DEPARTAMENTO DE CIÊNCIAS DA VIDA

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Year-round distribution suggests spatial segregation of Cory's Shearwaters (*Calonectris diomedea borealis*), based on breeding experience.

Rogério Velloso Missagia

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A small bird came toward the skiff from the north. He was a warbler and flying very low over the water. The old man could see that he was very tired. The bird made the stern of the boat and rested there. Then he flew around the old man's head and rested on the line where he was more comfortable.

"How old are you?" the old man asked the bird. "Is this your first trip?"

The bird looked at him when he spoke. He was too tired even to examine the line and he teetered on it as his delicate feet gripped it fast.

"It's steady," the old man told him. "It's too steady. You shouldn't be that tired after a windless night. What are birds coming to?"

The hawks, he thought, that come out to sea to meet them. But he said nothing of this to the bird who could not understand him anyway and who would learn about the hawks soon enough.

"Take a good rest, small bird," he said. "Then go in and take your chance like any man or bird or fish."

Ernest Hemingway, The old man and the Sea

Table of Contents

Abstract

Individual experience is considered an important factor in seabirds' ecology, determining the differences in distribution and behaviour of experienced and inexperienced individuals. Recent studies show that individuals with little experience are generally more pelagic and foraging explorers than more experienced birds. However, most part of these studies is focused on the breeding period of a given species, with little information regarding the post-breeding season, when extensive migrations and wintering processes take place.

This study analyzed the differences in spatial distribution and behaviour of fourteen individuals belonging to a population of Cory's Shearwaters (*Calonectris diomedea borealis*) breeding on Berlenga Island, offshore the Portuguese coast. The group was divided between experienced and inexperienced, based on individual breeding success, and each bird was tracked for one year, from September, 2011 to August, 2012, using *geolocators* (GLS). Carbon and nitrogen stable isotopes were analyzed from primary feathers and breast feathers. The results were processed with softwares for mapping and statistical analysis, and a modelling exercise was carried out, in order to verify possible variations in distribution induced by climatic changes over the next 100 years.

Results confirm that inexperienced birds present a more pelagic behaviour than experienced birds, with extensive migratory routes, marked by several stopovers, and a higher number of wintering grounds, while experienced individuals migrate through shorter routes, and present few wintering areas. Different foraging strategies were also encountered, with experienced individuals foraging close to coastal areas, while inexperienced birds foraged more on pelagic areas. The main environmental variables

influencing the spatial distribution of experienced birds were distance to land and sea surface temperature, while inexperienced individuals were influenced by wind speed during winter and sea surface temperature. The results from the modelling exercise show that global warming might exercise significant influence on the spatial distribution of Cory's Shearwaters, especially on experienced birds. These changes might generate situations of high inter- and intra-specific competition, reducing breeding success and disturbing the population dynamics of the species.

It is safe to conclude that individual experience is an important factor to determine the spatial distribution and behaviour of pelagic seabirds such as Cory's Shearwaters. However, this factor should not be analyzed individually, but together with any highly influential environmental variables.

Keywords: Spatial segregation, Breeding experience, *Calonectris diomedea borealis*.

Resumo

A experiência individual é considerada um fator importante na ecologia de aves marinhas, determinando as diferenças na distribuição e no comportamento de indivíduos experientes e inexperientes. Estudos recentes mostram que indivíduos com pouca experiência geralmente são mais pelágicos e exploradores do que aves experientes. No entanto, a maior parte desses estudos tem sido focada no período reprodutivo de determinada espécie, com pouca informação relativa à época pós-reprodutiva, quando ocorrem as grandes migrações e os processos de invernada.

Este estudo analisou as diferenças na distribuição e no comportamento de quatorze indivíduos pertencentes a uma população de Cagarras (*Calonectris diomedea borealis*) que se reproduz na Berlenga, costa ocidental portuguesa. O grupo foi dividido entre indivíduos experientes e inexperientes, com base no sucesso reprodutivo de cada um, e cada ave foi rastreada por um período de um ano, de Setembro de 2011 a Agosto de 2012, através de *geolocators* (GLS). Análises de isótopos de carbono e azoto foram efectuadas utilizando penas primárias e do peito. Os resultados foram processados com sistemas de informação geográfica e análise estatística, e um exercício de modelação foi feito com o intuito de verificar possíveis alterações induzidas por mudanças climáticas nos próximos 100 anos.

