

Acknowledges

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Abstract

A knowledge of pelagic seabird foraging patterns is important to evaluate key areas for marine pelagic top predators. The main objective of this thesis was to describe the foraging pattern of Cory's Shearwater, *Calonectris diomedea borealis* breeding in a small islet of Porto Santo, Madeira archipelago, Portugal. We identified the environmental predictors that determine the selection of foraging areas by Cory's Shearwater and estimated the possible change in the distribution of this species in the North Atlantic, considering the increase in sea surface temperature that is projected for this area during the next century. We used GPS tracking to monitor this population for two years (August 2011 and 2012) during the chick rearing period, and compared the results between these two years. With stable isotopic analysis (only for 2012) we described the ecological niche of adults and chicks and inferred their diet composition using a SIAR mixing model. Combining these information with environmental variables that are known to be important for seabird occurrence, we determined the mainly variables that influenced the Cory's Shearwater foraging choices using Maximum Entropy models.

Our results show a clearly distinct pattern between 2011 and 2012, with birds much more widespread throughout the North Atlantic Ocean in 2011 than in 2012, when birds concentrated their foraging effort in the African Coast. These results suggest that in 2011 the availability of food was much lower than in 2012, therefore Cory's Shearwater had to perform long journeys, which represents a higher foraging effort. The inter-annual variation of oceanographic characteristics sustains this idea of a poor productive year in 2011. The sea surface temperature was the main factor associated with the Cory's Shearwater behavioral foraging choices, which was expected because high levels of sea surface temperature are associated with low levels of pelagic marine

productivity. Information on diet composition shows that Cory's Shearwater adults fed mostly on cephalopods (*Histioteuthis* sp) but provisioned their chicks with higher trophic level prey (e.g. *Scomber* sp).

As a response to an increase in sea surface temperature, our results suggest a marked change in the Cory's Shearwater foraging distribution during the next century. Despite the high level of foraging plasticity that allows Cory's Shearwater to adapt to adverse environmental conditions, such changes imply a strong increase in foraging effort that may compromise breeding success and will influence population dynamics.

Dynamic habitats such as pelagic oceanic areas also need conservation and management considerations. This study contributes to express how important is to monitor the populations on top predators in the Atlantic North and their important foraging areas.

Key words: Foraging ecology, Porto Santo, *Calonectris diomedea borealis*

Resumo

O padrão da ecologia trófica de aves marinhas, representa uma contribuição importante para compreender quais as áreas de alimentação destas aves e o porquê de estas as escolherem. Permite ainda, conhecer de que modo é que, na presença de condições ambientais adversas, estas aves se comportam e adaptam.

Os principais objetivos desta tese centram-se em conhecer pela primeira vez, a ecologia alimentar da população de uma ave marinha, considerada como modelo de estudo, *Calonectris diomedea borealis* – Cagarra, de um ilhéu situado junto à ilha de Porto Santo, arquipélago da Madeira, Portugal, avaliar quais as características ambientais que determinaram a escolha dos seus padrões de alimentação e, considerando o aquecimento previsto para o Atlântico Norte durante o próximo século, inferir como é que as escolhas de áreas de alimentação pelas cagaras serão afetadas. Para dar resposta a estes objetivos, utilizamos dispositivos GPS e estudamos a distribuição no mar desta população durante dois anos (Agosto de 2011 e de 2012), durante o período de desenvolvimento das suas crias. Através da análise de isótopos (apenas referente a 2012), diferenciámos os nichos ecológicos das crias e dos adultos e inferimos quanto à composição da sua dieta através de modelos mistos SIAR. Combinando esta informação com variáveis ambientais conhecidas por explicar a presença de aves marinhas em determinados locais, através de modelos MaxEnt, concluímos quais as variáveis que representaram uma maior influência nas escolhas dos locais de alimentação pelas cagaras.

Os nossos resultados demonstram um padrão claramente distinto entre o ano 2011 e o ano 2012, sendo que em 2011 as aves apresentaram-se mais dispersas pelo Oceano Atlântico Norte, com comportamentos mais pelágicos, comparado com 2012 em que concentraram os seus esforços maioritariamente na costa de África. Estes

resultados sugerem que em 2011 a disponibilidade de alimento foi inferior a 2012 e, deste modo, as cagaras tiveram que realizar viagens maiores para se alimentarem exigindo um maior esforço da parte delas. A variação inter-anual das condições oceânicas sustém esta ideia de uma baixa produtividade em 2011 relativamente ao mesmo período em 2012. A temperatura à superfície da água foi o fator que representou maior relevância nas escolhas de locais de alimentação das cagaras, o que era de certo modo esperado dado que águas mais quentes estão associadas a águas com menos alimento. A informação da composição da dieta das aves demonstrou que os adultos se alimentaram preferencialmente de cefalópodes (*Histioteuthis* sp) mas alimentaram as suas crias de presas de alto nível trófico (e.g. *Scomber* sp).

A provável resposta das cagaras aos cenários de alteração da temperatura da água do mar previstos durante os próximos cem anos indica que os indivíduos de Porto Santo, apesar de apresentarem um elevado nível de plasticidade comportamental na procura de alimento que lhes permite adaptar a condições ambientais desfavoráveis, terão de efetuar um esforço muito superior para procurar alimento, o que poderá ser demasiado dispendioso comprometendo assim o sucesso reprodutor que por sua vez irá ter influência na dinâmica da população.

Habitats dinâmicos como os oceânicos necessitam de um maior esforço de conservação. Este estudo vem contribuir para expressar a importância de monitorizar populações de predadores de topo do Atlântico Norte e as suas áreas de alimentação.

Palavras-chave: Ecologia trófica, Porto Santo, *Calonectris diomedea borealis*

Chapter 1 - Introduction



1.1. Seabird as top predators

Marine pelagic ecosystems are perhaps the largest of all ecosystems on earth (Verity et al. 2002). In the vast ocean, there are a great number of organisms that depend on each other to survive, from the bottom photosynthetic organism to the higher strata, the top predators. Given the size of marine pelagic ecosystems their resources are patchy and scattered over large areas, and their location is often unpredictable (Weimerskirch et al. 2007). However, resources are often associated with certain oceanographic characteristics such as the upwelling phenomenon. This represents the rise of cold and deep waters that are rich in nutrient and so will contribute to an increase in phytoplankton, which will attract zooplankton, followed by small pelagic fish that feeds on them, which in turn attracts top predators such as large fish and seabirds (Figure 1).

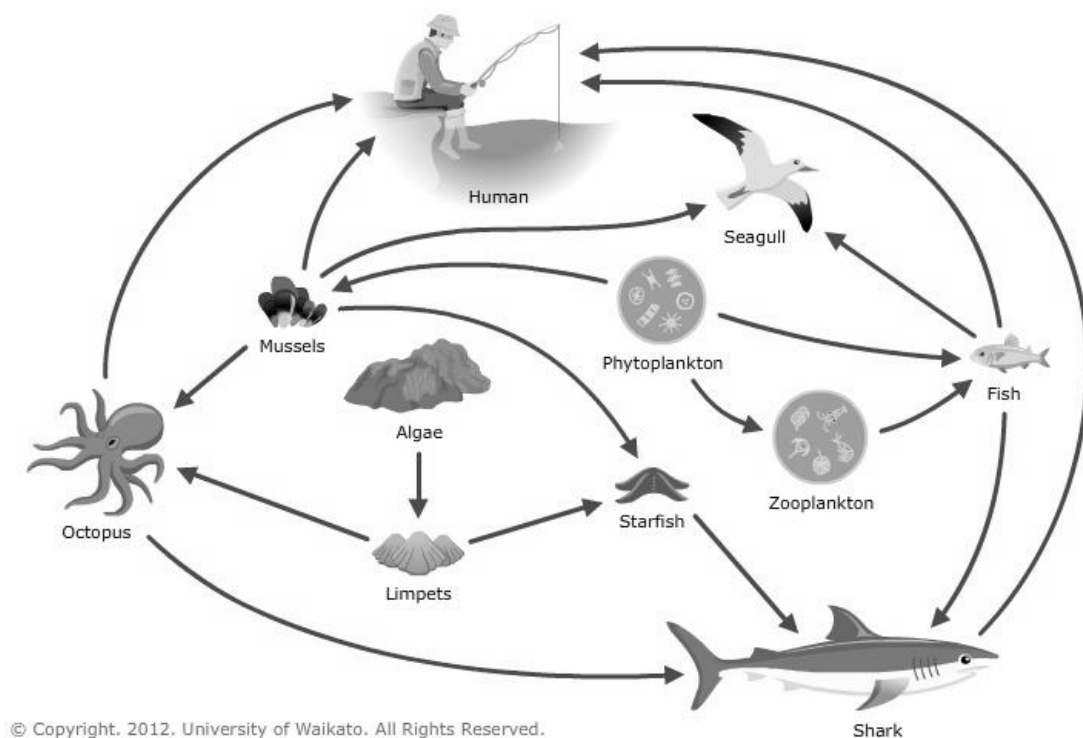


Figure 1 - Example of a marine food web (from: <http://www.sciencelearn.org.nz>)

The study of marine pelagic areas is difficult and expensive because research vessels are needed to collect information on environmental variables in situ (sea-surface temperature, salinity, etc), and on species distribution and abundance. Formerly, the attempts to locate foraging areas of marine top predators such as seabirds relied mainly upon visual observations and were, once again, obtained during oceanographic cruises (Cherel and Weimerskirch 1995). Seabirds are top consumers in marine food webs and offer opportunities to detect and assess biological effects of changes in physical parameters (sea surface temperature, salinity, bathymetry, Chlorophyll *a*, among others) of the marine ecosystem (Diamond and Devlin 2003). Furthermore, they are conspicuous animals and a suitable choice as sentinel organisms (Furness and Camphuysen 1997). If some unexpected changes occur in their numbers, in their usual diet, in their health or breeding success we can extrapolate that something is happening in the ecosystem, probably in the lower levels of the marine food web. Seabird ecology offer a unique insight into marine ecosystems status, functioning and health, because seabirds are highly visible animals traveling and foraging in productive marine hotspots, while other marine animals are mostly hidden underwater and more difficult to study (Furness and Camphuysen 1997). Most seabirds species are colonial and assemble annually in large numbers at relatively few locations in order to reproduce, a fact that allows populations census and to monitor trends of multiple coexisting species at various trophic levels simultaneously (Piatt and Sydeman 2007). Moreover, seabirds may be sampling agents for otherwise unstudied marine fauna at sites that are not easily or not usually surveyed by conventional means (i.e. vessel surveys). Besides, compared with vessel surveys, data on seabird food and feeding ecology have the advantage of being easily collected and inexpensive and allow a broader spatial and temporal coverage (Cherel and Weimerskirch 1995). In addition, seabirds as predators located in

Margarida Soares (2013) Foraging ecology strategies of Cory's Shearwater in Porto Santo Island.

the highest level of marine food webs shows potential as monitors of pollutants that accumulate at lower trophic levels (Furness and Camphuysen 1997).

1.2. Studying seabirds with GPS tracking and stable isotope analysis

Since 1990 there was an upgrade of the technology used to study seabird ecology at sea, with the use of satellite telemetry (platform terminal transmitters [PTTs]) (Weimerskirch and Jouventin 1990). Currently two types of devices are heavily used to study seabirds: Global location sensing or geolocation (GLS) and global positioning system (GPS). Geolocation uses changes in ambient light levels to estimate sunrise, sunset, day length, and, hence, longitude and latitude. GPS devices give us the possibility of recording locations every second at accuracies within meters of true location and, nowadays these devices are rather inexpensive and small enough to be used in several seabird species. Currently, attachment of miniaturized sensors linked to data loggers is increasing since these loggers do not call for long-distance signal reception. However, as with GPS or GLS recorders, the limitation is that birds have to be recaptured or pass close to a remote data-recovery system to download the information. The only time where birds faithfully return to the colony is during the breeding season, so most of the information available is restricted to this period of their life cycle.

According to BirdLife, international (www.birdlife.org/) data from satellite tracking and data loggers are already contributing significantly to conservation planning and monitoring, especially for the wide-ranging procellariiforms, penguins and sulids. This is also important for a better understanding of the changes in the ocean and to identify areas where birds might be threatened (e.g. oil and chemical pollution, hunting, fishery bycatch). Nowadays, projects using multiple sensors and combining different data sources are important for a more complete representation of what is happening at sea. For example, combining information on the location of foraging seabirds with ocean parameters such as sea surface temperature and chlorophyll *a* concentration, will

increases the comprehension of habitat requirements and prediction of foraging aggregations (Hyrenbach et al. 2002, Weimerskirch et al. 2005a).

Tracking devices may affect not only the flight performance but also the parameters being measured by them. Effects seem to be highly variable with the size, shape and placement location on the body, and with the foraging method of the seabird species. The deployment duration of tags in the bird's body must be taken under consideration as the effect of carrying a small device for a long time may not differ from that of carrying a heavier payload for a shorter time. Some of the negative effects registered include reduced diving abilities, increased foraging or commuting effort, stress, reduced growth and survival of chicks, reduced colony attendance and lowered probabilities of future reproduction (Burger and Shaffer 2008). To prevent a negative effect on the seabirds' behavior, the external devices should not exceed 3-5% of the bird's body mass (Phillips et al. 2003).

The spatial ecology of seabirds at sea will have a direct influence on the prey that these animals exploit and consequently on their diet composition. Presently, the use of stable isotopic analysis (SIA) to interpret the isotopic signatures of seabird's biological samples has increased in many studies. The main utility of stable isotope signatures is the fact that when they are incorporated in the proteins of consumers, they reflect those of the proteins in their diet in a predictable manner (Post 2002, Bearhop et al. 2004). Stable isotope signatures can be a prevailing alternative to the conventional ways of analyzing diets by collecting stomach contents or feces (Cherel et al. 2007), and may facilitate the monitoring of changes in marine ecosystems. Carbon ($^{13}\text{C}/^{12}\text{C}$, $\delta^{13}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$, $\delta^{15}\text{N}$) stable isotope ratios are the most common isotopes used in seabird stable isotope ecology (Ramos and González-Solís 2012). The utilization of $\delta^{15}\text{N}$ is based on the trophic richness of ^{15}N as long as it ascends on the trophic web

(Forero and Hobson 2003). In each trophic level the ^{15}N values increases 3-5% due to the production of urea, the ^{14}N is preferentially excreted than ^{15}N (Bond and Jones 2009). On the other hand, the use of $\delta^{13}\text{C}$ is based on the ^{13}C gradient, because there is an increase of ^{13}C in inshore areas when compared with offshore areas, allowing $\delta^{13}\text{C}$ to behave like a geographical indicator of foraging habitats (Forero and Hobson 2003, Quillfeldt et al. 2005).

