4.3	**0.01**
Long trip	0.1	4.2 ± 2.9	**0.01**
Short trip	0.2	22.7 ± 11.9	**0.01**
Curral Velho			
Chick-rearing	61.5	15.3 ± 11.3	**0.02**
Incubation	18.1	6.7 ± 1.9	0.20
Long trip	18.5	7.3 ± 3.8	0.19
Short trip	83.3	28.1 ± 12.6	**0.01**
Bulwer's petrel			
Raso			
Chick-rearing	1.1	15.6 ± 1.8	**0.01**
Incubation	0.1	6.4 ± 4.6	**0.01**
Long trip	1.9	9.7 ± 8.4	**0.01**
Short trip	0.4	19.6 ± 11.7	**0.01**
Cima			
Chick-rearing	0.1	18.4 ± 4.7	**0.001**
Incubation	0.2	5.2 ± 1.9	**0.02**
Long trip	0.1	6.9 ± 2.3	**0.02**
Short trip	—	—	—

Environmental drivers of the interannual use of core foraging areas

Within the core foraging areas of the population of Cape Verde shearwaters from Raso Islet, the net primary productivity as well as the mass content of epipelagic fish decreased significantly in 2015, 2018 and 2019 when compared with 2013 (Table 7). The mass content of zooplankton remained nearly constant among study years, only decreasing significantly in 2015. Unlike for the epipelagic fishes, the mass content of mesopelagic fishes did not vary between 2013 and 2018, only decreasing in 2019. The net primary productivity and the mass content of zooplankton were significantly lower in 2019 than in 2017 within the core foraging areas of the Curral Velho's population (Table 7). Whilst the mass content of epipelagic fishes decreased significantly in 2018 and 2019, the mass content of mesopelagic fishes remained stable. Within the core foraging areas of Bulwer's petrels from Raso, the net primary productivity and the mass content of zooplankton did not vary significantly during the years of the study (Table 8). However, the mass content of epipelagic fishes decreased significantly in 2018 and 2019 when compared to 2017. The mass content of mesopelagic fishes also decreased, but only in 2018. The net primary productivity of core foraging areas of Bulwer's petrels from Cima Islet also remained stable during the study years, but the mass content of zooplankton, epipelagic and mesopelagic fishes all significantly decreased in 2018 and 2019 compared to 2017 (Table 8).

Table 7. Results from models showing the effect of study year (2013-2019) on the (1) net primary productivity (NPP; mg m^{-2} day^{-1}), (2) mass content of zooplankton (ZOO; g m^{-2}), (3) mass content of epipelagic fish (EPI; g m^{-2}) and (4) mass content of mesopelagic fish (MES; g m^{-2}) within the Key Biodiversity Areas (KBAs) estimated for the overall foraging distribution of Cape Verde shearwaters from Raso Islet. Year 2013 was used as a reference against which other study years are compared. Significant differences are shown in **bold.**



	NPP			**ZOO**			**EPI**			**MES**		
	β ± SE	*t*–value	*P*	*β* ± SE	*t*–value	*P*	*β* ± SE	*t*–value	*P*	*β* ± SE	*t*–value	*P*
(Intercept)	3.4 ± 1.9	7.3	<0.001	2.9 ± 1.6	4.2	0.001	6.9 ± 3.2	3.9	0.001	4.2 ± 1.8	4.7	<0.001
2014	0.8 ± 0.3	1.5	0.19	2.9 ± 1.9	0.1	0.19	-0.8 ± 1.0	0.7	0.22	-0.6 ± 0.5	0.7	0.22
2015	-2.0 ± 0.8	1.0	**0.04**	-1.4 ± 0.5	1.4	**0.03**	-1.4 ± 1.1	4.2	**0.001**	-0.5 ± 0.3	0.5	0.19
2016	0.6 ± 0.3	0.5	0.29	0.5 ± 0.3	0.4	0.23	-1.7 ± 1.5	4.2	0.11	0.3 ± 0.2	0.7	0.21
2017	-0.9 ± 0.3	1.1	0.09	-1.0 ± 0.8	0.1	0.27	0.9 ± 0.8	0.4	0.21	1.1 ± 0.5	1.0	0.17
2018	-1.9 ± 0.7	3.9	**0.01**	1.2 ± 0.6	1.2	0.06	-2.8 ± 1.4	6.3	**<0.001**	1.2 ± 0.6	1.3	0.07
2019	-2.5 ± 1.6	4.2	**0.001**	1.1 ± 0.9	0.3	0.16	-3.1 ± 1.6	6.7	**<0.001**	-0.6 ± 0.5	1.9	**0.03**

Table 8. Results from models showing the effect of study year (2017-2019) on the (1) net primary productivity (NPP; mg m^{-2} day^{-1}), (2) mass content of zooplankton (ZOO; g m^{-2}), (3) mass content of epipelagic fish (EPI; g m^{-2}) and (4) mass content of mesopelagic fish (MES; g m^{-2}) within the Key Biodiversity Areas (KBAs) estimated for the overall foraging distribution of (A) Cape Verde shearwaters from Curral Velho (Boavista Island), (B) Bulwer's petrels from Raso Islet and (C) Bulwer's petrels from Cima Islet. Year 2017 was used as a reference against which other study years are compared. Significant differences are shown in **bold**.