Os resultados confirmam que aves inexperientes apresentam comportamento mais pelágico e exploratório do que aves experientes, com rotas migratórias extensas e várias paragens intermédias e maior número de zonas de invernada, enquanto indivíduos experientes migram por rotas mais curtas e possuem pouca variação no destino final. Diferenças nas estratégias de forrageamento também foram encontradas, com indivíduos experientes a alimentarem-se junto a áreas costeiras, enquanto aves

inexperientes se alimentaram em zonas pelágicas. As principais variáveis ambientais que influenciaram a distribuição de aves experientes foram distância a zonas costeiras e a temperatura superficial da água do mar (SST), enquanto indivíduos inexperientes foram influenciados pelas características do vento e SST. O resultado da modelação mostra que o aquecimento global pode exercer uma influência significativa na distribuição das Cagarras, especialmente em aves experientes. Essas mudanças podem gerar situações de elevada competição inter- e intra-específica, prejudicando o sucesso reprodutivo e a dinâmica populacional da espécie.

Podemos concluir que a experiência individual é um fator importante para se determinar a distribuição e o comportamento de aves marinhas pelágicas como as Cagarras. No entanto, este fator não deve ser analisado isoladamente, mas em conjunto com variáveis ambientais altamente influentes.

Palavras-chave: Segregação espacial, Experiência reprodutiva, *Calonectris diomedea borealis*.

List of Tables

List of Figures

Chapter 1 – Introduction

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1.1   Top predators foraging over the marine environment

Marine environments are among the largest, most varied and complex ecosystems on Earth (Verity et al., 2002). Although all ecosystems present some fundamental similarities, there are some important differences (Larkin, 1996). For example, terrestrial environments are subdivided into regional ecosystems based on major vegetation characteristics, while oceans are subdivided into several lesser ecosystems based on different characteristics of depth, oceanography, productivity and populations of organisms that are linked in trophic food chains and webs (Sherman, 1993). Pelagic areas are deep and unproductive ecosystems (blue is the color of the desert in the ocean), with liquid primary productivity ranging around $100g/m^2$/year, a very low index when compared to other marine ecosystems, as coastal areas might reach up to $500g/m^2$/year (Whittaker and Likens, 1973). However, marine top predators often present foraging strategies that allows them to effectively explore these low productivity areas, showing remarkable resilience and adaptability when searching for resources (Boyd et al., 2006).

Different marine ecosystems may support distinctive invertebrate and vertebrate communities in which top predators may specialize, becoming convenient indicators of particular biomes (Hunt & Schneider, 1987, Weimerskirch, 2007). Furthermore, marine productivity tends to be heterogeneously distributed, with high productive areas located close to specific areas such as shelf edges or coastal upwellings (Ainley and Boekelheide, 1990, Bakun, 1990, Crawford, 2007). Within these zones of high productivity, preys are found in patches of different sizes, depending of the process concentrating them and on the specific behaviour of the species. Marine top predators such as seabirds cope with this situation by adopting specific foraging strategies perfected by strong natural selection processes (Weimerskirch, 2007).

Marine apex predators are important top consumers in marine ecosystems, and may exercise significant influence in ecological processes of marine environments (Schreiber and Burger, 2001; Werner, 2010; Paiva et al., 2013). Previous studies showed that the decline of the populations of top predators can have cascading effects on lower trophic levels on both coastal and pelagic areas (Myers and Worm, 2003, Scheffer et al., 2005, Heithaus et al., 2008). These conditions qualify marine apex predators as good subjects for ecological studies, and favor the development of research programs aimed at identifying and analyzing any trends that could lead to the better understanding and management of marine ecosystems. The importance of this type of knowledge is indisputable, and also critical to prevent extinctions, deregulation of ecological processes and even disruption of ecosystem services (Block et al., 2011).