When assimilated through diet, isotopic forms are fractionated and incorporated into tissues as these are formed. This incorporation can be at a temporal or spatial scale. Each tissue has its own turn over so they integrate the isotopic information over various temporal scales and, if animals forage at different areas, tissues can also incorporate isotopes in various spatial scales. Depending on tissue-specific isotopic turnover, the measurements can reflect the average dietary records over days to years and enables to resolve nutritional variation at different time-scales (Cherel et al. 2007). The stable isotope signature of tissues usually reflects the diet over the period of tissue synthesis and different turnover rates will reflect dietary information over different time-scales. By carefully selecting the tissue, we can infer an animal's diet or habitat over a range of different time and spatial scales (Inger and Bearhop 2008). For instance, feathers allow us to analyse a period of information correspondent to the time of feather growth but, in contrast, red blood cells represents a period of a few weeks and plasma 3 days or so (Hobson 2005). To deduce geographical positions with isotopic analyses, the most reliable materials are those that are metabolically inactive so they retain signatures during a fixed growth period (Hobson 2005). Keratinous materials such as feathers are particularly useful because keratin is metabolically inactive and conserves dietary signals integrated over the period in which they grew (Forero and Hobson 2003). Moults

patterns of bird feathers are seasonally predictable and consistent over time (Ramos et al. 2009).

The advantage of using stable isotope analysis in ecological studies over stomach regurgitations is that it provides information about all the specimens ingested by the target species, and the collection of feather and/or blood samples is less stressful for the bird than the collection of diet samples by stomach flushing. Stable isotope signatures provide not only information about the food ingested but also about the food that was assimilated by the tissues. In this respect, conventional dietary analyses are more prone to misinterpretations of the proportions of some food sources, due to the diverse rates of digestion of different prey-types (Paiva et al. 2010a).

1.3. Energy cost of pelagic seabird foraging trips

Seabird pelagic foraging is limited by the environmental conditions, since productive areas of the oceans are variably distributed. Therefore, seabirds, as central place foragers, developed adaptations that allows them to balance between suitable breeding areas (mostly often desert islands which may be distant from productivity hotspots), long foraging trips, sharing incubation tasks or providing enough food to their chick and maintaining their own body condition (Navarro and González-Solís 2009). To defeat these constraints, many animals show a certain degree of behaviour plasticity in response to varying environments (Paiva et al. 2010b).

To provide food for their chicks and build reservations for themselves, seabirds routinely travel long distances from the nest, making trips of several hours to days , and travelling tens to thousands of kilometers from the breeding site on a single trip (Hedd and Gales 2005). Foraging success depends on foraging effort (energy expended or distance covered per unit of time) and thus should differ according to factors inherent to

the predator, such as foraging energy requirement, different involvement in breeding as well as bird age and experience (Weimerskirch et al. 2005b).

Many seabird species such as Cory's Shearwater *Calonectris diomedea borealis* use a dual strategy when breeding in areas that are poor in food resources. The birds combine short trips (1 to 3 days duration) in near-colony waters for chick provisioning, with longer trips (>5 days duration) to distant but highly productive area for self-provisioning. This is known to be an important strategy employed by Procellariiform species to solve the problem of distance and unpredictable food resources (Warham 1996). Studies conducted in the northern hemisphere demonstrate this strategy by seabirds: Laysan albatrosses *Phoebastria immutabilis* and black-footed albatrosses *P. nigripes* nesting in the Hawaiian islands employ bimodal foraging-trip strategies, with long trips visiting productive regions associated with frontal zones in colder waters at higher latitudes (Fernández et al. 2001, Hyrenbach et al. 2002). In addition, satellite tracking studies with wandering albatrosses suggests that long trips are more predictable and profitable, through the flight and foraging efficiencies afforded by the use of flattering wind conditions, while short trips take little advantage of wind and involve several expensive take-offs and landings (Davies et al. 2010). Spatial and temporal predictability of the trophic resources can modulate foraging-site fidelity. To optimize foraging performance, seabirds learn where and when resources are distributed within their potential foraging range and may return to the same feeding grounds during successive trips. In areas where resources are highly predictable, such as continental shelves or productive fronts, we expect site fidelity to increase (Navarro and González-Solís 2009). The bimodal foraging strategy is also used by birds during the incubation period, suggesting that the amount of investment into long trips may be a reflection of

the marine productivity around the breeding colonies and not only a way for birds to re-establish their body condition while feeding their chicks (Granadeiro et al. 1998a). Paiva et al. (2010a) reported in a study with Cory's shearwater *Calonectris diomedea borealis*, that the higher the concentration of Chl *a* around the breeding colony, the lower the percentage of long trips performed by birds. This suggests that local productivity (i.e. in the surroundings of the breeding colony) is a main factor influencing the investment of birds into an optimized dual foraging strategy.

Adding up to this dual foraging strategy, central place foragers display two main types of movements: commuting or looping. As described by Weimerskirch et al. (2007), an individual is commuting when he departs in a direct flight from the colony until reaching an area of interest, feeds there and returns to the colony using a direct flying path. This suggests that the individuals have a good familiarity with their environment which has been learned during immaturity and successive breeding experiences (Weimerskirch et al. 2007). When looping, the individual is foraging in loops, using different paths when leaving and when returning to the colony. This may indicate that the bird is searching continuously, stopping when it encounters a good foraging hotspot (Weimerskirch 2007).

1.4. How to minimize the costs to reach distant productive patches?

With the purpose of minimize flight costs, even in a bimodal foraging strategy, seabirds can take advantage of environmental factors like the wind, one of the main environmental dynamic movements. This is particularly relevant in the marine environment, where winds are stronger and more constant comparing to land winds. The strength of wind is expected to raise with increasing distance from the coast as a

result of the reduction in friction with the roughness of the coast, resulting in a higher wind effect for seabirds flying further off the coast (Mateos and Arroyo 2010).

Evidence from energetic and physiological studies points to the importance of wind speed in the foraging and life history of procellariiform seabirds. High wind energy is essential for dynamical gust soaring by albatrosses with greater body size predicted to require greater wind speeds in order to achieve optimal gliding performance (Davies et al. 2010). However, some birds may specialize in either powered flapping flight or soaring flight, whereas other birds (e.g. many gulls) use an extensive variety of flight strategies (Shamoun-Baranes and Van Loon 2006). Seabirds show diverse morphologies and flight techniques, such as gliding, continuous flapping or mixed techniques between gliding and pure flapping (Cramp and Simmons 1977). The wind can blow in the same direction of the bird travel – tailwind – or blows against the direction of the bird travel – headwind. A tailwind increases the speed and reduces the time spent travelling, whereas the headwind has the opposite effect, so flying with tailwind is energetically useful for birds, extending the flight range on a given amount of fuel by gaining ground speed or maybe saving energy by reducing air speed (Mateos and Arroyo 2010). Mateos (2009) showed that seabird flying into headwinds amplify air speed to compensate in part for the raise in wind speed. Approaching the coast, where wind intensity is lower, could be an additional strategy to reduce negative effects of flying into headwinds: under tailwind conditions seabirds flew to the sea, leveraging from increasing wind support further off-shore (Mateos 2009).

Another explanation, is given by Pennycuik (2002), which states that birds gain energy from the moving air, taking advantage of discontinuities in the wind flow and extracting from them pulses of kinetic energy. However, estimating energy consumption in flight is complex due to the variations of species soar (e.g. the large

species were seen flap-gliding only in very light winds, and on some occasions were observed soaring even in zero wind (Pennycuik 1982).

Sachs (2005) decomposed the soaring cycle in four phases. First, birds start from the valleys of the ocean waves and climb into the air, wheeling to wind, become exposed to a headwind (that slows them down relative to the water), with increasing air speed moving over their wings. Then, on an upward curve that takes them through cross winds, the birds change the flight direction to leeward (with even lower speed over the water). On the descendent phase, with predominantly tailwinds, they dive back (in a fast wind-powered motion) into a wave shelter. Finally, they enter a lower curve and change flight direction (flight powered by the previous phase) again to windward. By repeating these four phases, birds can save energy without having to put in much effort.

Foraging behaviour is an interesting case for studying flight strategy selection as the selection of a particular foraging behavior may strongly influence energy expenditure (Shamoun-Baranes and Van Loon 2006). By combining flight mechanics with ecological contexts such as winds, foraging, food transportation, it is possible to set an optimal speed which birds should adopt if they are optimizing a certain currency, that is, the net rate of energy intake or the foraging efficiency (Rosén and Hedenström 2001). Shamoun-Baranes and Van Loon (2006) provide evidence to support the hypothesis that flight and foraging energetic influence the selection of flight strategy when travelling between foraging sites. Moreover, one main factor that may influence flight strategy is the weather conditions. Meteorological conditions may not only influence the ability of a bird to flap or soar but also the energy expenditure or time needed for flight (Shamoun-Baranes and Van Loon 2006).

The Cory's Shearwater has long and slender wings adapted to combine gliding and active flight and that could be one really good help when using oceanic winds to

reduce flying costs (Rosén and Hedenström 2001). Navarro and González-Solís (2009) reported that Cory's shearwaters breeding in the Canary Islands and foraging over the continental shelf of Western Africa do so in total agreement with wind direction, which maybe indicate that the entire foraging path was improved to avoid headwinds and to use tailwinds with the purpose of reduce flying costs. However, birds travelling from the breeding colony to the continental shelf, and vice-versa, cannot choose their angle due to the northeast trade winds. Since the breeding colony and the continental shelf are rigid, birds have to handle with cross, tail and headwinds during departure or return trips. So, they conclude that differences in the wind angle with respect to the movement of the bird can affect the heading and shape of the departing and returning trips (Navarro and González-Solís 2009).

Paiva et al. (2010c) found that when prevalent winds were blowing from the north-east Atlantic, Cory's shearwater adults make use of those wind fields by adjusting their flight directions mainly towards north-west and south-west, flying with cross and tailwinds, respectively, and avoiding headwinds. This confirms that Cory's Shearwater use a shear soaring flying strategy while exploiting the environmental for food: adults foraged mainly with cross winds and their ground speed was not constant during all foraging trips, as it changed dynamically as a result of the ocean surface shear winds.

1.5. Objectives

We conducted this study in a small islet (Ilhéu de Cima) near Porto Santo's, Madeira archipelago, Portugal. The interest in this area is based on its low marine productivity in the surroundings and its distance from high productive areas (e.g. African coast). Until now there are no information about the foraging pattern and foraging areas of seabirds breeding in Porto Santo.

We use two years tracking information from the same period (i.e. August 2011 and 2012) of Porto Santo's Cory's Shearwaters to (i) understand how these seabirds forage at sea, (ii) which are the environmental predictors that determine the selection of foraging areas, and (iii) predict how projected warming of the North Atlantic Ocean would affect their foraging range over a decade, half century and in a century. We expected that birds should forage in distant highly productive grounds and anticipate that wind may be a very important factor used by the birds to reach those areas. With some data collected in 2012 we also assessed their chick estimated age.

Chapter 2 - Methods



2.1. Study area

Our study area encompasses most of the North-East Atlantic basin (Figure 2). Ocean circulation at this area is under the influence of a major gyre (Figure 2), as a circular current that is limited by tree coasts – in one side by the American coast and on the other side by the Portuguese and African coasts. The main surface currents that promote this gyre are created by the wind, which pulls warm (nutrient-poor) waters from the subtropical areas to the Gulf Stream. The warm waters, contours the American coast and converge at the top with the Arctic Labrador Current. This current brings cold (nutrient-rich) waters to the gyre. When the Arctic current encounters the warm waters, the Gulf Stream divides into 3 branches: one that take course up to the Norwegian coast and other that crosses Azores and finally one that create the Portugal/Canary current (Mann and Lazier 2006).

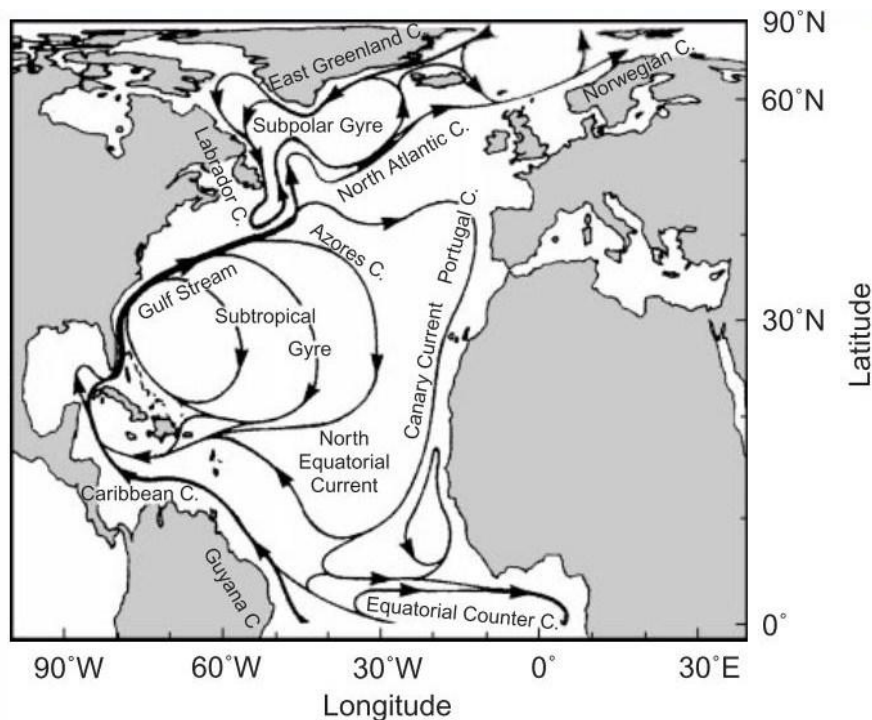


Figure 2 - Sketch of the general near-surface circulation of the North Atlantic Ocean (from: Barton 2001).

Branches of the Azores Current smoothly enter into the Portugal and Canary current. This last current separates from the African coast around 20°N to become the North Equatorial Current, that sooner or later feeds into the Caribbean Current and go back to the Gulf Stream. Where the eastward-Sowing Azores Current turns south as it nears the eastern boundary, two branches of the Canary Current are formed separated by Madeira (Barton 2001).

However, this pattern is more typical during the winter, as during summer, the location of some of the main North Ocean currents changes. This will affect the sea surface temperature (Figure 3) and the productivity (Figure 4) frontal regions pushing the north productive and cold waters from the poor warm waters in the south region. In the Portugal and Africa shelf's, during winter, the trade winds are at their peak strength so, the Portugal/Canary current presents strong coastal upwelling of nutrient rich waters. From winter to summer, the thermocline in the Portuguese coast has an elevated spatially variation due to the season variation in trade winds. Consequently, in this area, the upwelling is less strong (Paiva 2009).