A	NPP			ZOO			EPI			MES		
	β ± SE	*t*–value	*P*	*β* ± SE	*t*–value	*P*	*β* ± SE	*t*–value	*P*	*β* ± SE	*t*–value	*P*
(Intercept)	3.2 ± 1.5	3.9	0.001	2.6 ± 1.1	2.6	0.01	1.2 ± 0.8	2.2	0.01	0.8 ± 0.7	1.1	0.07
2018	0.3 ± 0.1	0.9	0.34	-0.3 ± 0.1	0.7	0.43	-3.2 ± 0.9	4.2	**0.001**	1.1 ± 0.5	0.7	0.10
2019	-2.9 ± 1.2	2.0	**0.01**	-1.4 ± 0.2	2.0	**0.02**	-3.8 ± 1.1	5.9	**<0.001**	1.0 ± 0.8	1.1	0.17
B												
(Intercept)	0.9 ± 0.5	1.4	0.08	2.8 ± 1.5	3.2	0.01	3.5 ± 1.2	4.1	0.001	3.6 ± 1.9	4.3	0.001
2018	0.2 ± 0.1	0.8	0.10	1.3 ± 0.5	1.0	0.16	-3.1 ± 1.3	2.2	**0.01**	-2.6 ± 1.4	1.4	**0.05**
2019	0.1 ± 0.1	0.3	0.20	-0.9 ± 0.5	0.9	0.10	-1.2 ± 0.4	1.8	**0.04**	0.6 ± 0.3	0.9	0.08
C												
(Intercept)	0.7 ± 0.4	2.5	0.02	-0.7 ± 0.3	1.3	0.07	-1.1 ± 0.8	2.0	0.01	-1.8 ± 0.8	2.3	0.02
2018	0.4 ± 0.2	0.5	0.16	-1.4 ± 0.7	1.9	**0.03**	-1.6 ± 0.3	6.3	**<0.001**	-2.3 ± 0.6	4.6	**<0.001**
2019	-1.1 ± 0.3	0.9	0.11	-1.9 ± 0.5	2.8	**0.01**	-1.9 ± 0.5	6.9	**<0.001**	-3.1 ± 0.5	5.9	**<0.001**

Overlap of the core foraging areas with the distribution of other marine predators

Cape Verde shearwaters from Raso had their core foraging areas overlapping with 19 out of the 24 species using the West Africa marine area, including four vulnerable species (Audouin's gull, Leatherback Sea turtle, Loggerhead turtle, Sperm whale), two near threatened species (Blue shark, Cape Verde petrel) and one endangered species (Shortfin mako shark). There are 11 bird species, two shark species, one dolphin species, two turtle species, and three whale species. Some species fully overlapped with the core foraging areas of the four categories (i.e. core foraging areas during chick-rearing, incubation, long trips and short trips), like the Audubon's shearwater and the Shortfin mako shark, some species overlapped very partially with the four categories, like the Cape Verde storm petrel, the Loggerhead turtle or the Northern gannet, and some species overlap both greatly and slightly with the categories. Indeed, the Blue shark, Brown booby and Cape Verde petrel overlapped almost totally with the short-trips category, by 50% with the chick-rearing but less than 10% for the long-trips and incubation (Figure 8).

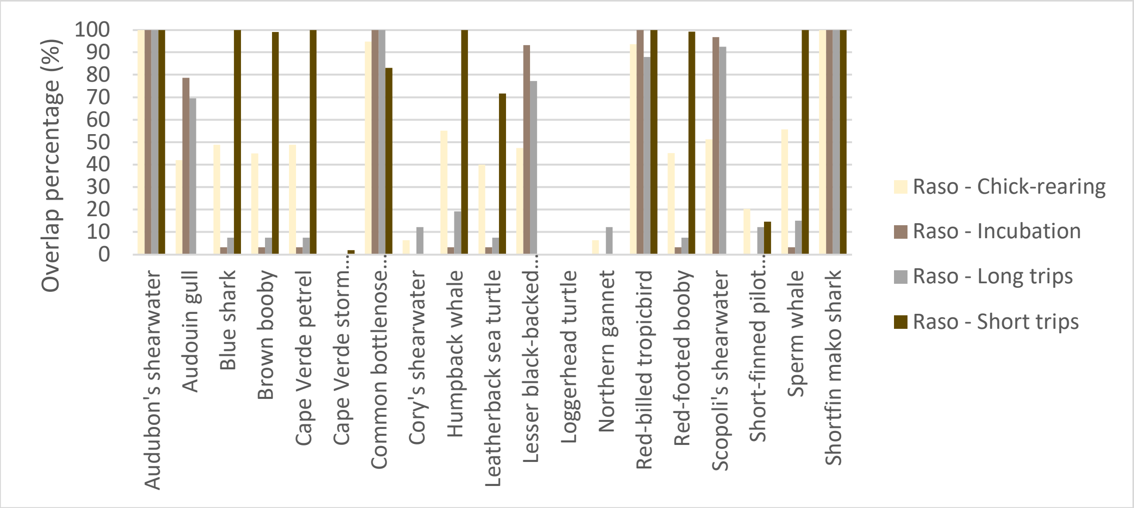


Figure 8. Overlap percentage of the core foraging areas for the Cape Verde shearwaters from Raso Island with the distribution of other marine predators.

Core foraging areas of Cape Verde shearwaters from Curral Velho overlapped with 18 species out of the 24 selected. Amongst them, there were three vulnerable species (Audouin's gull, Leatherback Sea turtle, Sperm whale), two near threatened species (Blue shark, Cape Verde petrel), and one endangered species (Shortfin mako shark). The same observation can be made concerning amount of the core foraging area covered by the species' distribution. In total there are 11 bird species, two shark species, one dolphin species, one turtle species and three whale species (Figure 9).

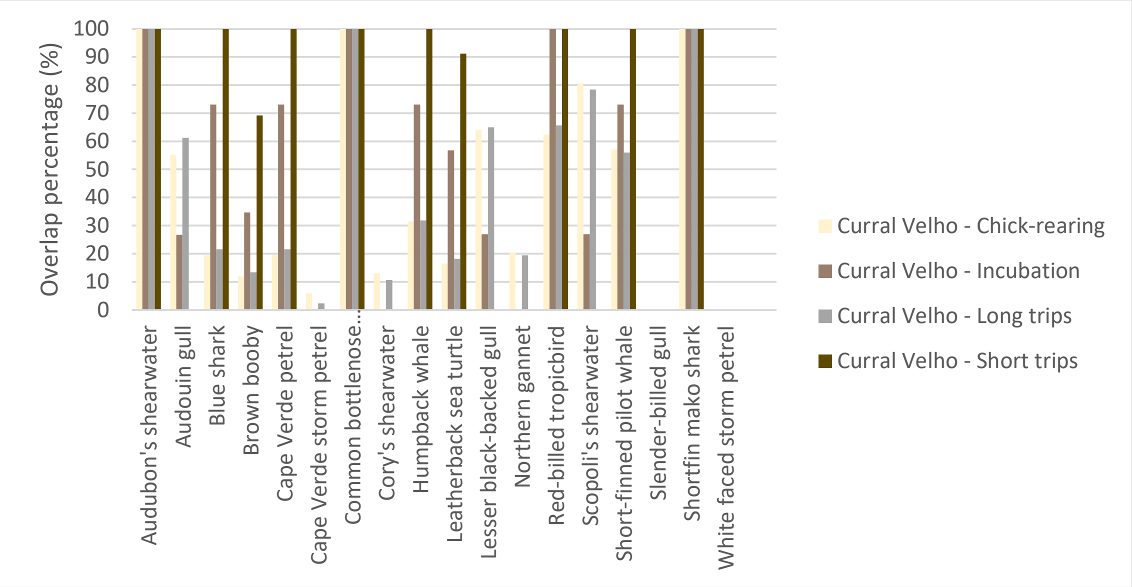


Figure 9. Overlap percentage of the core foraging areas for the Cape Verde shearwaters from Curral Velho Island with the distribution of other 'marine predators.