Among the marine top predators, seabirds are considered exceptional candidates for ecological research, having received a lot of attention from the scientific community (Votier et al., 2011). This is possibly related to the fact that seabirds are a cosmopolitan group, marked by several favourable conditions such as: 1) Long-distance migratory behaviour, with some species of seabirds travelling thousands of kilometers to reach wintering grounds. 2) High breeding site fidelity, increasing the chance of tracking data recovery. 3) Ground-nesting behaviour, facilitating any physical manipulation and recapture, when necessary. 4) The relatively extensive literature related to the biology and life history of several species (Warham, 1996, Schreiber and Burger, 2001). Nevertheless, modern ecological studies continue to increase this knowledge base, elucidating many important aspects of seabirds' ecology, like foraging strategies (e.g. Granadeiro et al., 1998, Paiva et al., 2010a, Thiebot et al., 2011, Votier et al., 2011; Alonso et al., 2012), migration patterns (e.g. Catry et al., 2004a, Gonzalez-Solís et al.,

2007, Dias et al., 2010), and the future of the group under impeding climatic changes (e.g. Smith et al., 1999, Barbraud and Weimerskirch, 2001, Crick, 2004).

1.2 Procellariiformes and the Marine Environment

The study of seabirds dates back to the 18th century naturalists and explorers, like Charles Darwin and Alfred Russell Wallace, renowned for their contributions in different fields of natural sciences. Due to the technical and informational constraints of the period, and to the life history of the group (below), the early research on pelagic seabirds was restricted to morphological and taxonomic studies performed in single specimens, paying no regards to populational or ecological studies. The first modern systematic study of pelagic seabirds' distribution was performed by P. Jespersen in 1924, as part of a marine biological survey (Tasker et al., 1984). In the following decades, the estimated distribution was based on the sighting of species in ocean transects, technique pioneered by V.C. Wynne-Edwards and showed in his 1935 work: *On the habits and distribution of birds on the North Atlantic* (Warham, 1996).

The 1960s were marked by the emergence of modern techniques for tracking animals, with the improvement of telemetric systems (Phillips, 2004; Haug, 2012), making data collection in ecological research faster, more precise, and with higher replicability and comparison potential. These advances were regarded as a turning point in ecological studies with pelagic seabirds (Phillips et al., 2004), allowing scientists to complement the existing knowledge (based on reproductive cycles) with the previously inaccessible wintering and migratory data.

The Procellariiformes is a well-represented order of seabirds well known for their long migratory journeys. The order comprises four families: Pelecanoididae (diving petrels), Diomedeidae (albatrosses), Hydrobatidae (storm petrels) and Procellariidae (shearwaters). The group is also the most long-lived among birds (Bried, 2003, Werner,

2010), and present extreme life history strategies, like the laying of a single egg per breeding season, followed by a long incubation and chick rearing period (Warham, 1990, Schreiber & Burger, 2001). Because of their biological traits, cosmopolitan distribution and role as top predators in marine food chains; procellariiformes are regarded as an indicator for changes and monitoring of ecological processes in marine ecosystems (Werner, 2010, Paiva et al., 2013). However, most of the information regarding the group is based on the reproductive phase of their life cycles, when the birds have their distribution restricted to their breeding colonies, and are easier to handle and track (Paiva et al., 2010, Haug, 2012). During the non-breeding season, seabirds are not bound to return to their nests, and usually take on migratory routes that can cover many thousands of kilometers into remote oceanic areas. Due to the inherent difficulty in equipping and tracking seabirds for a long period of time, and through such distances, information about the wintering period is still scarce (Wilson et al., 2002).

The migratory flexibility of seabirds is also a point of great concern, as growing evidence suggests that the group is significantly vulnerable to the environmental changes (Perón et al., 2012, Louzão et al., 2012). Species that possess a certain degree of adaptability to these changes will allow the persistence of certain populations, gaining time for natural selection to act, or for the restoration of more favorable environmental conditions (Dias et al., 2010). The migratory fidelity of marine animals is a relatively new topic of research, opposed to the considerable existing knowledge on migratory flexibility of terrestrial animals (Catry et al., 2004b, Catry et al., 2011, Dias et al., 2010).

1.3   Influence of environmental variables on seabirds

It is tempting to correlate the present and future distribution of marine top predators mostly to the population dynamics of the prey they feed upon (Tremblay et al., 2009). This premise is not wrong, since it has been proven before that apex predators are well adapted to efficiently forage for resources, be it in high productivity zones (Louzao et al., 2006, Morato et al., 2008), or in areas with low foraging potential (Weimerskirch, 2007). However, these distributions are often correlated to a plethora of other environmental aspects and oceanographic characteristics inherent to specific marine ecosystems, which might add conditional layers to the otherwise simple predator-prey relation.