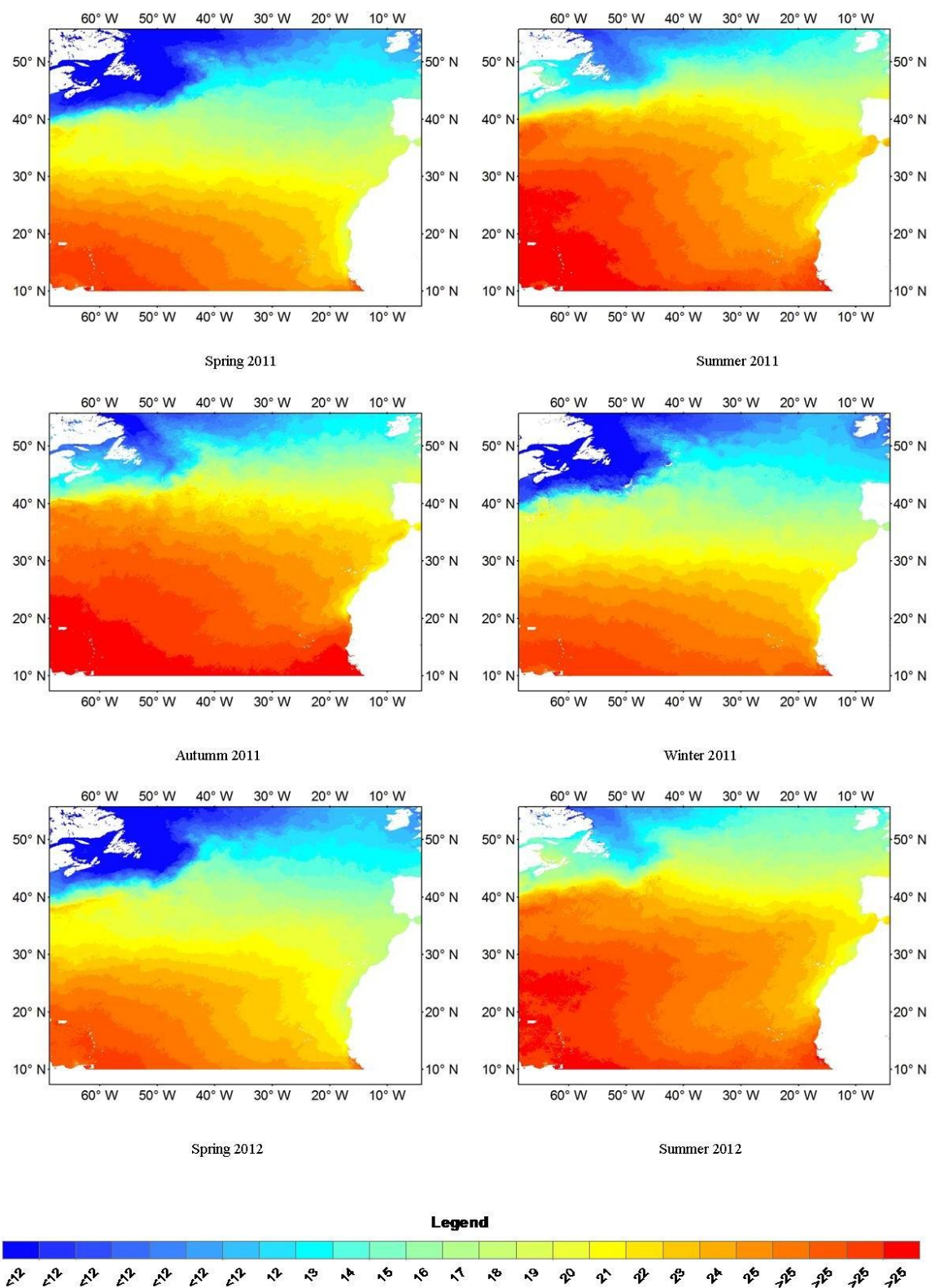


Figure 3 – Monthly average composites for Sea-Surface Temperature (°C) in the North-East Atlantic. (from: <http://coastwatch.pfeg.noaa.gov/>)

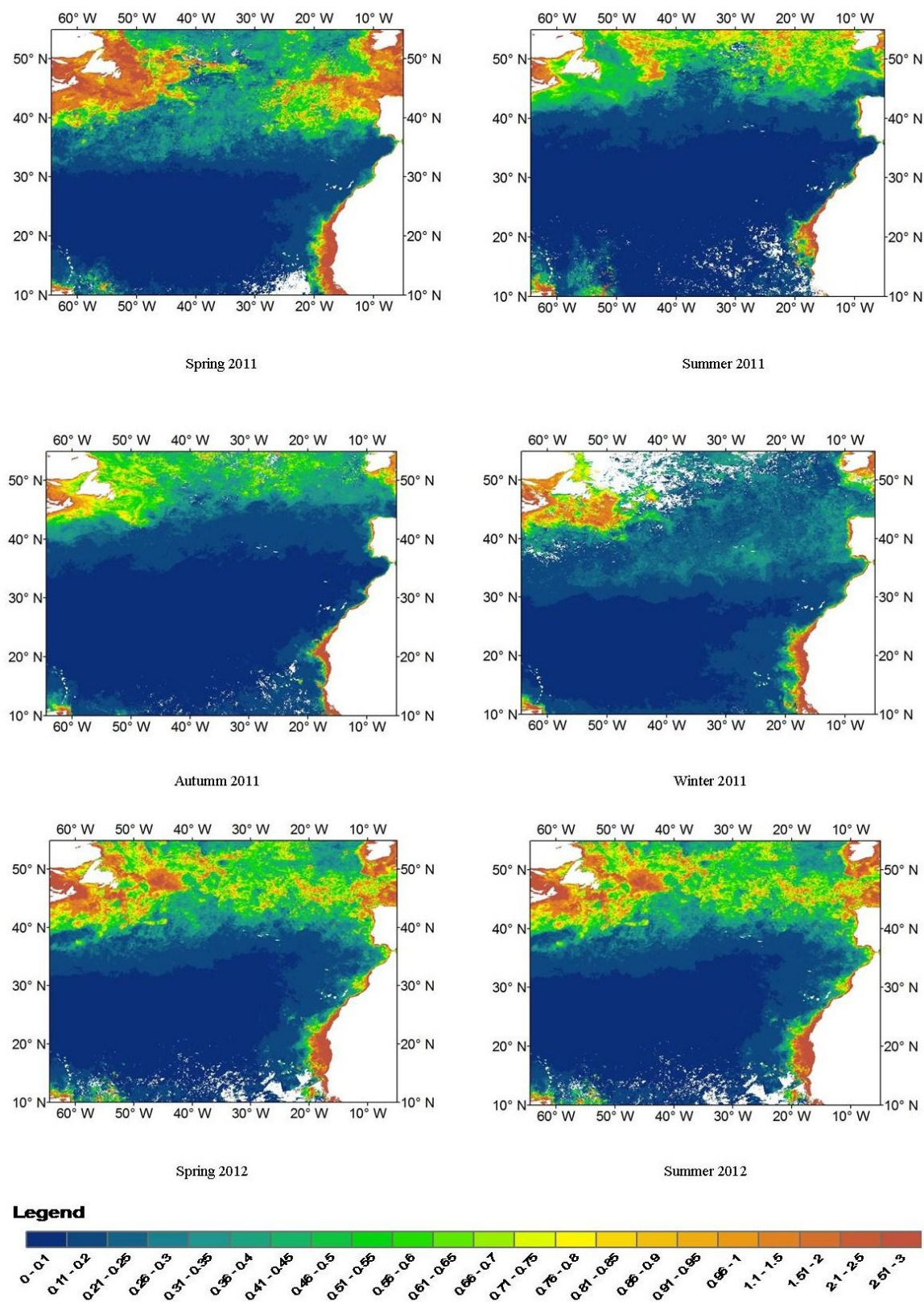


Figure 4 – Monthly average composites for Chlorophyll a concentration (mg/m³) in the North-East Atlantic (from: <http://coastwatch.pfeg.noaa.gov/>)

Also, taking in account Figure 4, it is known that the chlorophyll generated in the African upwelling system may be spread into the eastern Canary region or transported by filaments some hundreds of kilometers offshore (Barton et al. 1998). Although the center of the North Atlantic gyre presents low productivity, there are some hotspots in the ocean that concentrates some productivity (Figure 5). These hotspots can be seamounts, banks, canyons or the Middle Atlantic Ridge (MAR).

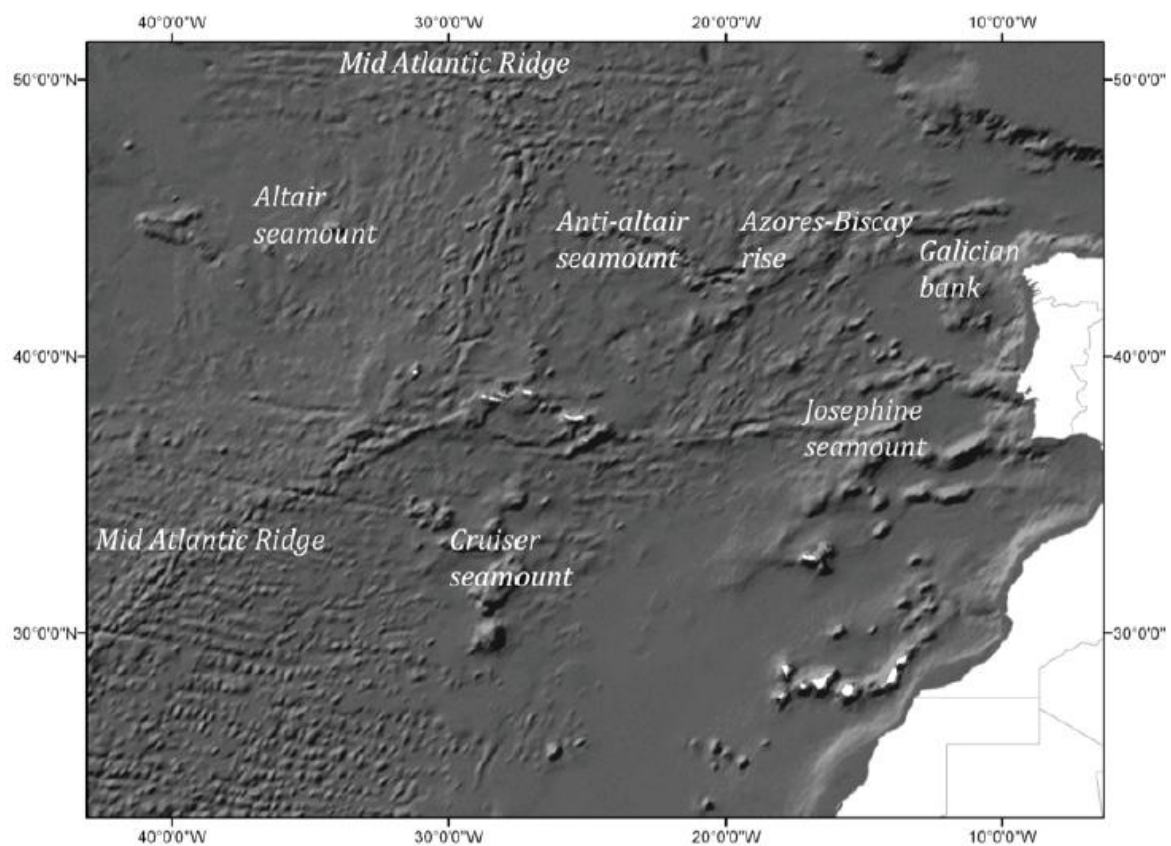


Figure 5 – Location of some of the bigger seamounts, banks and the Mid-Atlantic Ridge the North Atlantic region (from: Paiva 2009).

Seamounts are defined as any topographically distinct seafloor feature that is at least 200 meters higher than the surrounding seafloor, but which does not break the sea surface (Morato et al. 2008). They promote local and regional upwelling phenomena that

will increase the productivity and biodiversity into different levels of the food chain (Mann and Lazier 2006).

In the Northern hemisphere there also exists a prominent and recurrent pattern of atmospheric variability, the North Atlantic Oscillation (NAO), one of the oldest known world weather patterns. It refers to changes in the atmospheric sea level pressure difference between the Arctic and the sub-tropical Atlantic that are most noticeable since November until April, and are associated with changes in the mean wind speed direction (Visbeck 2003).

2.2. Study species and breeding colony

Calonectris diomedea borealis (Cory, 1881), represented in Figure 6, is a procellariiform seabird not endangered according to IUCN conservation status. It is one of the most representative North Atlantic seabird species with a large population size estimated in 600 thousands to 1.2 million individuals according to Birdlife International (<http://www.birdlife.org/>). They spread in the North Atlantic between the Berlengas Archipelago, Azores Archipelago, Madeira Archipelago and Canary Archipelago. This distribution is based in seasonal variation patterns such prey availability and the existence of islands as breeding areas. Formerly, Cory's shearwater were abundant in all these islands of the North Atlantic Ocean but with the colonization by humans, and the consequent introduction of terrestrial predators such as rats and cats, the birds became restricted to sea-cliffs and islets with low accessibility and without rats (e.g. Ilhéus de Porto Santo).

Cory's Shearwater arrives at the North Atlantic during March and starts preparing the breeding season. They select a nest and defend it from other Cory's Shearwater individuals. In order to build their body reservation for egg formation,

females embark on an approximate 20 days pre-laying exodus (Jouanin et al. 2001). During the next two months, both male and female will incubate and protect the egg and after the chick is born (in the end of July), both parents feed the chick for about 2 months, although the regularity of chick provisioning decreases as chicks age (Ramos et al. 2003). So, during chick-rearing, Cory's Shearwaters must find food in the ocean around the breeding colony and, since that, become central place foragers. The central-place foraging theory predicts that prey items close to the colony will be preferred over prey items distant from the colony in this case due to the need of feeding their chicks (Elliott et al. 2009). Also, they have to find food for themselves and, a combination of short trips (1 to 3 days duration) in near-colony waters to feed their chicks with long trips (>5 days duration) to distant waters with higher productivity to feed themselves, will prevail during chick rearing. When autumn comes, they start preparing a trans-equatorial migration to the South Atlantic where they spend the winter.



Figure 6 – A. adult Cory's Shearwater. B. Beak detail. C. Cory's Shearwater Chick

Madeira archipelago consists in two islands: Madeira and Porto Santo. Surrounding Porto Santo's Island there are five small uninhabited islets – Ilhéu de Fora, Ilhéu das Cenouras, Ilhéu de Cima, Ilhéu de Baixo, Ilhéu de Ferro. They are all covered with Macaronesian flora and fauna. The present study was performed at Ilhéu de Cima (33°03'19''N 16°16'54''O) (Figure 7), a rocky islet with 111 meters of altitude. The islet possesses some endemic fauna and flora and represents the breeding site for

different seabird species, such as *Calonectris diomedea borealis*, *Oceanodroma castro*, *Puffinus baroli* and *Bulweria bulwerii*.