Core foraging areas of Bulwer's petrels from Cima Islet overlapped with a total of 10 species out of the 24 selected for the analysis, which is almost half of the number of species overlapping with the core foraging distribution of the Cape Verde shearwaters. Amongst these species, there is one vulnerable species (Sperm whale), two near threatened species (Blue shark, Cape Verde petrel) and one endangered species (Shortfin mako shark). There are four bird species, two shark species, one dolphin species and three whale species. All species overlapped almost completely with all three core foraging areas, expect for the Humpback whale that covers less than 20% of the three sites (Figure 10).

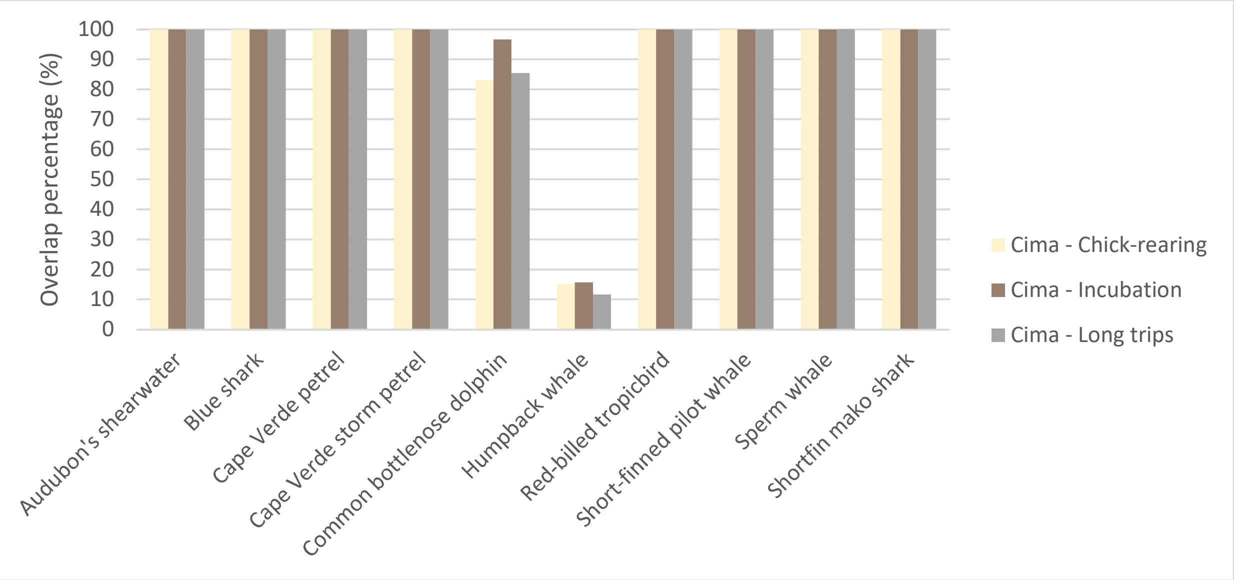


Figure 10. Overlap percentage of the core foraging areas for the Bulwer's petrels from Cima Islet with the distribution of other marine predators.

Core foraging areas of Bulwer’s petrels from Raso overlapped with the distribution of 15 out of the 24 species using the West Africa region. There were two vulnerable species (Leatherback Sea turtle, Sperm whale), two near threatened species (Blue shark, Cape Verde petrel) and two endangered species (Chilean devil ray, Shortfin mako shark). However, the endangered Chilean devil ray’s distribution overlaps with only 0.3% of the core foraging area during the chick-rearing phase. Like for the population from Cima Islet, the percentage overlap is either high (>80%) or low (<25%), except for the Common bottlenose dolphin and the Leatherback Sea turtle which have more varying coverage, even between categories. In total, there are seven bird species, two shark species, one ray species, one dolphin species, one turtle species and three whale species (Figure 11).

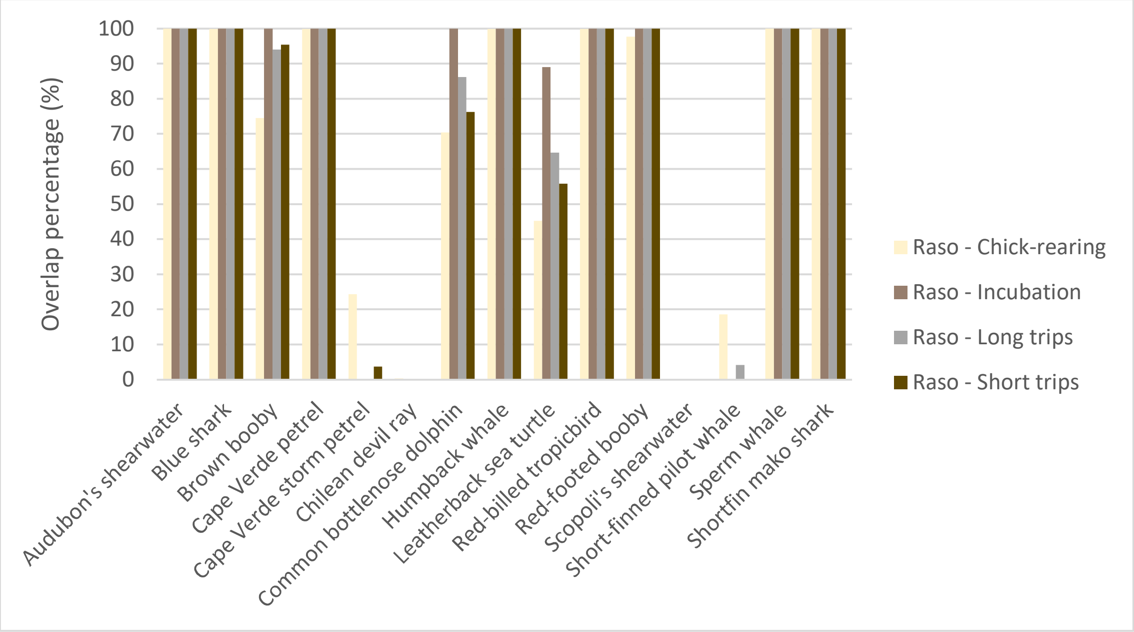


Figure 11. Overlap percentage of the core foraging areas for the Bulwer's petrels from Raso Island with the distribution of other marine predators.