The recent development of modern analytic tools and computer technology allowed the improvement of studies centered on habitat selection and population dynamics of several marine species. What started with simple correlation testing between species distribution and a few directly measured oceanographic variables, evolved into studies that incorporate several bio-physical variables and apply a range of analytical tools such as classic hypothesis testing, statistical modelling, spatially explicit approaches and multivariate analysis (Ballance et al. 2006, Tremblay et al. 2009). Essentially, modern, technologically improved studies allow investigators to not only discover which environmental variable affects certain species (if any), but also how strong is the effect, to which extent it is applied (scale-wise), and if here are any external influences by other variables. Making use of these techniques, recent researches showed that seabirds are influenced by a number of environmental factors like temperature (Paiva et al., 2010b), salinity (Ainley et al., 2005), wind conditions (González-Solís et al., 2009) and distance to land (Briggs et al., 1987). Nevertheless, it is virtually impossible to qualify a single factor as the most influencing in any scenario,

and scientific assumptions tend to consider groups of variables as the determinant of a given hypothesis.

1.4   Foraging strategies of experienced and inexperienced

All animals need food in order to survive, and the manner in which different species acquire this resource has been researched for many years. The early works on the theme are based on mathematical models proposed to explain the patterns behind the foraging behavior (Schoener, 1971, Pyke et al., 1977) and to this day are well supported by data collected from modern studies. Learning processes in foraging strategies of animals have been described before (Kamil and Roiblat, 1985) and are extensively documented in a number of vertebrates (Galef and Giraldeau, 2001). These processes are especially important for long-lived vertebrates – like seabirds – in which experience-related variations in foraging strategies and breeding success may be particularly marked.

The recent development of more accurate, lighter and cheaper trackers and loggers made possible the research of spatial and temporal distribution of seabirds, along with behavioral analyses and their relation with environmental characteristics that might influence their habitat use (Wilson et al., 2002, Phillips et al., 2004). Information gathered by these studies allowed scientists to draw comparisons between different groups of individuals inside the same population, exploring the possible variations in ecological aspects of groups divided by standards like sex (e.g. Lewis et al., 2002, Ramos et al., 2009a) or age (Dias et al., 2010, Votier et al., 2011).

The differences in behavior between experienced and inexperienced are important for a number of reasons. For example, seabirds are among the most long-lived group of birds – with long periods of immaturity – which may result in populations with

many non-breeders (sometimes over 50% of the individuals). Therefore, the disparity in feeding behavior between these groups may reduce the effects of intra-specific competition between breeders and non-breeders during a period when food availability may be lower (Schreiber and Burger, 2001, Thiebot et al., 2011), increasing the survivability of both populational segments. Also, as younger birds tend to show greater dispersion rates, they might possess a higher adaptive capacity towards climatic changes (Kokko and Lopez-Sepulcre, 2006, Haug, 2012).

Different levels of experience can have significant influence in the behavior of a species. When compared with breeding individuals, immature Northern Gannets (*Morus bassanus*) may present a higher dispersal behavior when foraging, and can even move between colonies during the breeding season of their first 2 − 3 years of life (Votier et al., 2011). Breeders of a certain species tend to forage closer to the colony, which is expected when taking into account the spatial and temporal constraints of the mature birds during the breeding period, while providing for their offspring (Navarro et al., 2007, Thiebot et al., 2011, Alonso et al., 2012). In a related study, younger Wandering Albatrosses (*Diomedea exulans*) showed similar levels of success than older individuals when searching for food, making use of different time-related strategies − immature individuals tend to forage more intensely and land more prey during the night (Weimerskirch, 2005).

Different experience levels can also affect the demographic characteristics of certain seabirds, especially when acting alongside shifting environmental variables. First time breeders of Black-browed Albatross (*Talassarche melanophrys*) showed lower reproductive success and lower survival rates when compared with older, more experienced individuals (Nevoux et al., 2007). That study suggests that inter-annual environmental variations are closely related to this phenomenon, influencing both

groups in different ways – while experienced individuals showed more resilience to harsh conditions, keeping the same survival rates throughout the reproductive season, younger birds had increased mortality rates and lower reproductive success. However, these differences were mitigated during more favourable environmental conditions.