Figure 7 – Ilhéu de Cima, Porto Santo, Madeira (33°03'19''N 16°16'54''O).

2.3. Fieldwork

The study was performed during August of 2011 and 2012 (early chick-rearing phase for the species) at Ilhéu de Cima, Porto Santo, Madeira. Potential nests to monitor were selected based on the presence of a newborn chick. In 2011, 18 potential nests with chicks were selected and GPS loggers were attached to adult birds, but only at 12 sites we were able to remove the logger, since the other individuals did not return or lost the device. In 2012, 11 potential nests with chicks were selected and weighed, and 10 of these 11 nests were selected for logger attachment: 17 loggers were attached to birds but only 13 were recovery but 4 of them were damaged, making impossible to download the data. The adults were all ringed and weighted in a bag using a Pesola® balance (± 20 g), at the time of the first capture, upon logger attachment, and again when retrieving the logger. Biometric measures as wing and tarsus length and blood samples were also collected (Figure 8). In 2012, the chicks from telemetered adults, were weighted every

day at the same hour (when parents were at sea) in order to measure the growth rate during the chick-rearing period.

In 2012, we collected blood and feather samples in order to perform Stable Isotope Analysis (SIA) and thus investigate the trophic ecology of Cory's Shearwater in Porto Santo. When retrieving the loggers, blood samples were collected from the adults' tarsal vein using a 1ml syringe (~0.7ml from each individual). Up to five growing breast feathers were collected from each chick of the adults being telemetered. All these biological samples were collected under licence of the Natural Park of Madeira.



Figure 8 – Fieldwork procedures at the breeding colony. From left to right, measurement of wing and tarsus lengths and collection of blood samples.

2.3.1. Loggers: deployment & specifications

The mini-GPS loggers consist of a GPS receiver, data-logger, antenna, user interface circuits, and a CR2 (3V) battery (see (Steiner et al. 2000) for original design of devices) and are programmed to collect one location (estimated horizontal error of +/- 4 meters) every 5 minutes. In order to decrease the weight, the surrounding plastic case of the device were removed and replaced by a 7 cm long thermo-retractable rubber sleeve, which was then sealed with heat.

The devices were attached to the bird with TESA tape (Wilson et al. 1997) to the contour feathers along and in between both scapular feathers avoiding troubling neck movements (Figure 9). The total handling time of the bird did not exceed 10 minutes and then birds were returned to their nests.



Figure 9 – Process of logger deployment. Logger deployment (left) and deployed (right) on a Cory's Shearwater.

2.4. Tracking data analysis

2.4.1. Trip filtering

Each GPS device was on the bird for multiple days so the data obtained from each device were analyzed and divided into individual foraging trips by (1) calculating the distance to colony from each GPS position and (2) considering that the bird was at the colony when the distance was 0 m or close to that value (and thus the beginning of a new foraging trip when distance to colony starts to increase again). Points that may be associated with birds maneuvering to arrive to the colony, resting at sea, in the colony surroundings and being at the colony, were removed by applying a distance-to-colony filter of 2 km. Trip duration was also calculated, since the GPS logger give us information not only about distance but also about time, and were divided in short (= 1 day) and long (≥ 2 days) by analyzing the frequency histogram of trip duration. The relocations, between consecutive tracking points, were filtered on running flight speed.

A filtered flight dataset was performance to remove periods where birds were on the water surface, resting and drifting so, a lower threshold of 9km/h (i.e. based on the frequency distribution of speed records; (Guilford et al. 2008)) was set for the flight

data set that were used for estimation of home ranges (HR). In addition, we also create a data set to estimate foraging areas (FA). This last one was done by calculation path sinuosity for all the relocations, defined as the ratio of the actual flight speed given by the GPS logger to the velocity between every third fix (Grémillet et al. 2004). We performed a histogram of the sinuosity distribution to determine the break-off value for this parameter, which was identified at 2.7.

2.4.2. Kernel estimations

We used utilization distribution (UD) kernels to characterize the areas where birds spent more time searching for food. The utilization distribution term refers to the relatively frequency distribution for the points of location of an animal over a period of time (Van Winkle 1975). Home ranges (UD95) and foraging areas (UD50) were calculated from the flight-filtered and foraging-filtered datasets, respectively, using UD kernel methods (Worton 1989) estimated using R packages *adehabitat* and *adehabitarHR* (Calenge 2006). For comparison between the years and between long and short trips, the ad-hoc method was used with the aim to find a reasonable smoothing factor (h) that will set the detail of each kernel (Kappes et al. 2011). The ad-hoc method requires kernel calculation of a representative subsample setting the h value as “reference” and the optimal value will then give. Since the sample in this study is small and Haug (2012) used a smoothing factor of 3100 m with Cory's Shearwaters at data from North Atlantic, this value presents more strength and so was used here. We subset, from the total data, trips with: velocity ≤ 9 km/h (to exclude resting or social behaviors), a distance to colony ≤ 2 km and a sinuosity ≤ 2.7 (chosen by analyzing the flight distribution frequency histogram). With the purpose of find out if there was any spatial segregation, the overlap between kernels of 2011 and 2012 and between kernels of long

and short trips were calculated. Overlaps were also calculated between each year and each trip to evaluate the individual consistency. All this overlaps were performed in R with the *kerneloverlap* function of the *adehabitat* package.

2.5. Oceanography predictors and habitat use analysis

To understand the seabird species occurrence, we used 20 environmental variables that has been previously described as correlated with seabird distribution and abundance (Table I) (Louzao et al. 2009, Tremblay et al. 2009). All the variables were downloaded as monthly composites from <http://coastwatch.pfeg.noaa.gov/> for North Atlantic area, as ASCII files, except the oceanic wind intensity (m/s^{-1}) that was extracted from the SeaWinds database (QuikSCAT; <http://winds.jpl.nasa.gov/>; 0.125° spatial resolution, approximately 11 km). Files were the converted to raster using Spatial Analyst tool in ArcGis 10.0.

With the aim of assessing the entire possibilities we included the SST and Chl *a* anomalies (calculated from a average for each season over a 20-year period), spatial SST and Chl *a* gradients (calculated as $[(\text{maximum value} - \text{minimum value}) \times 100 / \text{maximum value}]$ with the maximum being the highest and minimum the lowest seasonal mean SST or Chl *a* value over a 3x3 grid cell window) but as well was included bathymetry gradient (reflects the presence of seamounts). Chl *a* peak (CHPK) was calculated from the binominal layers of Chl *a* concentrations in the study period during the 10 last years and cells with a Chl *a* concentration $> 1 \text{ mg/m}^2$ were attributed a value of 1 and lower values a value of 0 (Louzao et al. 2012, Suryan et al. 2012) with the purpose of understanding how Chlorophyll-a was distributed in the areas where birds forage.

Environmental predictors described in former steps were used in an habitat modeling exercise, in order to understand which environmental predictors trigger the foraging behaviour of Cory's Shearwaters and thus build habitat suitability maps based on the best set of habitat models. We used the MaxEnt program, version 3.3.3k (further information in Phillips et al. 2006), a software that allows the modeling of ecological niches from presence-only species records (Elith et al. 2011) by analyzing the relationship between species records at sites and the environmental characteristics of those sites. Another use of MaxEnt is to find correlations of species occurrence, mapping current distributions and is one of the most used techniques to predict suitable habitat patches (comparing probability densities in covariate space) (Elith et al. 2011).

In the beginning, all GPS positions were binned into a spatial grid with cell size of 4x4 km (0.0417°) to match the spatial resolution of remotely sensed environmental data. Thus, every grid was coded with a value of 1 if the bird was actively foraging (i.e. flight positions with sinuosity ≥ 2.7) or 0 if he was just flying. MaxEnt models were run separately for each year (i.e. 2011, 2012), after performing a correlation matrix where between each pair of highly correlated variables (i.e. $\geq 75\%$), just one was selected to enter the model building process. MaxEnt models were run with the following settings: logistic output format (resulting in values between 0 and 1 for each grid cell, where higher values represents more similar climatic conditions), duplicates removed and 50 replicate runs of random (bootstrap) subsamples with 30% random test percentage. The results were summarized as the average of the 50 models.

Output results of MaxEnt include a Jackknife chart, a Receiver Operating characteristic Curve (ROC) or a probability map. The first one allows evaluating the contribution of each environmental layer to the final result. The ROC curve describes the model's accuracy measured by the Area Under the ROC Curve (AUC), which in

turn estimates the likelihood that a randomly selected presence point is located in a raster cell with a higher probability value for species occurrence than a randomly generated point (AUC > 0.90, good for $0.80 < \text{AUC} < 0.90$, acceptable for $0.70 < \text{AUC} < 0.80$, bad for $0.60 < \text{AUC} < 0.70$ and invalid for $0.50 < \text{AUC} < 0.60$) (Araújo et al. 2005).

2.5.1. Projecting scenarios

A model that was trained on some environmental layers can be “projected” through applying it to another set of environmental layers with modifications (i.e. predicted values of an environmental parameter after n years). Projections are an useful tool to employ when modeling species distributions under changing climatic conditions (Péron et al. 2012). Here, we projected our best 2011 and 2012 foraging models to a climate change prediction where the Sea Surface Temperature increases 0.18°C per decade, according to one of the most conservative scenarios (A2) of the Intergovernmental Panel on Climate Change (IPCC; <http://www.ipcc.ch>). We predicted the foraging distribution of Cory's shearwaters to periods of: a decade (+ 0.18°C); 50 years (+ 0.9°C) and 100 years (+ 1.18°C) using the MaxEnt program to build those predictions.

Table I – Biologically relevant explanatory variables used for habitat modelling (MaxEnt) and data manipulation and source. Dynamic variables were downloaded on a monthly basis. Since they differed in spatial resolutions, they were aggregated to match the standard grid of 0.04° cell size. Static variables were extracted once and aggregated.

Variable	Derived Metric	Units	Manipulation	Source
Sea Surface Temperature	Minimum	°C	Temporal minimum from monthly climatologies (2002-2012)	Aqua-MODIS
Sea Surface Temperature	Mean	°C	Temporal mean from monthly climatologies (2002-2012)	Aqua-MODIS
Sea Surface Temperature	Maximum	°C	Temporal maximum from monthly climatologies (2002-2012)	Aqua-MODIS
Sea Surface Temperature	Range	°C	Temporal range from monthly climatologies (2002-2012)	Aqua-MODIS
Sea Surface Temperature	Mean	°C	Temporal mean from monthly climatologies (June-August)	Aqua-MODIS
Sea Surface Temperature Anomaly	Mean	°C	Temporal deviation of sea surface temperature compared to a 20 year average of sea surface temperature	Aqua-MODIS
Sea Surface Temperature Gradient	Mean	%	Temporal gradient from monthly climatologies (2002-2012)	Aqua-MODIS
Sea Level Anomaly	Mean	m	Temporal deviation of sea surface height compared to a 20 year average of sea surface temperature	AVISO
Chlorophyll <i>a</i> concentration	Minimum	mg m ⁻³	Temporal maximum from monthly climatologies (2002-2012)	Aqua-MODIS
Chlorophyll <i>a</i> concentration	Mean	mg m ⁻³	Temporal maximum from monthly climatologies (2002-2012)	Aqua-MODIS
Chlorophyll <i>a</i> concentration	Maximum	mg m ⁻³	Temporal maximum from monthly climatologies (2002-2012)	Aqua-MODIS
Chlorophyll <i>a</i> concentration	Range	mg m ⁻³	Temporal maximum from monthly climatologies (2002-2012)	Aqua-MODIS
Chlorophyll <i>a</i> concentration	Mean	mg m ⁻³	Temporal mean from monthly climatologies (June-August)	Aqua-MODIS
Chlorophyll <i>a</i> concentration Anomaly	Mean	°C	Temporal deviation of Chlorophyll <i>a</i> concentration compared to a 20 year average of Chlorophyll <i>a</i> concentration	Aqua-MODIS
Chlorophyll <i>a</i> concentration Gradient #	Gradient	%	Temporal gradient from monthly climatologies (2002-2012)	Aqua-MODIS
Bathymetry	Mean	m	Spatial mean	ETOPO 1
Bathymetry spatial gradient	Gradient	%	Spatial gradient	ETOPO 1
Chlorophyll <i>a</i> concentration peak	Sum	-	Sum of higher productive cells (> 1 mg m ⁻³) over a period of 10 years (2002-2012)	Aqua-MODIS
Distance to land	Minimum	km	Distance to the nearest coastline	ArcGis
Distance to colony	Minimum	km	Minimum distance to the breeding colony	ArcGis
Wind speed	Mean	m s ⁻¹	Temporal mean from monthly climatologies (June-August)	QuikSCAT

2.6. Stable isotope analysis (SIA)

The trophic ecology of adults and chicks was investigated during the breeding season of 2012. Feather samples were washed in successive rinses with a 2:1 chloroform : methanol solution in order to clean all the impurities at the feathers surface and to prevent possible contamination of SIA results, then wrapped in aluminum foil and storage in an aspirating hood for 24h at 50°C. After dry, they were cut in small pieces and stored in eppendorfs. Whole blood samples were also dried in an aspirating hood for 24h at 50°C.

Whole blood and feathers samples were all weighed to 0.35-0.40 mg and encapsulated in tin cups, with all utensils being cleaned with ethanol after processing of each sample to avoid contamination. Isotope ratios of carbon and nitrogen were then determined through standard methodology (Bearhop et al. 2006, Phillips et al. 2009) by continuous-flow isotope ratio mass spectrometry, using an EA-IRMS (Isoprime, Micromass, UK) at the Institute of Marine Research (IMAR), Coimbra.

2.7. Data analysis

Chicks age was estimated based on established relationships between weight, tarsus length and wing length of Zino et al. (1987) and Zino (1971) for Selvagens and Granadeiro (2001) for Berlenga Island. Chick growth rate from chicks of parents equipped with loggers was compared with that from chicks of parents without loggers with a t-test.

All variables were visualized using quantile-quantile plots to see the normality and Cleveland dotplots to check homoscedasticity (Zuur et al. 2010) and, when necessary, some logarithmic transformations were adopted. All statistical analyses were performed using the software R. Computations were carried out using several functions

within different R packages (e.g. *MASS*, *maptools*, *adehabitat*) and some custom-built functions. Presented are means \pm standard deviation and results were considered significant at $P \geq 0.05$.

Inter-annual differences on the trips characteristics (e.g. maximum distance to colony, kernelUD areas, etc) of adult Cory's Shearwaters were tested with generalized linear mixed models (GLMMs), because several foraging trips were recorded for the same individuals, leading to a potential pseudo-replication problem.. GLMMs provide a flexible approach for analyzing non-normal data when random effects are present (i.e. pseudo-replication of the data; Bolker et al. 2009).