Overlap of the core foraging areas with fishery activities

Across all years, the main vessel type operating within the core foraging areas of Cape Verde shearwaters from Raso seem to be trawlers, but the pole and line method appeared in 2018 and increased rapidly in 2019 reaching a 80% overlap with the core foraging area during the short trips of the birds (Figure 12). Longlines do not have an important activity in this area, reaching a maximum overlap of ~15%. During 2013, 2014 and 2016 fishery activities exhibited a maximum overlap of 30% by seiners for the core foraging area of the shearwaters' long trips in 2016, but did not reach more than 20% for the remain categories of core foraging areas and fishing methods.

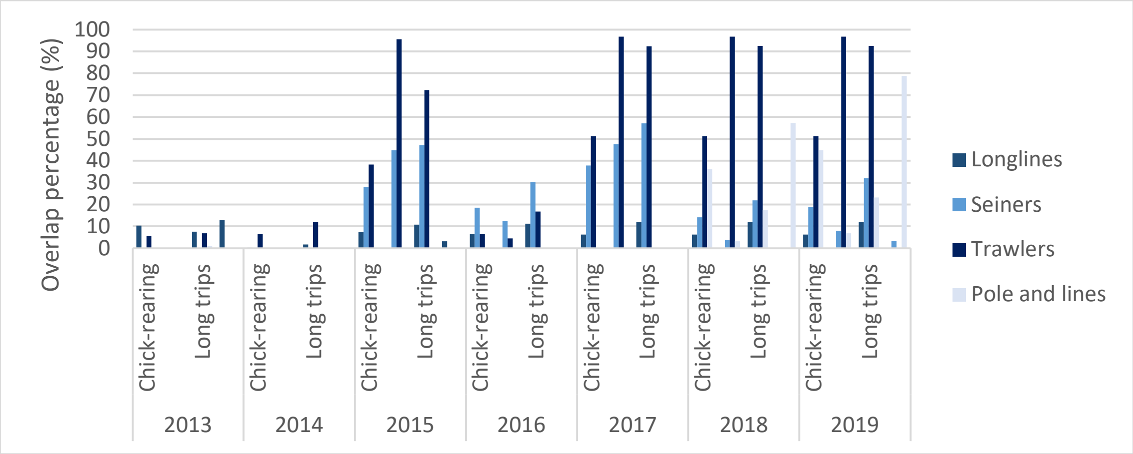


Figure 12. Overlap percentage of the core foraging areas for the Cape Verde shearwaters from Raso Islet with areas of core fishery activities.

During the three years of the study, the fishery activities did not vary much within the core foraging areas of Cape Verde shearwaters from Curral Velho. Indeed, seiners' activity inside the areas decrease after 2017 whilst trawlers' activity increased, but 2018 and 2019 were very similar in terms of overlap percentage between the four fishing methods and seabird core foraging areas (Figure 13). Fishery activities overlapped the most with the core foraging areas of long trips during the incubation period.

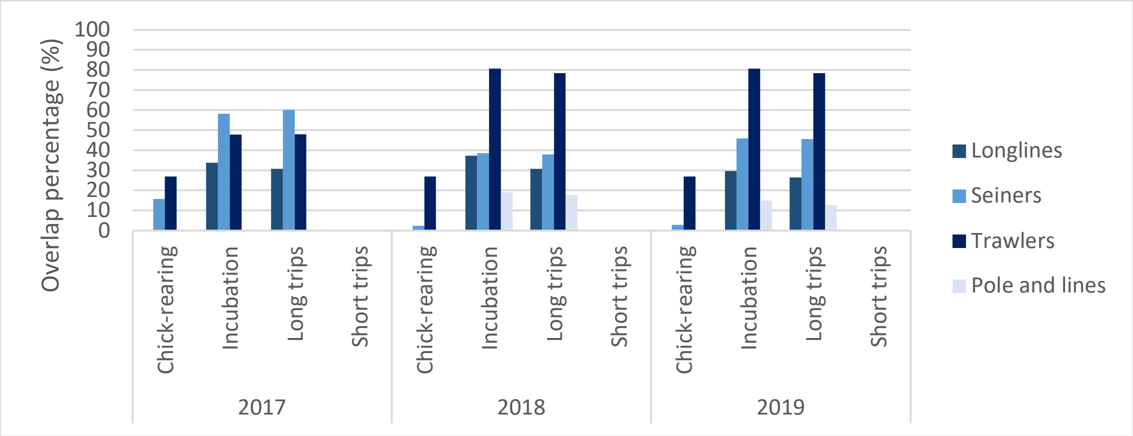


Figure 13. Overlap percentage of the core foraging areas for the Cape Verde shearwaters from Curral Velho Island with areas of core fishery activities.

Within the core foraging areas of Bulwer's petrels from Raso, pole and line were the dominant fishing methods during 2018 and 2019. In 2017, only longliners operated within the core foraging areas of the long-trips during the chick-rearing period (Figure 14). In 2019, there was more vessel diversity, with the appearance of seiners in the seabirds' core foraging areas. The fishery activities also seemed to increase in intensity, with a percentage overlap ~16 times higher in 2019 than in 2017.