The effects of environmental variation on experience-related characteristics of seabirds are an important topic of research for modern ecologists, as the group faces major climatic shifts, like the El Niño-Southern Oscillation Events (ENSO) (Schreiber and Burger, 2001). The severe weather resulting from this type of event may cause the death of many birds, a dire prospect when taken into account the vulnerability of younger individuals, and their potential as future recruits and major determinants of long-term population persistence (Votier et al., 2011). Until now, the majority of the information on how birds' experience influences their foraging strategies results from data collected during the reproductive season (Thiebot et al., 2011, Votier et al., 2011). To fully understand the experience-related ecology of seabirds, it is essential to explore the same topic during the non-breeding periods. During this phase, birds are not restricted to one area, and are subject to significant environmental variation, resultant from extensive migratory events.

1.5   Study rationale

This study was part of an ongoing monitoring of a population of Cory's Shearwater (*Calonectris diomedea borealis*) breeding on Berlenga Island, offshore the Portuguese west coast. However, few analyses were made regarding differences in behaviour and distribution between individuals with different experience levels. In this study we equipped Cory's Shearwaters with GLS loggers during one full year and analyzed carbon and nitrogen stable isotopes from feathers in order to compare the following characteristics between experienced and inexperienced birds: 1) Daily foraging behaviour. 2) Migratory profiles and the location of wintering grounds. 3) Foraging strategies based on stable isotopes analysis. 4) Influence of environmental variables on the at-sea spatial distribution throughout the year. 5) The at-sea distribution under influence of climatic change for the next 100 years.

Based on the known ecology of other species of seabirds, we expect to find significant variations between Cory's Shearwaters with different experience levels, especially regarding migratory processes, wintering grounds, and foraging strategies. Variations between groups are also expected to be correlated to environmental predictors, mainly productivity drivers such as chlorophyll-a, and physical aspects like distance to land and wind profile. The final results of this work are expected to contribute to explain the at-sea distribution of seabirds and other marine top predators, while also helping establish "individual experience" as a very important characteristic for population studies of pelagic seabirds.

Chapter 2 – Methods

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2.1   Study Species - Cory's Shearwater (*Calonectris diomedea borealis*)

The Procellariformes is a well-represented order of seabirds that comprises four families: Pelecanoididae (diving petrels), Diomedeidae (albatrosses), Hydrobatidae (storm petrels) and Procellariidae (shearwaters). The group is known as the most long-lived among birds (Bried, 2003, Werner, 2010) and present extreme life history strategies, with the laying of a single egg per breeding season, followed by a long incubation and chick rearing period (Warham, 1990, Schreiber and Burger, 2001). During the chick rearing period, the parents take alternate foraging trips to provide food for the brood and replenish their own nutritional reserves, often travelling tens to hundreds of kilometres from the breeding site on a single journey (Magalhães, 2008).

The Cory's Shearwater (*Calonectris diomedea borealis*, Fig. 1) is a colonial, long-distance migrant seabird (Procellariiformes: Procellariidae) with breeding grounds located on the northeast Atlantic and Mediterranean islands like Azores, Cape Verde, Selvagens and Berlengas (Granadeiro, 1993, Navarro et al., 2007). Their reproductive behaviour is characterized by great energetic investment from both parents, spread through 8 months (March to April), with a long egg incubation period (54 days) and long chick rearing (90 days), when the parents alternate duties of tending to the offspring and foraging for food (Navarro et al., 2007).

The first three months of the reproductive cycle are known as the pre-laying period; when the parents leave the nesting area to feed, replenishing the energy lost during the migration from the non-breeding areas (see below) and stocking up on nutritional reserves that will sustain them through the early stages of the reproductive process (Werner, 2010, Paiva et al., 2013). The foraging strategy employed by the species is based on a cycle between short ($1 - 2$ days) and long trips ($3 - 9$ days), with

short trips used to provide for the chick, while long trips are realized to replenish the adults' nutritional reserves. For more information on foraging strategies, refer to Granadeiro et al., (1998), Navarro et al., (2007), Magalhães et al., (2008), Navarro and González-Solís, (2009), Paiva et al., (2010a), Paiva et al., (2010b), Paiva et al., (2010c).