The SIA results were analyzed with a MANOVA, a statistical test used when the experimental design consist in more than one dependent variables, followed by a Two-way ANOVA with biological tissue (growing feather and whole blood) as a factor. To establish the isotopic niche among periods with the stable isotope data we applied a recent metrics – SIBER (Stable Isotope Bayesian Ellipses in R) - based in a Bayesian framework that confers a robust comparison to be made among data sets concerning different sample sizes (Jackson et al. 2011). The area of the standard ellipse (SEAc, an ellipse that has 95% probability of containing a subsequently sampled datum) was adopted to compare between adults and chicks isotopic signatures and their overlap in relation to the total niche width (both groups combined), and a Bayesian estimate of the standard ellipse and its area (SEAB) to test whether group 1 is smaller than group 2 (i.e. p , the proportion of ellipses in chicks that were lower than in adults; see Jackson et al. 2011 for more details). We used the computational code to calculate the metrics from SIBER implemented in the package SIAR (Parnell et al. 2010) under R 2.15.2.

All the metrics were calculated using *standard.ellipse* and *convexhull* function from SIBER, implemented in the *siar* package. *Siar* (stable isotope analysis in R) is a

package designed to solve mixing models for stable isotopic data within a Bayesian framework. This model allows the possibility of estimate probability distributions of various sources contributions to a mixture and, at the same time, accounting for the observed variability in source and mixture isotopic signatures, dietary isotopic fractionation, and elemental concentration (Polito et al. 2011) Here the SIAR model was used to quantify chicks and adults diet composition. To build the model, we used the isotopic signature of whole blood (adults) and growing feathers (chicks), a trophic enrichment of 0.30 and 2.85 ‰ for carbon and nitrogen (i.e. values from controlled experiments available in the literature;(Hobson and Clark 1992, Bearhop et al. 2002)) between the prey trophic level and the consumers isotopic signature and potential prey isotopic signatures taken from the literature (see Table II). A standard deviation of $\pm 1.0\text{‰}$ was taken into account, considering potential differences in fractionation factors among species.

Table II– Isotopic values for the main prey items composing the stomach content of the different populations of Cory's Shearwater feeding in the North Atlantic.

Species	^{15}N	^{13}C	Reference
<i>Trachurus picturatus</i>	11.75 ± 0.62	$- 19.58 \pm 0.22$	(Ceia et al. 2013)
<i>Histioteuthis</i> sp	7.23 ± 0.24	$- 18.44 \pm 0.16$	(Paiva et al. 2010a)
<i>Trachurus trachurus</i>	12.5 ± 0.15	$- 17.66 \pm 0.21$	(Paiva et al. 2010a)
<i>Belone belone</i>	10.93 ± 0.18	$- 17.48 \pm 0.06$	(Paiva et al. 2010a)
<i>Sardina</i> sp	10.68 ± 0.08	$- 19.12 \pm 0.622$	(Paiva et al. 2010a)
<i>Scomber</i> sp	9.57 ± 1.72	$- 19.32 \pm 0.16$	(Paiva et al. 2010a)
<i>Exocoetus volitans</i>	9.89 ± 0.57	$- 17.92 \pm 0.22$	(Paiva et al. 2010a)

Circular correlations between wind and flight direction were used in order to understand in more detail the influence of the wind fields on the flight and foraging patterns of Cory's Shearwaters when exploiting their main foraging ground during long trips, the Canary Current near the coast of Africa. All statistical analyses were

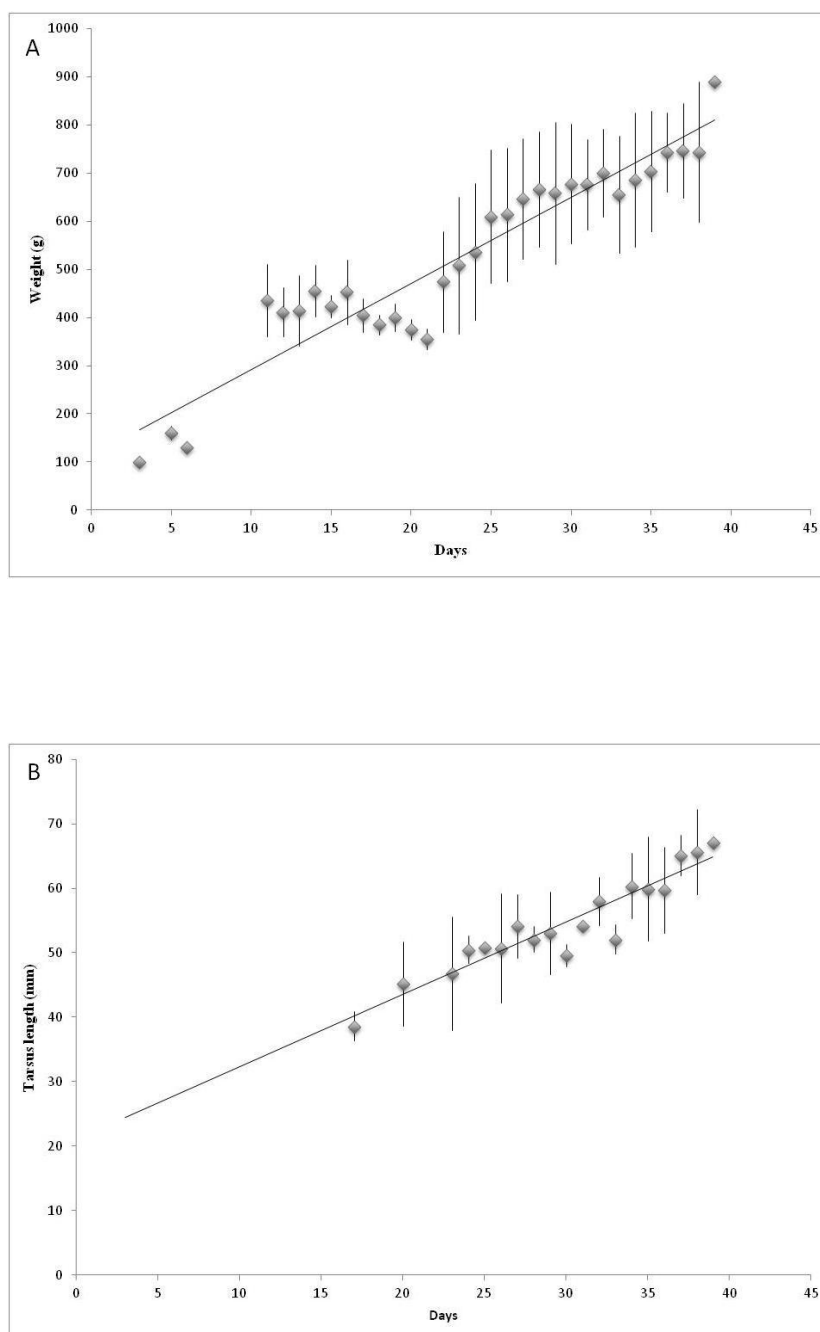
performed using the Package *circular* v 0.4-3 (Correlation Coefficient for Angular Variables, Watson two samples Test of Uniformity) in R.

Chapter 3 - Results



3.1. Chicks growth

With the purpose of estimating chick age, the average of weights, wing and tarsus length was calculated for each chick and a regression was used to obtain the approximate chick age (Figure 10).



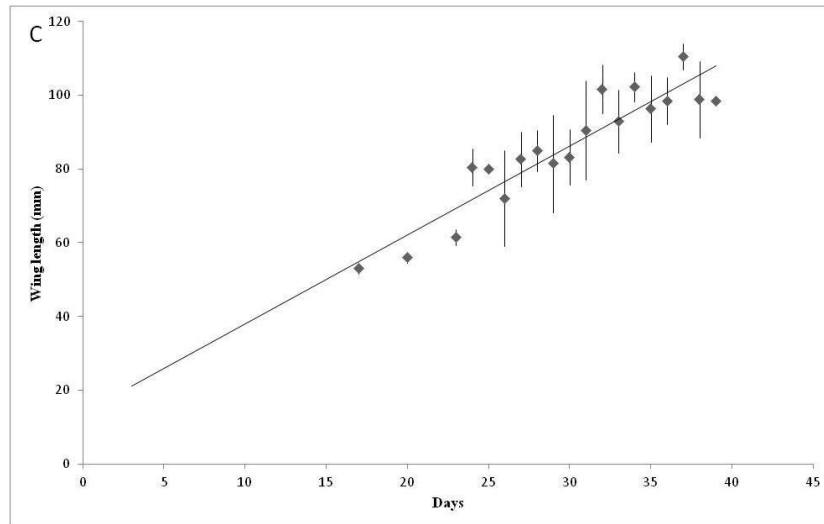


Figure 10 - Cory's Shearwater chicks estimated age by weight (A), tarsus length (B), wing length (C).

Although the sample size was very small, the fledglings from birds carrying devices (N=8) had a similar growth rate (growth rate estimated between 30 and 40 days) to that of birds without devices (N=3; birds with loggers = 4.2 ± 0.4 g versus birds without loggers = 3.9 ± 0.5 g; $t_9 = 0.81$, $p = 0.22$).

3.2. Foraging pattern and spatial segregation

In both years, birds established a dual foraging strategy, alternating between short trips around the colony and long trips spread by the Atlantic North Ocean. Spatial segregation was assessed considering overlap of the 95% kernel UD (home range) and the 50% kernel UD (core foraging area) kernels between years short and long trips (Figure 11 and 12).

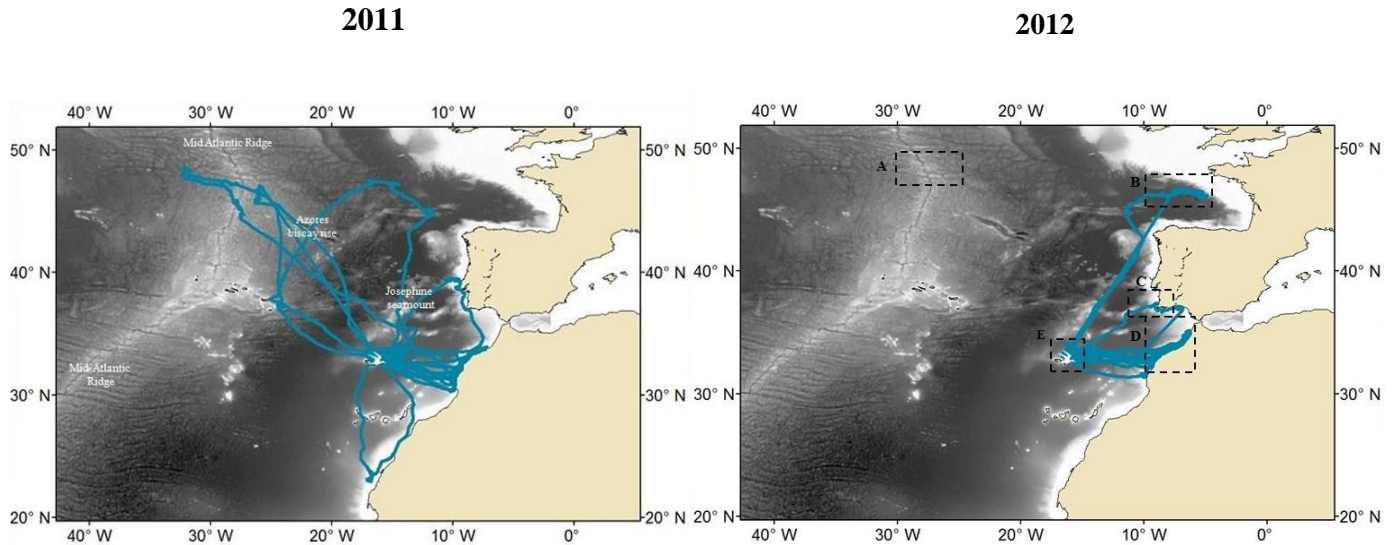


Figure 11 – Foraging patterns of long trips performed by Cory's Shearwater of Porto Santo's, Madeira during August of 2011 and 2012. and A – Mid Atlantic Ridge area, B – Gulf of Biscay area, C – Portugal Current, D – Canary Current (i.e. main foraging destinations of 2011 and 2012) and E – Porto Santo area (i.e. surroundings of the breeding colony).

In short trips of 2011 the spatial segregation of birds was highly variable comparing to 2012. Though, the home range was almost the same, the core foraging area was considerably higher in 2011 than in 2012 when the short trips show an increasing consistency. Kernels overlap sustains this idea since the values for short trips in 2011 were 28.7% comparing to the 45.8% of 2012. Moreover, individual consistency in 2011 was only 31.8% contrasting the 64.8% in 2012.

Considering long foraging trips, once again 2011 showed a widely spread pattern comparing to 2012. In 2011 the main foraging areas were the Azores, North of Azores, African coast (above the Canary archipelago), Portuguese cost (i.e. Berlengas archipelago) and some other hotspots spread by the Atlantic (e.g. Seine, Josephine, Ashton, Agadir seamounts). Yet, the core foraging areas (UD50) were the African coast, the Azores and the Altair seamount. On the other hand, in 2012, Cory's Shearwater core

foraging areas were only, once again, the African coast and the Gulf of Biscay. Overlaps supports this results given in 2011, as only 36.9% of the long trips were for the same spots and, in 2012, there was an overlap of 78.7%. Approximately the same proportions were found for the individual consistency (2011: 24.3%; 2012: 77.2%).