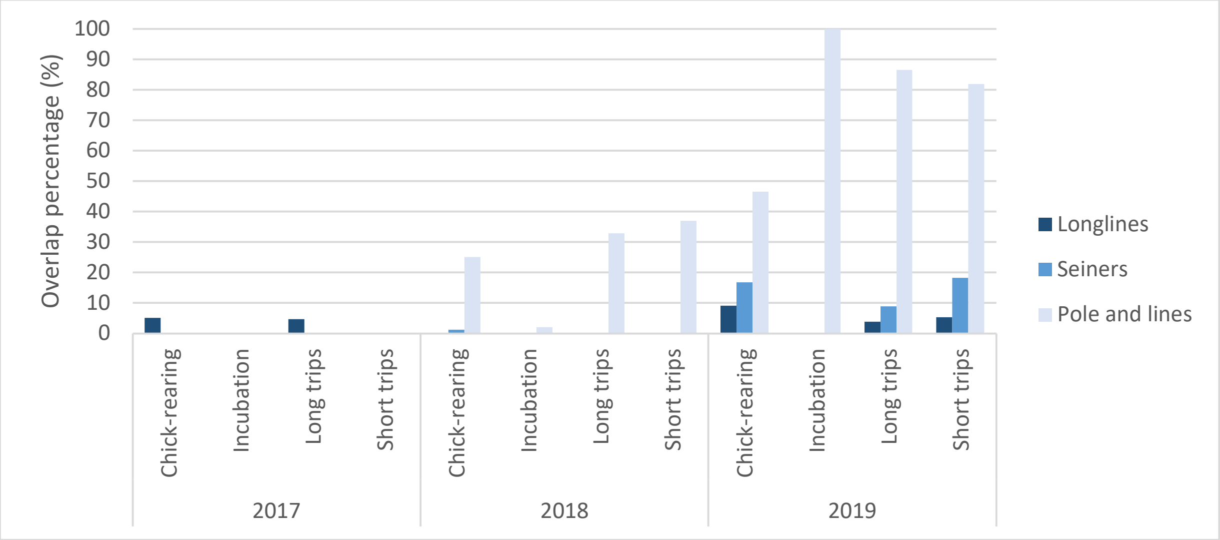


Figure 14. Overlap percentage of the core foraging areas for the Bulwer's petrels from Raso Island with areas of core fishery activities.

Within the core foraging areas of Bulwer's petrels from Cima Islet, the only fishing vessels were longliners and seiners, but the seiners were only present in 2019 with an overlap lower than 1% (Figure 15). Overall, fishery activities did not overlap more than 15% with the core foraging areas for the Bulwer's petrels from Cima Islet.

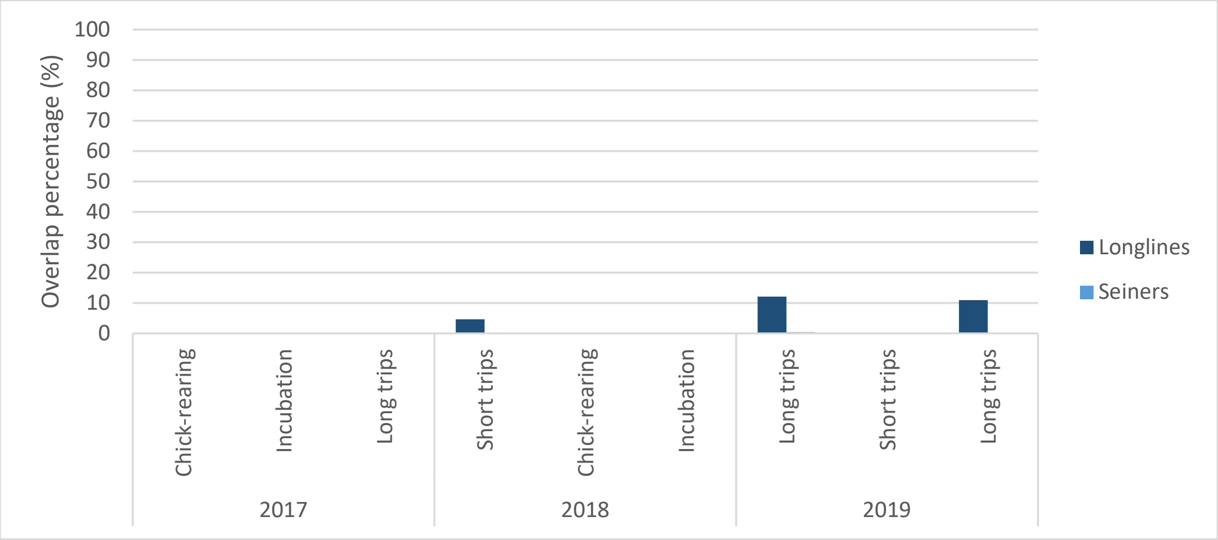


Figure 15. Overlap percentage of the core foraging areas for the Bulwer's petrels from Cima Islet with areas of core fishery activities.

DISCUSSION

Foraging patterns and consistency in space use

The foraging distribution of the two populations of Cape Verde shearwaters (from Raso and Cima Islets) had many similarities, and almost only naturally differed in their starting locations. Indeed, shearwaters performed short trips to forage within their colony surroundings and long excursions to forage off West Africa. They showed different foraging behaviours during the incubation and chick-rearing periods. They generally exhibited a dual foraging behaviour, which has been previously described for the species (Paiva et al, 2015), alternating especially during chick-rearing, between several short forays for chick provisioning with a long excursion to off West Africa mostly for self-provisioning (i.e. to restore their body condition). From 2013 to 2019, Cape Verde shearwaters had four core foraging areas: one around each colony, one off Mauritania and one off North Senegal. During incubation both populations foraged mostly on the sites off West Africa than in the colony surroundings, whilst the opposite was naturally observed during chick-provisioning. This behaviour is coherent with the foraging behaviour of the species during the different breeding phases. Moreover, Cerveira et al. (2020) found Cape Verde shearwaters of Raso Islet to exhibit foraging plasticity, investing in a higher number of long trips towards off West Africa in years of poor oceanographic conditions within the Cabo Verde archipelago, and shorter trips around the colonies during years of good oceanographic conditions. Despite this differential strategy, the areas targeted between years were very similar as shown by the general pattern of values around 0 on the ANOSIM (similarity) analysis.