During winter, the species travels thousands of kilometres to feed in warmer climates, being found mainly in South Africa, Brazil, and southern central Atlantic (Camphuysen & Van Der Meer, 2008, Ramos et al., 2009b). Even with their well-known migratory routes, the life and behaviour out of breeding season is still an object of research, becoming less of a question mark as technological improvements become available to perform the necessary studies (Dias et al., 2010, Ramos et al., 2009c). In the last decade, research groups started to slowly fill in these knowledge gaps with data collected from birds populations of several different breeding sites.

Studies on Cory's Shearwater migration patterns showed that this species presents a migratory plasticity, with individuals wintering in different locations between years and sometimes showing great disparity in their destination, shifting places from North to South Atlantic, western to eastern South Atlantic and even from the Atlantic to the Indian Ocean (Dias et al., 2010, Catry et al., 2011, Dias et al., 2012). Because of its flexibility, this species might be in better situation to resist current climatic variations than other long-distance migratory birds with inflexible migratory strategies (e.g. the Manx Shearwater *Puffinus puffinus*, Guilford et al., 2009). Also, this characteristic can help understand the mixing of populations during the winter quarter and the impacts of population-level threats, building the foundation of conservation policies and programs not only for Cory's Shearwaters, but for other seabirds as well (González-Solís et al., 2007). The post-reproductive period of Cory's Shearwater is slowly being unfolded, providing information about flight dynamics (Dall'Antonia et al., 1995), foraging

strategies, physiological traits (Ramos et al., 2009b) and general behaviour (Catry et al., 2011).

Figure 1 – Cory's Shearwater (*Calonectris diomedea borealis*) in flight.

2.2   Study Area

2.2.1 Berlengas archipelago

The Berlengas archipelago is located in the Portuguese coast, at approximately 10Km west of the town of Peniche, in the north Atlantic. The largest Island of the archipelago is Berlenga Island (39°12'40''49N, 09°30'29''W), a granitic skerry that reaches and altitude of 88m, with maximum length of 1,5Km on its widest, and a total area of 78,8ha (Haug, 2012, Santos et al., 2012). Two groups of smaller Islets called Estelas and Farilhões are also part of the archipelago and, together with Berlenga, are the three main dry land extensions of the area.

In 1981, the Portuguese government attributed the status of natural reserve to the area. Since then, the islands passed through successive improvements on total area covered and conservation importance, which culminated in June 28th 2011, when the Berlengas Natural Reserve (R.N.B.) was included in the World Network of Biosphere Reserves (W.N.B.R.), under positive ruling of UNESCO (Santos et al., 2012). The whole archipelago presents high biodiversity, with 76 fish species currently referenced for the reserve area (Rodrigues et al., 2008). This, allied with the favourable combination of bathymetric features and ocean and wind circulation (namely the Azorean anti-cyclone and the Portuguese continental shelf upwelling), characterizes the area as rich feeding and breeding grounds for several seabird species (Paiva et al., 2010b, Werner, 2010). Presently, the archipelago hosts approximately 850 breeding pairs of Cory's Shearwaters, distributed among Farilhões Islets (500-550 pairs) and Berlenga Island (300 pairs) (Lecoq et al., 2011).

Fieldwork was conducted in Berlenga Island, with logger retrieval during September in 2011 (deployment of loggers), and end of August − September, 2012 (recovery of loggers). The birds on the colony are used to human interactions, and were caught by hand from their burrows for logger retrieval during night-time, while nesting and less prone to stress. The tracked individuals belong to a long-term study on the species, and were previously ringed and monitored for information such as sex and reproductive success, adding to the separation between experienced and inexperienced.

2.2.2 The Atlantic Ocean

Due to the migratory processes of Cory's Shearwater, most tracking data collected contains information that extends the study area to encompass a large portion of the Atlantic Ocean, with individuals present in coastal areas of North America, South America and Africa. Oceanographic characteristics over such large areas are under influence of several environmental determinants, showing remarkable variation in ecological aspects like temperature and productivity which, in turn, can play a major role in marine species distribution and behaviour (Warham, 1996, Louzão et al., 2006, Paiva et al., 2010c).