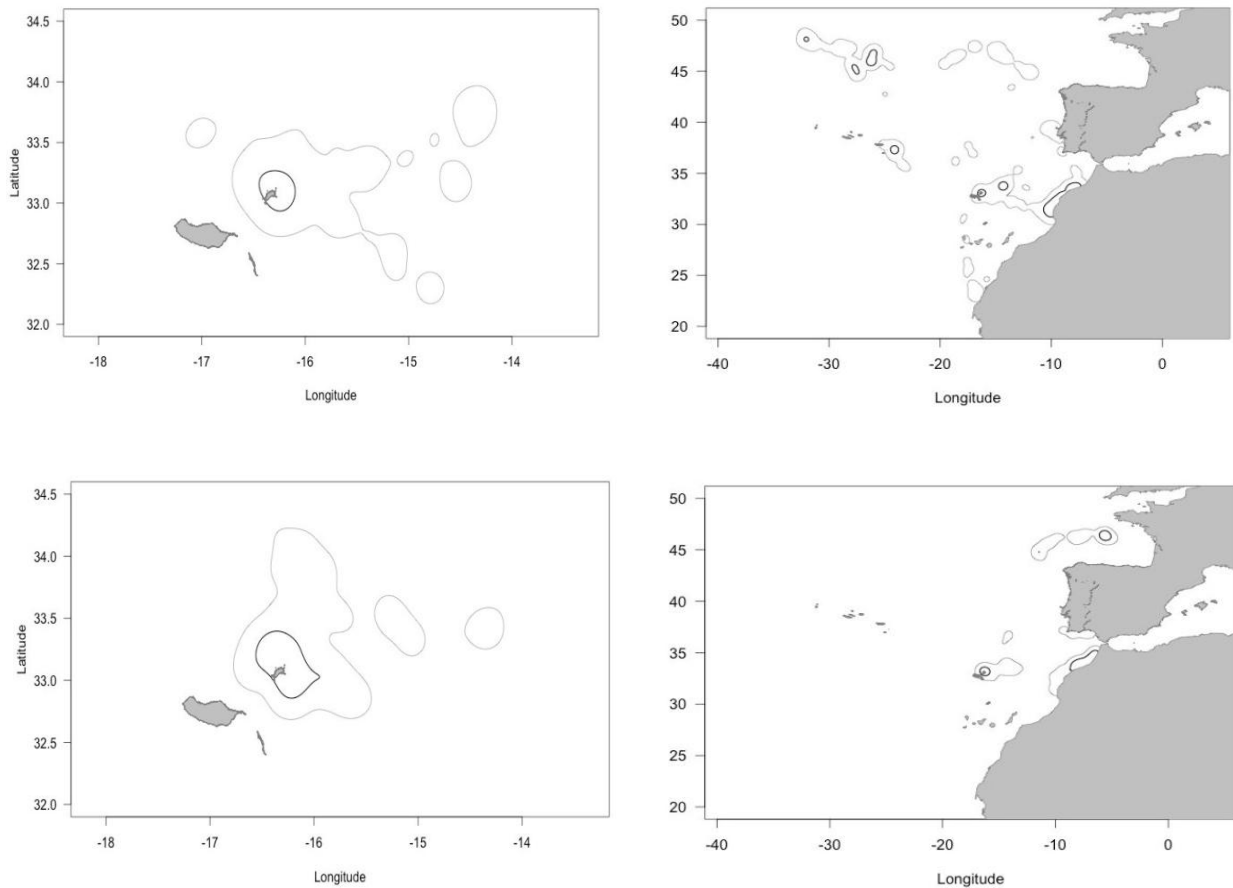


Figure 12. Kernel Utilization Distributions (UD; short and long trips from left to right) plots. Darker grey represents UD50 and low grey forms represents UD95.

Considering the main foraging grounds used by Cory's Shearwaters from Porto Santo, the inter-annual comparison of oceanographic characteristics shows significant differences between years (Table III). SST was significantly higher in the Gulf of Biscay, Portugal and Canary Currents during summer of 2011 than in 2012. Consequently, Chlorophyll *a* concentration was significantly lower at the same places

during 2011 than during 2012 (Table III). SST and productivity regimes (Chl *a* concentration) were similar between 2011 and 2012 within the Mid-Atlantic Ridge and Porto Santo areas. The surroundings of Porto Santo (i.e. breeding location) were (always) the foraging ground with warmer water regimes (SST) and less productivity (Chl *a* concentration), when compared to the other four main foraging grounds (Table III).

Analyzing trip parameters (Table IV) it is possible to notice that the short journeys were similar for both years. However, some statistical differences are found when comparing 2011 with 2012. Regarding short trips, they present differences in the percentage of commuting patterns between years, which means that in 2011 they used a looping pattern during short trips, which is also consistent with a higher sinuosity in this year (Table IV). Moreover, as previously mentioned, the home range and the core foraging areas illustrate as well these comparisons since there were statistical differences being 2011 the year when birds had to attain a higher foraging effort (Table IV, Figure 11). Long trips also reveal the same outcome with significant differences between years. This upholds the results obtained previously with the inter-annual variation that shows 2011 as a year of high foraging effort. However, Cory's Shearwater does not present a sinuosity index with disparity with 2012 along with the home range that also do not indicate differences. The core foraging areas were markedly larger in 2011 than 2012 (Table IV, Figure 11).

Table III. Inter-annual comparison of oceanographic characteristics at the main foraging regions of Cory's shearwaters. Oceanographic regimes are averages of mean values for June - August (Summer season) of each year. Chl *a* – Chlorophyll *a* concentration (mg m⁻³). SST – Sea surface Temperature (°C). NAO – North Atlantic Oscillation. General Linear Models (GLMs) were used to compare mean oceanographic values and NAO index between years. Presented are Mean ± SD.

Variable	2011	2012	GLM, F	df	P
<u>(A) Mid-Atlantic Ridge</u>					
Chl <i>a</i>	1.67 ± 0.23	1.07 ± 0.19	3.42	1,2134	0.08
SST	19.32 ± 2.09	18.98 ± 1.91	2.55	1,2134	0.10
<u>(B) Gulf of Biscay</u>					
Chl <i>a</i>	0.65 ± 0.15	1.21 ± 0.13	5.42	1,1924	0.02
SST	19.22 ± 3.22	17.23 ± 4.12	6.65	1,1924	0.01
<u>(C) Portugal Current</u>					
Chl <i>a</i>	1.50 ± 0.12	2.98 ± 0.33	10.95	1,724	0.001
SST	20.01 ± 0.21	18.21 ± 0.12	5.96	1,724	0.01
<u>(D) Canary Current</u>					
Chl <i>a</i>	1.53 ± 0.16	2.79 ± 0.13	6.72	1,1424	0.01
SST	20.14 ± 1.67	17.21 ± 2.12	10.87	1,1424	< 0.001
<u>(E) Porto Santo</u>					
Chl <i>a</i>	0.35 ± 0.12	0.37 ± 0.09	2.73	1,524	0.10
SST	24.11 ± 4.23	25.30 ± 3.50	2.41	1,524	0.12

Table IV- Foraging trip parameters for Cory's Shearwater from Porto's Santo, Ilhéu de Cima during August 2011 and 2012, equipped with GPS devices.

Trip type	Year	N° Birds	N° trips	Trip Duration (days)	Maximum distance (km)	Cumulative distance (km)	% Commuting trips	Sinuosity Index	25% KernelUD área	50% KernelUD área	75% KernelUD área	95% KernelUD área
SHORT	2011	11	25	1.0 ± 0.2	60.8 ± 58.4	217.7 ± 129.8	62.1 ± 5.1	1.9 ± 0.3	97.2 ± 23.7	276.6 ± 90.2	613.2 ± 189.1	1091.2 ± 265.3
SHORT	2012	6	19	1.1 ± 0.4	63.8 ± 63.0	243.2 ± 170.3	77.0 ± 3.7	1.7 ± 0.2	65.2 ± 23.8	156.3 ± 42.8	367.0 ± 134.1	801.4 ± 190.2
GLMM: F1,42	—	—	—	2.13	1.98	2.01	4.11	4.21	18.23	14.22	8.24	6.12
p	—	—	—	0.15	0.17	0.16	0.05	0.05	< 0.001	< 0.001	0.01	0.02
LONG	2011	11	12	9.3 ± 3.3	1048.1 ± 520.5	3489.5 ± 1673.0	72.6 ± 3.4	1.4 ± 0.1	3415.3 ± 511.2	9524.5 ± 623.7	23142.9 ± 882.3	68521.3 ± 1953.5
LONG	2012	6	6	10.5 ± 2.1	1071.7 ± 337.9	3365.2 ± 1072.8	81.2 ± 2.8	1.5 ± 0.1	2283.1 ± 556.1	7624.1 ± 842.6	21012.7 ± 892.6	64331.4 ± 2312.6
GLMM: F1,16	—	—	—	2.98	1.74	1.02	6.65	1.11	10.28	8.24	5.12	3.51
p	—	—	—	0.1	0.21	0.33	0.02	0.31	< 0.001	0.01	0.04	0.08

3.3. Stable isotopic analysis (SIA)

There was an overall difference in the trophic ecology of adults and chicks (Wilks $F_{2,18} = 21.24$, $P < 0.001$; Figure 13). Both the carbon and the nitrogen isotopic signature of chicks was significantly higher than that of their parents (C: $F_{1,19} = 24.42$, $P < 0.001$; N: $F_{1,19} = 14.59$, $P < 0.001$, respectively).

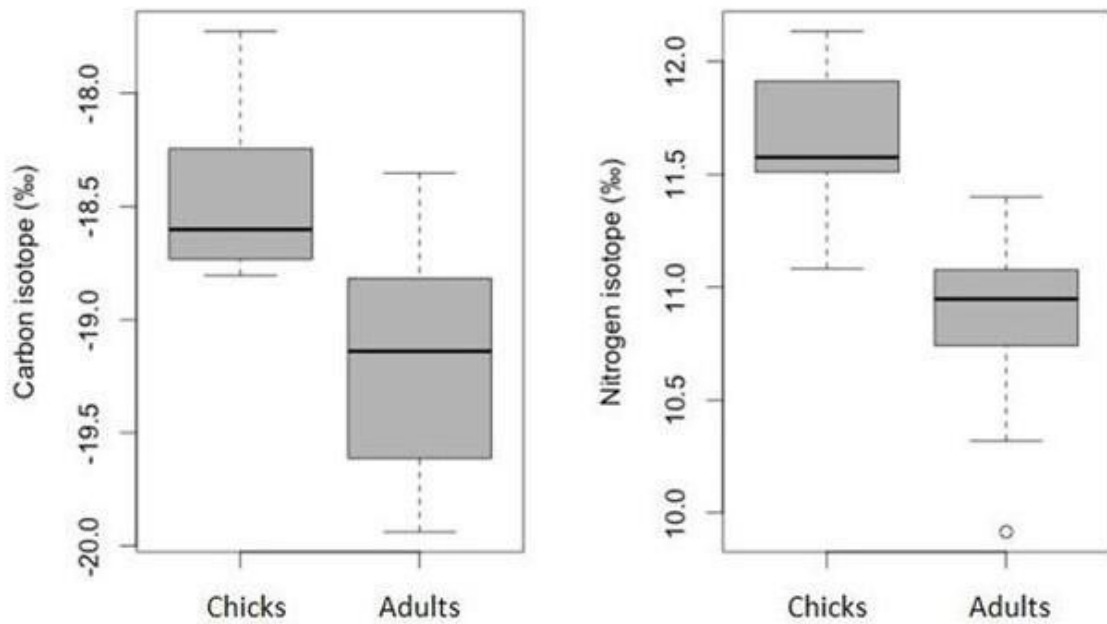


Figure 13 – Isotopic values for Carbon and Nitrogen isotopes of Cory's Shearwater adults and chicks during August 2012.

Results from the Stable Isotope Bayesian Ellipses (SIBER model) confirm that the isotopic niche of adults is more pelagic than the area exploit by birds to feed the chicks. The trophic level of parents is lower than the trophic level for the chicks, which agrees with the other results. The isotopic niche area of adults and chicks did not overlap and the Standard Ellipse Area (SEAc) shows a significantly higher niche area for the adults (SEAc: 0.76) than for the chicks (SEAc: 0.26; SEA_B , $P = 0.01$).

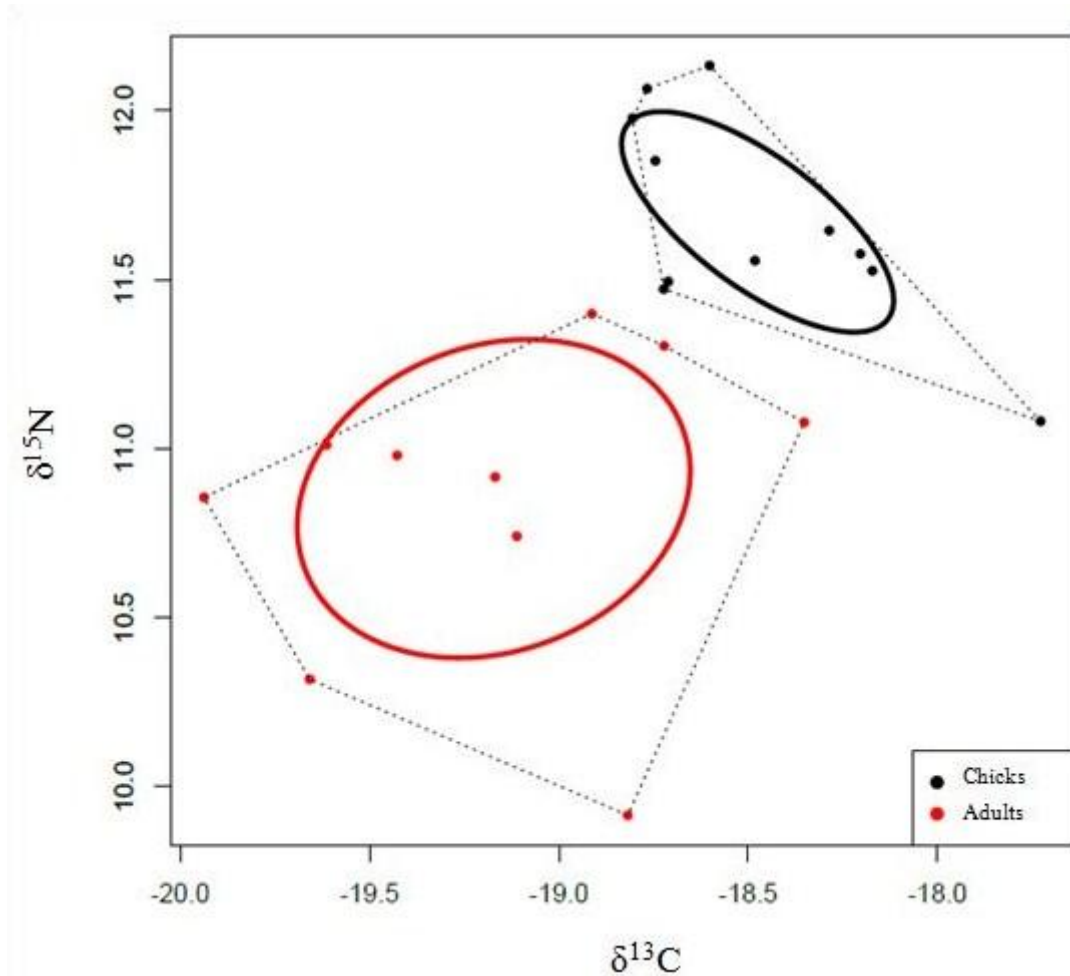


Figure 14 – Isotopic niche area on stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in red blood cells (adults) and growing feathers (chicks) of Cory's Shearwaters breeding in Ilhéu de Cima during August 2012.

Results from the SIAR model (Figure 15) estimate that the prey with the higher proportion in the birds' diet was represented by *Histioteuthis* sp (mean for chicks=0.53; mean for adults=0.69) in both of the groups but in chicks, *Sardina* sp was also an important prey (mean=0.11), and in adults *Scomber* sp seems to be a relevant food source (mean=0.09).