As for the Bulwer's petrels, the two colonies displayed similar generally oceanic foraging distributions, albeit a certain degree of between populations spatial segregation. Indeed, whilst both colonies foraged around the breeding colony, off West Africa and in more pelagic area west of Cabo Verde, the population of Cima foraged in southern areas when compared to the more northern distribution of Raso's population. This might have happened because there is a considerable difference in the breeding phenology of these populations, although their proximity in breeding locations (~180 km apart). Ecological/ evolutionary drivers behind this are still under investigation, but led to a temporal mismatch on tracking data collection, with the tracking information of Raso's colony being recorded two months later than Cima's colony. Thus, the mesopelagic fish distribution might have changed during these months, and Bulwer's petrel already showed some adaptative skills to prey availability (Dias et al., 2016). Compared to former studies where Bulwer's petrels travelled very long distances, up to 1700 km from the colony during the breeding period (Dias et al., 2016), individuals of our study travelled shorter distances with a maximum of 979 km from the colony. Despite being overall more pelagic than the Cape Verde shearwater, the core foraging areas of Bulwer's petrels were larger but centred around the colonies. During chick-rearing, core foraging areas overlapped almost perfectly with the long trip areas especially for Cima's population, whilst during incubation the areas are even smaller than those for short trips. Populations of this species showed some inconsistency in their foraging spatial distribution among years in their foraging patterns, which might also be linked to the oceanographic conditions and the adaptative behaviour of the petrels to find their preys (Dias et al., 2016; Waap et al., 2017).

Overlap of KBAs off West Africa with the estimated core foraging areas

KBAs off West Africa overlap with most of the core foraging areas and particularly the areas of the Cape Verde shearwater, both populations of Raso and Curral Velho. Indeed, the Raso/ São Nicolau – marine KBA covers most of the areas for Raso's population, and the smaller KBAs of Ilhéu Branco, Ilhéu Raso and Beaches of Sao Nicolau Island also overlap with these areas. However, for Curral Velho's population, whilst the core foraging areas near Curral Velho Island and Dakar are well covered by the Ilhéu de Curral Velho – marine, and the Northern Senegal shelf-break KBAs, the core foraging areas by the Northern Mauritanian coast are only slightly overlapping with the Canary current shelf-break (South) KBA, which is too North to wholly cover the sites. This zone was implemented as a KBA in 2016 because it has been identified as an area of ecological importance due to the presence of eight birds including the Audubon's and Cory's shearwaters and the Northern gannet, but neither the Cape Verde shearwater nor the Bulwer's petrel (Key Biodiversity Areas Partnership, 2022). As for the Ilhéu de Curral Velho – marine KBA, it was implemented in 2017 due to the presence of the Cape Verde shearwater (Key Biodiversity Areas Partnership, 2022). The Northern Senegal shelf-break KBA was implemented in 2016, also due to the presence of the Cape Verde shearwaters, respecting two criteria (B1: more than 10% of the global population and more than 10 reproductive units of any species, D1a: more than 1% of the global population size of a species over a season and during more than one key stage in the life cycle) (Key Biodiversity Areas Partnership, 2022). So, this explains the high overlap of the core foraging areas around Curral Velho (Boavista Island) and Dakar (Senegal), and it shows the possibility of extending the Canary current shelf-break (South) KBA to include the important foraging areas of the two study species.

As for the Bulwer's petrel, only 6 out of the 11 coastal KBAs near Cabo Verde are overlapping with the estimated core foraging areas, because individuals of these populations are comparably more pelagic, these KBAs only covered a small amount of the core foraging areas, especially for the population of Cima Islet with a maximum coverage of less than 13%. This low coverage could be explained by the characteristics of the KBAs. Indeed, Ribeira de Fajã de Água is a terrestrial MPA with a small sea extension that was implemented because of the presence five endangered and critically endangered plant species (Key Biodiversity Areas Partnership, 2022), not taking into account the distribution of any marine taxa. Ilhéus do Rombo is a terrestrial and marine KBA which was implemented in 2017 for the presence of four bird species and one reptile endemic to Cabo Verde, the Delalande's Skink (*Chioninia delalandii*). Both are relatively small areas, more than 1900 times smaller than the core foraging areas of Cima's population of Bulwer's petrels, so the core foraging areas are covering these small KBAs entirely. The terrestrial and marine area around Ilha do Fogo is a larger KBA implemented in 2017 around Fogo Island due to the presence of the Cape Verde petrel (*Pterodroma feae*) (Key Biodiversity Areas Partnership, 2022). However, the KBA is larger at the North of the Island whilst the Bulwer's petrels tend to forage more on the South, thus the low percentage of overlap. On the other hand, during the incubation period the core foraging distribution of Bulwer's petrels from Raso Islet was totally covered by the Raso / São Nicolau – marine KBA whilst during the chick-rearing period only 25% of the area was covered by Raso / São Nicolau – marine, Ilhéu Branco and Ilhéu Raso KBAs. This could be explained by the size of the sites, the core foraging area during chick-rearing being 51 times larger than during incubation. And the KBAs are relatively small: Raso / São Nicolau – marine is 2560 km², Ilhéu Branco 15.55 km² and Ilhéu Raso is 10.47 km² (Key Biodiversity Areas Partnership, 2022), so they are respectively 3, 522 and 776 times smaller than the core foraging area of this population during the incubation period.

So, the KBAs currently implemented near Cabo Verde are much smaller than the important foraging areas for the populations of Cape Verde shearwaters and Bulwer's petrels. Considering the potential of these two seabirds to be umbrella species for other marine taxa, the current network of KBAs off West Africa are not yet covering all the important sites for marine biodiversity, but it seems to be improving with new implementations covering more important ecological areas. Moreover, the identification of KBAs is only the first step in a conservation plan as the criteria only consider the biological characteristics and no other components like economic or social factors, which are evaluated during the identification of MPAs.

Overlap of MPAs off West Africa with the estimated core foraging areas

Out of the 9 MPAs near the coast of Senegal and Mauritania, only one overlaps with the core foraging areas of the Cape Verde shearwaters. This MPA is situated on the sea-floor trench of Kayar, where there is a rich upwelling enriching the waters in phytoplankton. These two features allow a great diversity of fish species, like the Spotted seabass (*Dicentrarchus punctatus*), the Common octopus (*Octopus vulgaris*) or the near-threatened White grouper (*Epinephelus aeneus*). Because of overfishing in the region of Kayar, fish stocks decreased drastically, like the Spotted seabass that has not been caught since 1968, leading to economic issues with the fish prices dropping and conflicts between fishermen communities (PAG AMP CAYAR, 2011-2015). In order to counter this, the government of Senegal implemented rules, some concerning fisheries like the surveillance of traditional fisheries up to 6 nautical miles from the coast, where industrial trawlers are forbidden (PAG AMP CAYAR, 2011-2015). However, this MPA and its regulations remain coastal and do not take into consideration other taxa such as reptiles or birds. Yet, one of the measures is to monitor birds, marine mammals, and turtles so the data collected in our study could add to the knowledge of the biodiversity around Kayar and protecting a larger area around the upwelling could contribute to the issues targeted in this MPA.