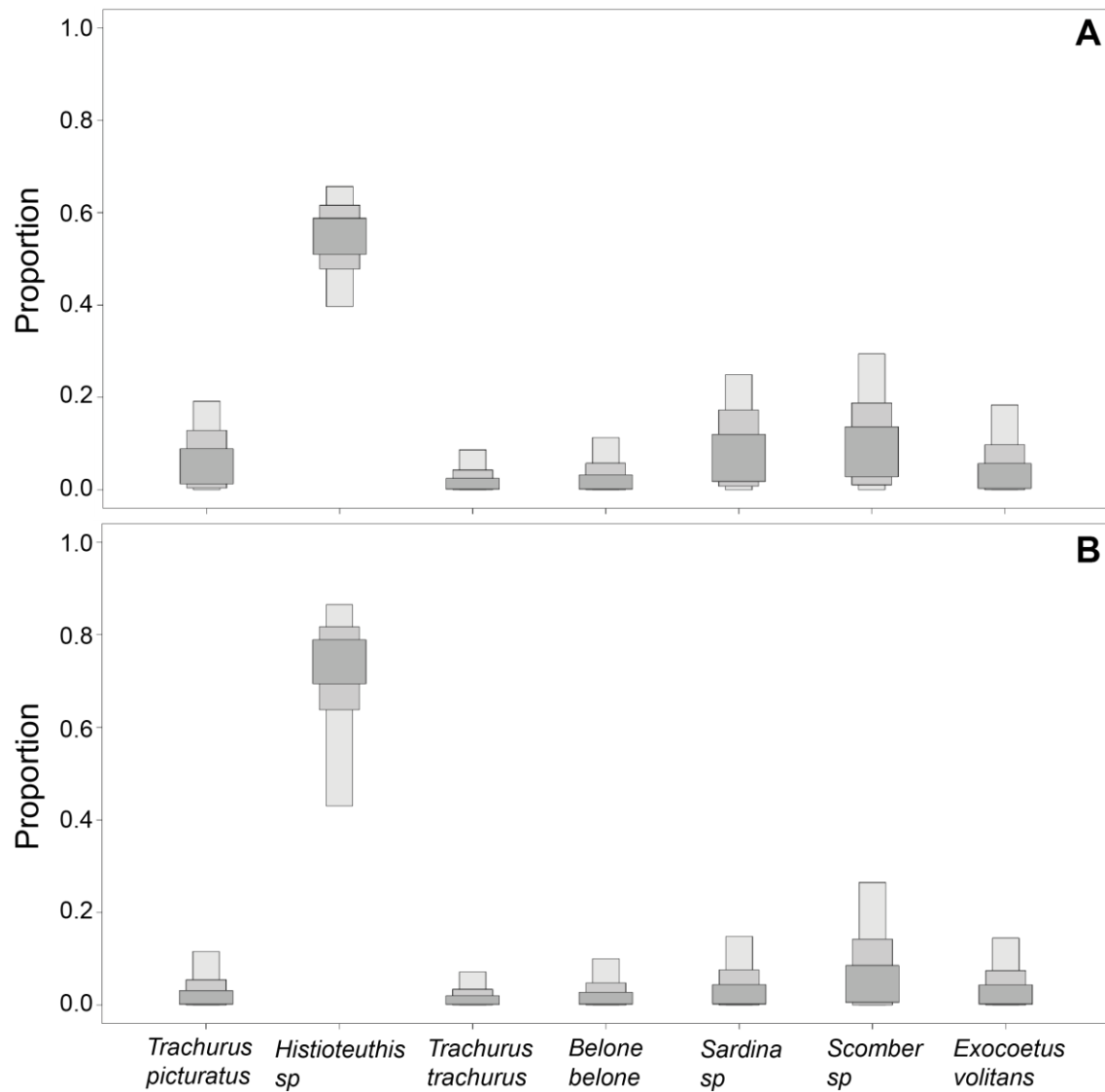


Figure 15 – Range of possible proportions of the main diet species on the trophic ecology of Cory's Shearwater (A) chicks and (B) adults during 2012. Increasing bar widths represent 50, 75 and 95 % Bayesian credibility intervals computed by Stable Isotope Analysis in R (SIAR; (Parnell et al. 2010)).

3.4. Species distribution modeling

The models obtained from the MaxEnt program for 2011 and 2012 were fitted and accomplish excellent AUC values, showing that both models have an excellent

predictive capacity (Table V). SST (mean and range) seems to be the most relevant trigger of foraging habitat selection by Cory's Shearwaters in both years. Moreover and again during both 2011 and 2012, birds seem to be highly depend on habitats close to coastal areas (distance to land). In 2011, wind speed during summer and also bathymetry gradient were also relevant triggers of the habitat selection by birds. While in 2012, sea level anomalies seem to explain the habitat use of this species.

Table V– Estimates of model fit and relative contributions of the environmental variables to the MaxEnt model, normalized to percentages for 2011 and 2012. Most relevant parameters (over 2 %) are shown in bold. SST – Sea Surface Temperature (°C). Chl *a* – Chlorophyll *a* concentration (mg m⁻³).

	<u>Parameter contribution</u>		<u>Permutation importance</u>	
Model parameter	2011	2012	2011	2012
<u>Test AUC</u>	0.97	0.98		
<u>Parameter contribution</u>				
SST mean	47.0	40.0	53.4	56.0
SST range	17.9	7.3	14.3	8.4
SST summer	6.1	1.7	0.8	1.1
SST gradient	0.1	0.0	0.2	0.1
SST anomaly	0.1	0.2	0.1	0.8
Chl <i>a</i> mean	1.1	0.6	0.9	3.8
Chl <i>a</i> peak	0.8	0.2	0.6	1.5
Chl <i>a</i> range	0.7	1.5	0.3	1.1
Chl <i>a</i> summer	0.0	0.0	0.0	0.1
Chl <i>a</i> anomaly	0.0	0.0	0.0	0.0
Chl <i>a</i> gradient	5.3	3.8	2.0	1.2
Distance to land	12.9	35.5	23.8	16.3
Wind speed summer	2.7	1.1	0.7	0.8
Bathymetry	1.9	1.6	1.4	6.0
Bathymetry gradient	2.2	0.8	0.6	0.7
Sea level anomaly	1.2	5.6	0.9	2.1

3.5. Projecting scenarios

Most relevant result from the application of the A2 scenario to the current distribution of Cory's Shearwaters in both 2011 and 2012 is the northward shift in the foraging distribution of this population breeding in Porto Santo (Figure 16). Considering the 100 years projection based on the 2011 at sea foraging distribution of birds, adult Cory's Shearwaters would forage for food in habitats further North of Azores, along the Mid-Atlantic Ridge, Northern of the Portuguese coast and North of the bank of Biscay. The 100 years projected distribution of birds departing from the habitat suitability map of 2012, illustrates an increase use of areas around the Biscay bank region and also the South-West coast of the United Kingdom by foraging individuals (Figure 16).

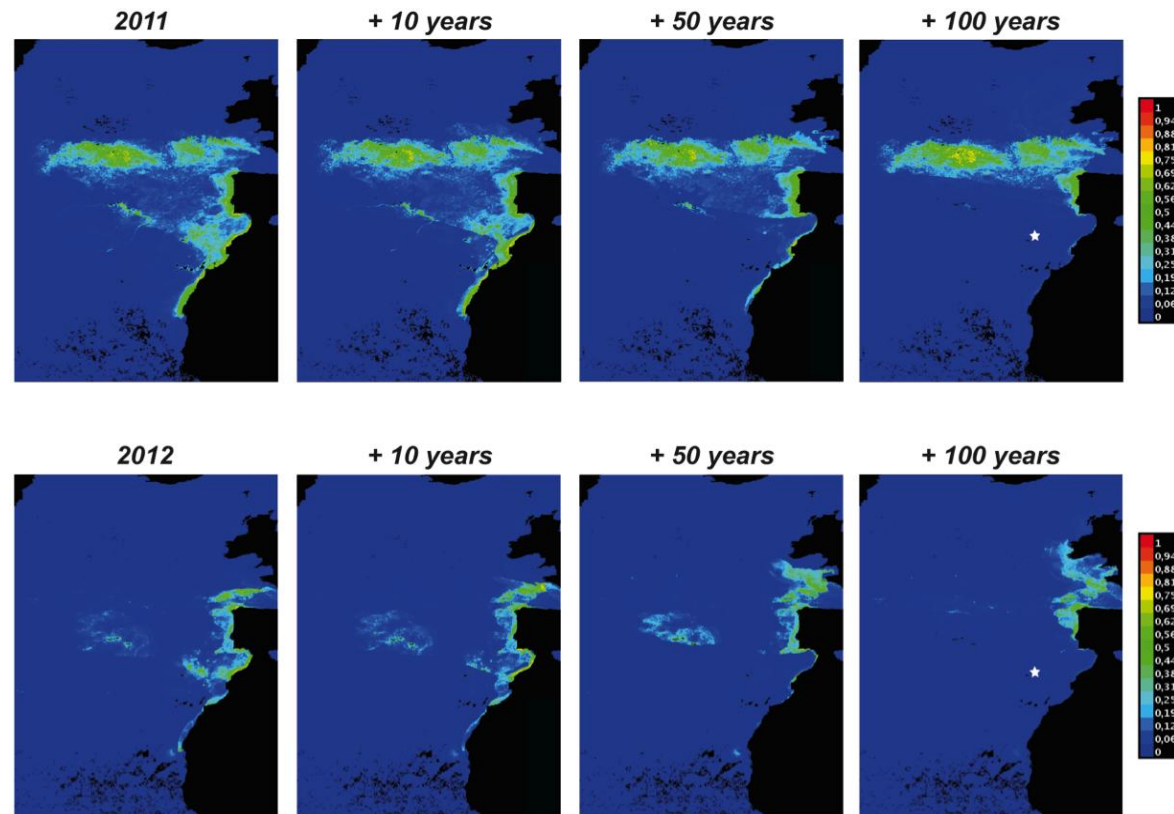


Figure 16 - Current and future foraging distribution of Cory's shearwaters breeding in Ilhéu de Cima (Porto Santo Island) as predicted by the habitat suitability MaxEnt models for 2011 and 2012 (see methods for details). Future predictive models based on scenario A2 from the Intergovernmental Panel for Climate Change (IPCC) for 10, 50 and 100 years from 2011 or 2012 onwards. White star represents the breeding colony.

3.6. Wind contribution

As previously postulated, wind can be one important influence on the route choice when seabirds decide to leave the colony. Considering the bearing of the individuals foraging to the Canary Current (CC; African coastal neritic system), they were strongly correlated with prevalent perpendicular/lateral winds (mean difference between wind and flight bearings = 42° ; Circular Correlation coefficient, $r = 0.981$, $F_{1,45} = 6.6$, $P < 0.001$). Within the CC, when foraging for food on a daily basis, birds kept their preference to forage with lateral strong winds (Circular Correlation coefficient, $r = 0.610$, $F_{1,65} = 4.6$, $P < 0.001$, Figure 17).

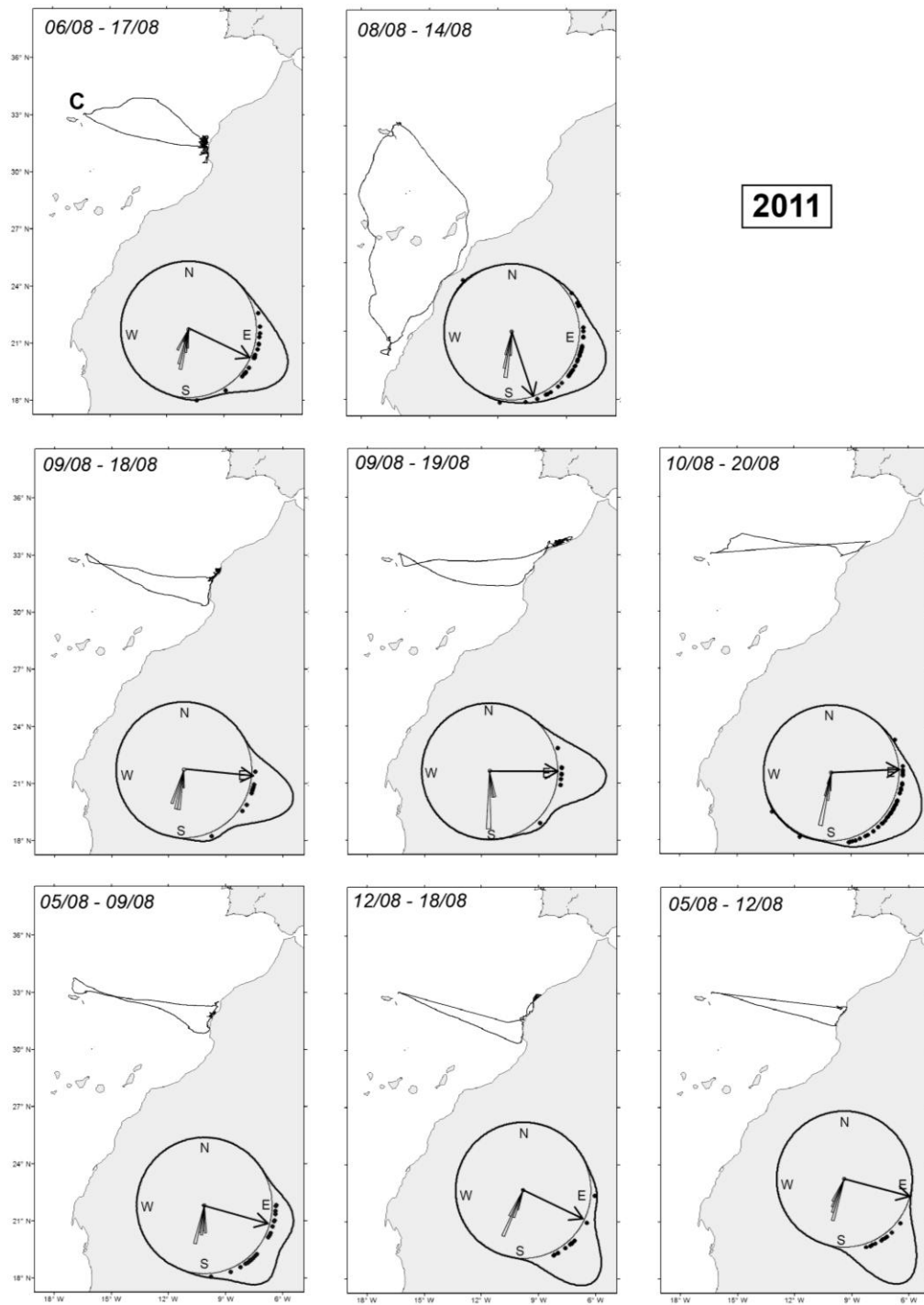


Figure 17 - Relationship between flight patterns and wind fields, when individuals use their main long trips foraging ground; the Canary Current (CC). The arrow represents the mean flight direction when departing from the colony to the CC. Dots above the circular graph represent unitary flight directions taken when within the CC and the histogram depicts and summarizes more frequent flight directions. Bars radiating from the center of the circular graph show more prevalent wind directions and intensity (length of the bars) for all the track duration (dates at the top of each map). C – Ilhéu de Cima (breeding colony).

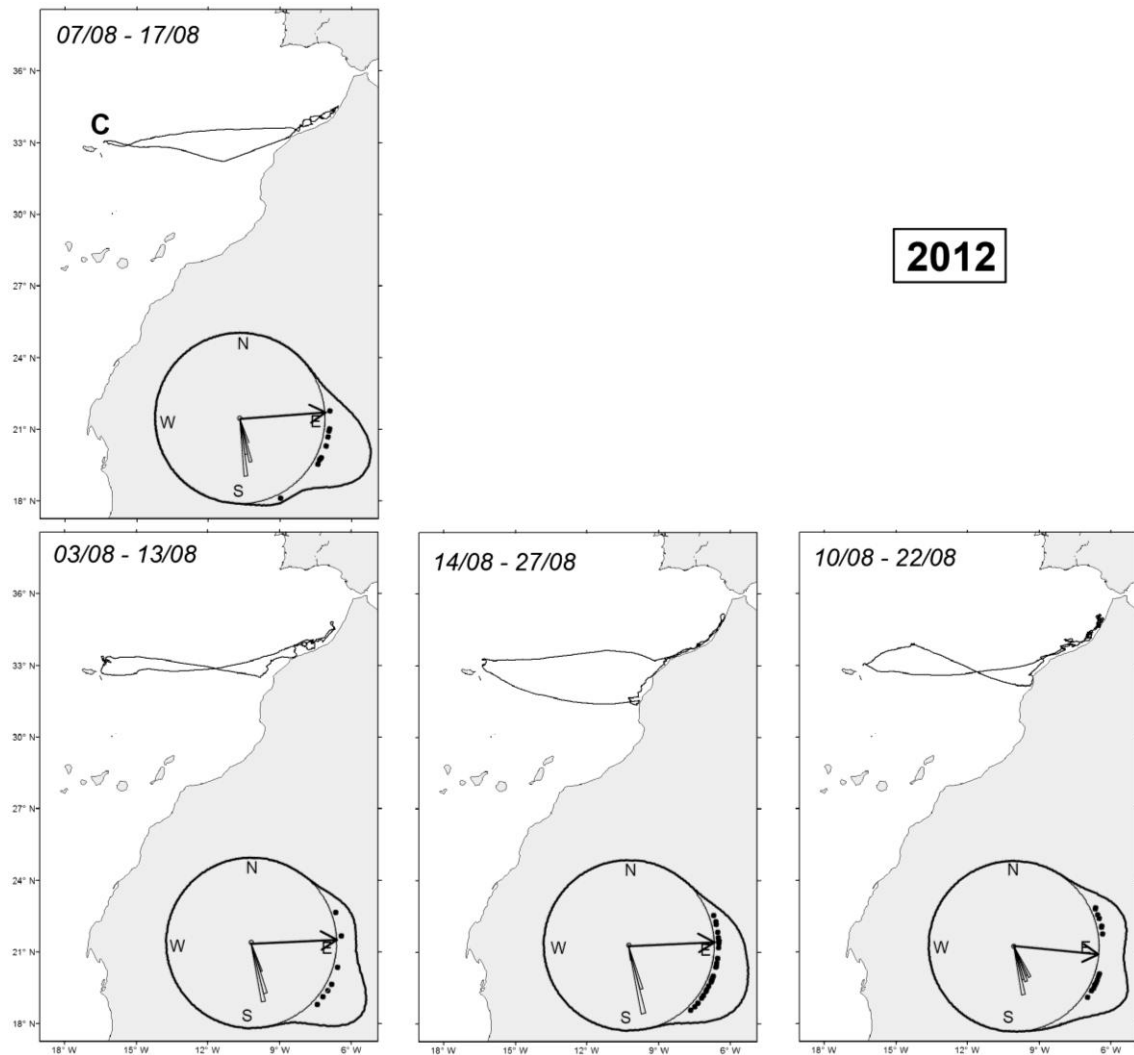


Figure 17(continuation) - Relationship between flight patterns and wind fields, when individuals use their main long trips foraging ground; the Canary Current (CC). The arrow represents the mean flight direction when departing from the colony to the CC. dots above the circular graph represent unitary flight directions taken when within the CC and the histogram depicts and summarizes more frequent flight directions. Bars radiating from the center of the circular graph show more prevalent wind directions and intensity (length of the bars) for all the track duration (dates at the top of each map). C – Ilhéu de Cima (breeding colony).

Chapter 4 - Discussion



4.1. Foraging pattern

The results obtained from tracking reveal clearly distinct foraging patterns between 2011 and 2012. In the first year, Cory's Shearwater showed a higher dispersive pattern in the long trips but also in the short trips. During long foraging trips birds exploited locations in the North Atlantic, Azores, the mainland Portuguese coast and mostly the African coast, and all these areas are identified as high productive grounds. Earlier results have shown that different populations of Cory's Shearwater do not disperse indiscriminately from their colony towards the open ocean, but concentrated their foraging effort in known productive areas on their long trips (Paiva et al. 2010d) so we anticipate a similar pattern. During short trips birds remained around the colony with a random exploration.

This dispersive pattern is consistency with the differences found when analyzing the trip sinuosity index because birds, in short trips around the colony, foraged without a path (i.e. random foraging). Moreover, the commuting trips were lower in 2011, both in short and in long trips. This straight movement is known to be the most efficiency when searching for prey over larger scales (Zollner and Lima 1999), and the lower proportion of them here, suggests that birds accomplish more looping movements (i.e. continuously searched for food and stopping when spotting a feeding opportunity (Weimerskirch et al. 2007)). Given that, we may argue that birds in 2011 worked harder than those in 2012. In 2012, the long foraging trips were restricted almost to the south Portuguese and African coasts and even the short trips present less randomness than in 2011. The UD area (25-95%) estimated is another evidence for the opposite pattern between years, since there were large differences between them. However, in long trips there were no significant differences because the total home ranges in the North Atlantic

were almost the same (confirm trough maximum distance traveled), what changed was the foraging effort in those grounds. Paiva et al. (2013), came across the same pattern in 2011 with female Cory's Shearwater from Berlenga Island, where during 2007-2010 birds presented a similar foraging pattern, but in 2011 there was a dramatic shift in their foraging distribution. They postulate that these behavioral choices may be related to the decrease in primary productivity in the preferred foraging grounds used by Cory's Shearwaters in the previous study years, which is associated with alterations in large-scale oceanic phenomenon, driven by NAO. Ceia et al. (2013) in Berlenga Island tracked both male and female Cory's Shearwaters during 2010-2012 and found a similar pattern; i.e. in 2011 birds showed a wide dispersing foraging pattern. However, in 2012 their results concurred with our study given the overlap between exploited foraging grounds. Taken altogether, these comparisons suggest that 2011 was a poor year for foraging Cory's Shearwaters throughout the North Atlantic region. Apparently this was driven by a climatic phenomenon that occurred during the 2010 winter when the NAO index presented one of the lowest values in the latest years (Osborn 2011). Low NAO index values indicate a cold winter which represents cold waters and strong winds. Although cold waters usually stand for upwelling phenomena, when strong winds are also present and the spawning events several small pelagic fish species (Santos 2001) are occurring their eggs may be dispersed offshore and do not survive which results in lower recruitment of fish prey (Paiva et al. 2013).

When linked behavioral decisions with scale dependent processes, our models establish sea surface temperature (SST) as the variable that kept the major influence in triggering the occurrence of bird foraging events. This is expected since low SST is related to high marine productivity, and the climatic oscillations in this parameter affect

the availability of fish stocks. Moreover, it can explain why 2011 was an unfortunate year for birds finding food: the winter events combined with high SST (comparing to 2012) generate a decreased in marine productivity during the summer months. Being SST and Chl *a* local indicators of productivity on a fine time scale, they will influence the food chain and, in this particular case, since SST is higher the Chl *a* consequently is lower, all the food web as to dislocate to oceanic environmental in order to subsist. Distance to land was selected as another significant variable; this was somehow expected because Cory's Shearwater feeds mostly on epi- and meso-pelagic fishes (Granadeiro et al. 1998b) that are more abundant in less deep waters (i.e. near land) than in deep oceanic regions. Also, near the coastline the Ekman transport created by offshore winds move the warm waters near the surface towards offshore regions and replace them with cooler waters from below that are enriched in nutrients (Mann and Lazier 2006). Nevertheless, chlorophyll *a* gradients were also important to explain the occurrence of foraging birds, as they occur on pelagic systems in regions of surface convergence and divergence which raises nutrients to the top layer of the water column, creating marine patches at scales of 10-100 km (Weimerskirch 2007) and it has been proven that Cory's Shearwater respond positively to Chl *a* gradients (Paiva et al. 2010e). Besides these important factors, in 2011, wind and bathymetry gradient showed a considerable influence in foraging activities of birds. Bathymetry gradient can be explained given the fact that Cory's Shearwaters exploit shallower waters in their trips around the colony, and can be used as a proxy of other small scale oceanographic processes (i.e. shelf break fronts,(Mann and Lazier 2006)). Concerning wind influence, previous studies have proven that ocean winds drive seabirds local-scale movements and the route decision can be made upon the perception of local wind conditions

(Felicísimo et al. 2008, Mateos and Arroyo 2010). Cory's Shearwater can improve the entire foraging path to avoid headwinds and use tailwinds to reduce flight costs (Navarro and González-Solís 2009). However, in 2012, wind was not an important model contributor, departure from the colony was strongly correlated with prevalent perpendicular/lateral winds when traveling to the African coast, which is consistent with the shear-soaring cycle that make use of cross winds (Sachs 2005, Paiva et al. 2010c). In most cases, birds flew directly to the closest area on the African shelf and then dispersed (Ramos et al. 2013). When foraging for food on a daily basis, birds kept their preference to forage with lateral strong winds, as occurred in 2011.

4.2. Foraging ecology

As expected, Cory's Shearwater adopted a dual foraging strategy (Weimerskirch and Cherel 1998) during the early chick-rearing phase. Birds carried out long trips with the purpose of feeding themselves and built reservations to support periods of low or even no feeding, when they searched for food near the colony to feed their chicks (Weimerskirch and Cherel 1998). Weimerskirch (1998) conducted a study in south of New Zealand with sooty shearwaters (*Puffinus griseus*) that breed in areas 1550 km away from productive areas: by performing long journeys to productive grounds Cory's Shearwaters and other pelagic seabirds store energy for themselves but also for the chicks and then use this stored energy to cover the costs of performing several short trips in nearby less productive waters to provide food to their chicks. These conclusions may also apply to our study colony in Porto Santo.

The results obtained with the chicks growing rates support this idea of a dual foraging strategy. The rates were linear which was already demonstrate with the more

data from the same study species but in other colonies in the North Atlantic, such as Selvagem Grande (Zino 1971, Zino et al. 1987) or Berlenga (Granadeiro et al. 2001) Islands. This was also consistent with the growing rate of other procellariiform seabirds of similar size (Harris 1966, Cruz and Cruz 1990), which confirms that short journeys provide enough food to chicks and their long trips do not lead to starvation. The isotopic signatures for adults and chicks, shown a high trophic level prey for chicks than for adults which was previously found by Alonso et al. (2012) in isotopic signatures of Berlenga chicks and adults that present the same foraging pattern as ours.

Regarding the stable isotopic analysis, through SIAR we saw that *Histioteuthis* sp was estimated as a very important prey for adults. When feeding in oceanic systems, the nitrogen isotopic signature is lower than when foraging in neritic systems (Paiva et al. 2010a). Furthermore, there is a direct relationship between blood carbon signatures of birds and those of their main prey species (Cherel et al. 2005, Paiva et al. 2010a), suggesting a direct influence of prey trophic level in determining consumer trophic position (Inger and Bearhop 2008). Adding to this, a low isotopic signature when feeding in oceanic systems associated to when they feed on cephalopods (e.g. *Histioteuthis* sp), and if the proportion of cephalopods is higher than that of pelagic fish species in the birds' diet, the $\delta^{15}\text{N}$ of blood is lower (Paiva et al. 2010e).

4.3. Future scenarios

Cory's Shearwater showed an important plasticity of adapting to the environmental conditions (e.g. considering the foraging pattern in 2011), but, when breeding, birds must return often to their colony. However, if environmental conditions deteriorate will their plasticity be enough to reach alternative foraging grounds? Pichegru et al. (2009) states that

Cape Gannets (*Morus capensis*) facing such changes will favor adult survival and may compromise breeding success, which ultimately will influence population dynamics.

Nowadays the studies on climatic changes are increasing and it is possible to predict the future distribution of seabirds given appropriate scenarios of spatial changes in environmental conditions. Here, we tested this with Cory's Shearwater and showed that in the next 100 years the African coast may decrease its productive potential as a consequence of the increase in SST. How will North Atlantic seabirds, such as Cory's Shearwaters, that rely mostly in that area (Ramos et al. 2013) adapt to this new scenario? Our predictions are that this will lead to an effort that Cory's Shearwater may not face without breeding failure and therefore demographic parameters will be compromised if birds try to continuously use historic favorable places (i.e. Canary Current). The nitrogen trophic signatures showed a higher level for chicks, which means that they need highly trophic preys in order to grow up healthy. Studies on Cape Gannets have shown that when chicks are fed predominantly on low energy fishery discards, their chicks survival rate was very low (Grémillet et al. 2008). In addition, a combination of environmental changes and overfishing (Furness and Tasker 2000, Frederiksen et al. 2004, Crawford 2007) mean that seabirds may have an increasing difficulty in finding enough food. On the other hand and according to our spatiotemporal projections, Cory's Shearwaters appear to show some foraging plasticity (Paiva et al. 2010a) and will likely forage further north in the Atlantic ocean (i.e. North of Azores archipelago, Galician islands). The expected problem here will be (1) the increasing distance between the breeding colony and the foraging grounds (in a central-place foraging period this may jeopardize the breeding success of this population); (2) the lack of potential breeding grounds for them in areas further North in the Atlantic ocean, which will enhance the intra- and inter-specific competition not only for resources but also for breeding habitats.

The oceanic environment is a dynamic habitat (e.g. currents, frontal systems, eddies), and it needs a stronger conservation efforts and management considerations. Considering these key marine areas for seabirds of Porto Santo's and taking in account that these areas are also important for other colonies in the North Atlantic, it is important to combine tracking studies and habitat modeling to maintain a constant monitoring of these populations and their foraging areas.

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