Concerning the MPAs surrounding Cabo Verde, there are currently 31 protected areas, and only 7 are overlapping with core foraging areas of Cape Verde shearwaters and Bulwer's petrels. Around Raso Islet, Bulwer's petrel core foraging areas are overlapping with two MPAs: the Reserva natural de Santa Luzia and the Reserva natural integral Ilhéus Branco e Raso. For each breeding phase and trip duration, the overlap does not exceed 2%, which is particularly small knowing that Bulwer's petrels overlapped between 25% and 100% with KBAs. As seen previously, the KBA overlapping the most with Bulwer's petrels is the Raso / São Nicolau – marine KBA which is not under any protective regulations despite having been identified as an ecologically important area. The core foraging areas of the population of Cape Verde shearwaters overlapped only with the Reserva natural integral Ilhéus Branco e Raso. Bulwer's petrels and Cape Verde shearwaters showed the same tendency of having their core foraging areas highly covering this MPA during their long and short trips, during the chick-rearing period though much less during the incubation phase. Indeed, during this period, birds seem to forage mostly in a small area in the South of Raso islet, where there is no MPA in place.

Around Cima Islet, the core foraging areas of the Bulwer's petrels overlapped with two MPAs: the recently implemented Parque Natural da Baia do Inferno e do Monte Agra (PNBIMA), on the South-West coast of Santiago Island, and the Reserva Natural Integral de Ilhéus do Rombo. However, this overlap does not exceed 0.2%, so the important foraging areas of Bulwer's petrels from this population are barely protected.

The population of Cape Verde shearwaters from Curral Velho had their core foraging areas overlapping with three MPAs: the Reserva natural integral de Ilhéu Curral Velho, the

Reserva natural de Tartaruga, and Oceania, the recently implemented large marine pelagic MPA. These core foraging areas are the most protected compared to the other colonies, which is due to the large polygon that covers a large area on the South-East of Boa Vista, where the Cape Verde shearwaters frequently forage.

Moreover, the MPAs of Cabo Verde were organised in three categories, depending on their protection priority and level of management costs (República de Cabo Verde, 2016). None of the MPAs mentioned before are in the high priority category. For Raso Island, the Reserva natural de Santa Luzia is classified as moderate priority whilst the Reserva naturel integral Ilhéus Branco e Raso is classified as low priority (República de Cabo Verde, 2016). For Cima Islet, the Reserva natural integral Ilhéus do Romba is classified as low priority (República de Cabo Verde, 2016) and the Parque Natural da Baia do Inferno e do Monte Angra has not been classified yet. Two of the MPAs overlapping with the core foraging areas around Curral Velho (Reserva batural integral Ilhéus de Curral Velho, Reserva natural Tartaruga) are classified as moderate priority (República de Cabo Verde, 2016), the large polygon has not been classified yet. So, Curral Velho is not only the site with the highest overlap, but also the site with the highest investment in the MPAs.

Overall, the core foraging areas are not under protection, leaving the Cape Verde shearwaters, the Bulwer's petrels, their prey, and coexisting species under the threat of anthropogenic activities, like fisheries. However, the situation could evolve positively, by continuing to add new MPAs and increasing the protection efforts. The numerous KBAs around the archipelago as well as the results of this study already show that the region off West Africa is ecologically important and has a rich biodiversity. However, the economic and social challenges also need to be considered. Indeed, even though tourism plays a major part in Cabo Verde's economy, representing 25% of the GDP in 2018 (Ministère de l'économie, des finances et de la relance, 2020), fisheries are still important and their decrease would impact the economy and the lives of the locals depending on them (Ferreira et al., 2021). Nevertheless, a synergy between MPAs, tourism and fisheries can be explored. Indeed, in the Paraty Bay MPA, in Brazil, whilst fisheries are still in conflict with MPA regulations, fishermen involved in tourism have a higher income that the ones who do not (Lopes et al., 2015). So, Lopes et al. (2015) came with the idea of implementing a mosaic of uses including fisheries and tourism to obtain sustainable and non-conflicting use of marine ecosystem services.

Overlap of the core foraging areas with the distribution of other marine predators

The core foraging areas of the Cape Verde shearwater and the Bulwer's petrel overlapped in total with 21 species out of the 24 selected for the analysis. These 21 species can be separated into six taxa: bird, dolphin, whale, ray, shark and turtle. This diversity, in terms of taxa but also species, underlines the ecological importance of the estimated core foraging areas. Indeed, the presence of a great variety of predators implies the presence of numerous preys. The Chilean devil ray can dive up to 2000m deep and is thought to predate at depth on fish or squid in high-density layers (Thorrold et al., 2014). The leatherback sea turtle populations of West Atlantic use the region off West Africa as foraging grounds where the zooplankton biomass is higher and their foraging success increase (Fossette et al., 2010). They are shallow divers around Cabo Verde and West Africa where the zooplankton biomass is high but dive up to 300m when the biomass is low (Fossette et al., 2010). Thus, the core foraging areas of both Cape Verde shearwaters and Bulwer's petrels encompass/ are also used by a great taxa biodiversity on different vertical layers, from above the ocean with the avifauna to deeper levels with diving species and underwater predators.

Moreover, the 21 species include two endangered species (Chilean devil ray, Shortfin mako shark), two near-threatened species (Blue shark, Cape Verde petrel), and four vulnerable species (Audouin's gull, Leatherback Sea turtle, Loggerhead turtle, Sperm whale). This highlights the potential of protecting the core foraging areas of the Cape Verde shearwaters and the Bulwer's petrels for the protection of other threatened species. Indeed, these species are facing similar threats to the two species studied on this thesis. The endangered Chilean devil ray also faces the threat of accidental by-catch by tuna purse seines and longline fisheries (Couturier et al., 2012).

A collapse of the survival of a population of Northern gannets from Rouzic Island in France was observed by Grémillet et al. (2020) who hypothesised that accidental by-catch and intentional harvest are the most likely causes of mortality, especially for the individuals spending their inter-breeding period off West Africa which is a distant-water fishing hotspot (Cabral et al., 2018). The endangered Shortfin mako shark also suffers from accidental by-catch from fishery activities and Cabo Verde was distinguished as one of the regions where the impact of Spanish longline vessels on these sharks it's the highest (Duarte, 2020). Therefore, the vessels threatening the Cape Verde shearwater and the Bulwer's petrel are also the ones threatening other taxa distributed off West Africa.

Some species' distributions do not overlap temporally with the core foraging areas, or only overlapped partially, like the Lesser black-backed gull recorded off West Africa from September to April (Stienen et al., 2017), the endangered Chilean devil ray that was monitored near Cabo Verde in November-December (Thorrold et al., 2014), or the Humpback whale that winters by the archipelago between January and May (Hazevoet et al., 2011) though some individuals of Humpback whales were recorded near Cabo Verde outside the winter season, during the months of June, July and August (Reiner et al., 1996; P. López Suárez; B. Gravanita). Therefore, these areas are not only ecologically important during the breeding period of the Cape Verde shearwater and the Bulwer's petrel but also during the rest of the year, hence the necessity of protecting these sites.

Moreover, these species have been recorded consistently over the years. From 2008 to 2018, the Shortfin mako shark showed a high fidelity to productive areas including Cabo Verde (Duarte, 2020), the humpback whale comes to Cabo Verde to breed and was observed in Cabo Verde each year between 2010 and 2013 (Ryan et al., 2014), sightings can go back to the 19th century (Smith and Reeves, 2003).

Environmental drivers of the interannual use of the core foraging areas

In 2019, the decline of epipelagic fishes within the core foraging areas of Cape Verde shearwaters from Curral Velho (Boavista Island) matched with the decrease of net primary productivity and mass content of zooplankton, but not in 2018. So, whilst in 2019 the decrease of net primary productivity might have led to the decrease in zooplankton and then epipelagic fishes, there must be another reason for the productivity pattern of 2018, which could be a higher fishery intensity around Curral Velho and off West Africa. Moreover, the lower net primary production could be due to anthropogenic pressures like global warming or reduced nutrient input (Capuzzo et al., 2017). As for the foraging areas of Cape Verde shearwaters from Raso, there also was a decrease of the net primary productivity, the mass content of zooplankton and epipelagic fishes in 2015 compared to 2013. However, in 2018 and 2019, although there was a decrease of the net primary productivity and epipelagic fishes (and mesopelagic fishes for 2019), the mass content of phytoplankton remained similar to the average value of 2013. Cape Verde shearwaters' main preys are epipelagic fish, like the Madeiran sardinella, the bigeye scad or the keeltail needlefish (Rodrigues, 2014), so if the mass content of epipelagic fish keeps decreasing with the years, individuals foraging behaviour will be affected. They also prey on benthopelagic preys like squids (Rodrigues, 2014), but these can also live near the surface, and thus can be subject to the same threat as epipelagic fishes. Within the core foraging areas of Bulwer's petrels from Raso, the environmental drivers are quite constant during the study years, except for the mass content of epipelagic fishes which decreased after 2017. This might not have a big impact on the Bulwer's petrels' diet as they rely mostly on mesopelagic fishes (Zonfrillo, 1986; Neves, Nolf and Clarke, 2011, Waap et al. 2017). There was however a significant decrease in mesopelagic fishes in 2018, compared to 2017 which could impact their distribution and might explain the slight inconsistency in the foraging patterns between years. Moreover, Bulwer's petrels' second main preys are cephalopods (Zonfrillo, 1986; Neves, Nolf and Clarke, 2011) and Cabo Verde was recently identified as a cephalopod biodiversity hotspot holding at least 102 cephalopod taxa (Merten et al., 2021), so they might have compensated the lower number of mesopelagic fishes by preying on cephalopods. The same observations can be made within the core foraging areas of Bulwer's petrels from Cima Islet, except that the decrease of biomass also appears at lower level of the food chain, with the mass content of zooplankton decreasing significantly after 2017. Here, the decline in mass content of phytoplankton might be a reason for the lower mass content of mesopelagic and epipelagic fishes, but it cannot be explained by a decrease in marine productivity, as the net primary productivity remained stable during the study years.

For the four population's core foraging areas, there was a significant decrease in mass content of epipelagic fishes in 2018 and 2019 which could have been caused by a decrease of available zooplankton, but it is only observed within the core foraging areas of Bulwer's petrels from Cima Islet. So, this decline in fishes could be due to higher fishery activities around the archipelago and off West Africa.

Overlap of the core foraging areas with fishery activities

Overall, the fishing vessels off West Africa, especially trawlers, overlapped with most of the core foraging areas of the Cape Verde shearwaters. However, the fishery activities barely overlapped with the core foraging areas of Bulwer's petrels from the two populations, breeding phases or trip types (short or long forays). Only the pole and lines fisheries overlapped with Bulwer's petrels from Raso during the last two years of the study. This difference between the two species is related to the foraging behaviour of the birds because the Cape Verde shearwaters were observed preying on fishes drove to the surface by tuna around fishing vessels (Bugoni et al., 2010). They use fisheries to find prey more easily, therefore they are expected to interact more with fisheries (Montrond 2020). Moreover, closely related species like the Cory's shearwater (*Calonectris diomedea*) feed on fishery discards (Belda and Sánchez, 2001; Bicknell et al., 2013), which might also be the case for the Cape Verde shearwater. Reducing fisheries in the core foraging areas of the shearwaters like in the MPA of Kayar where trawlers are banned a few kilometres from the coast (PAG AMP CAYAR, 2011-2015), or banning discards could reduce the bycatch rates of the seabirds and thus reduce their mortality rate (Anderson et al., 2011; Dias et al., 2019). This strategy could be particularly effective given the fact that fishery waste is considered as the equivalent of junk-food for seabirds because of the negative indirect effects it has on seabirds like reducing the nestlings' survival and the growing pattern of the chicks (Grémillet et al., 2008; Romano et al., 2006). Moreover, there are currently several seabird bycatch mitigation measures, either at a testing phase (e.g. blue-dyed bait at pole and line fishing; Cocking et al., 2008) or fully implemented and validated (e.g. hookpod to mitigate seabird bycatch on longlines; Sullivan et al., 2018) which should help reduce seabird and other marine taxa (e..g seaturtles) bycatch off West Africa and worldwide (Løkkeborg et al., 2011, Mangel et al., 2018).

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