The North Atlantic Basin is under influence of a major circular current known as the North Atlantic Gyre (Fig. 2). This wind-based gyre is formed by the western action of the Gulf Stream towards East, feeding into the North Atlantic Current and the Azores Current, closing the cycle into a large, clockwise rotating subtropical gyre (Barton, 2001). The water cycling present in the area is responsible for the displacement and exchange of warm (and nutrient-poor) water extracted from subtropical areas by the Gulf Stream, and cold water (nutrient-rich) injected into the system via the Arctic Labrador Current (Barton, 2001, Soares, 2013).

The North Atlantic Gyre cycling profile is not the same throughout the year, with seasonal variations occurring during summer. This effect is caused by the increase of the sea surface temperature, and results in a significant shift of productivity values of areas close to the Portuguese coast towards areas located in the Arctic Circle (Paiva et al., 2010b, Soares, 2013). Consequences of these effects on the at-sea distribution and behaviour of Cory's Shearwater in the North Atlantic can be found throughout the literature (e.g. Granadeiro et al., 1998, Paiva, 2009, Roscales et al., 2011), being generally focused on the breeding period.
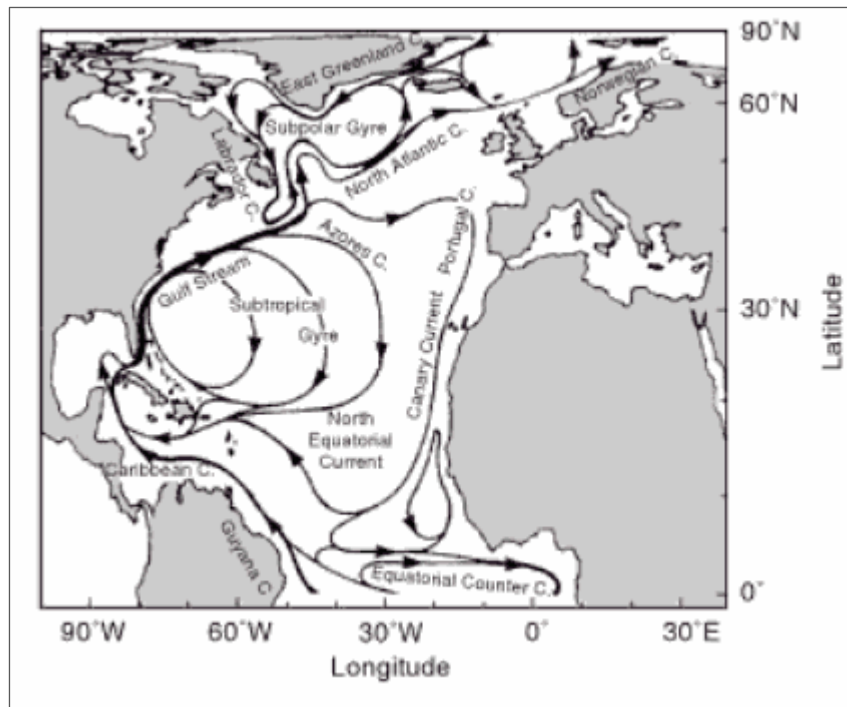
Figure 2 – General near-surface circulation patterns of the North Atlantic Ocean (Barton, 2001).

The upper-level circulation of South Atlantic waters is determined by the Subtropical Gyre, in a counter-clockwise flux generated by a considerable array of geostrophic currents. The Eastern boundary of that circulation profile is marked by the Agulhas Southern Retroflection (A.S.R.), an important current (although small in comparison with other fluxes) as it acts as an inter-oceans mediator between the Atlantic and the Indian oceans (Peterson and Stramma, 1991). The A.S.R. creates a northern flux that is inserted into the Benguela Current, flowing north towards the equator, where it is divided into the South Equatorial Counter Current (flowing eastward, back to African waters), and into the Brazil Current. The latter flows southward along the Brazilian coast and is redirected by the Falkland Current and the massive Antarctic Circumpolar Current, closing the Subtropical Gyre flux profile (Fig. 3).
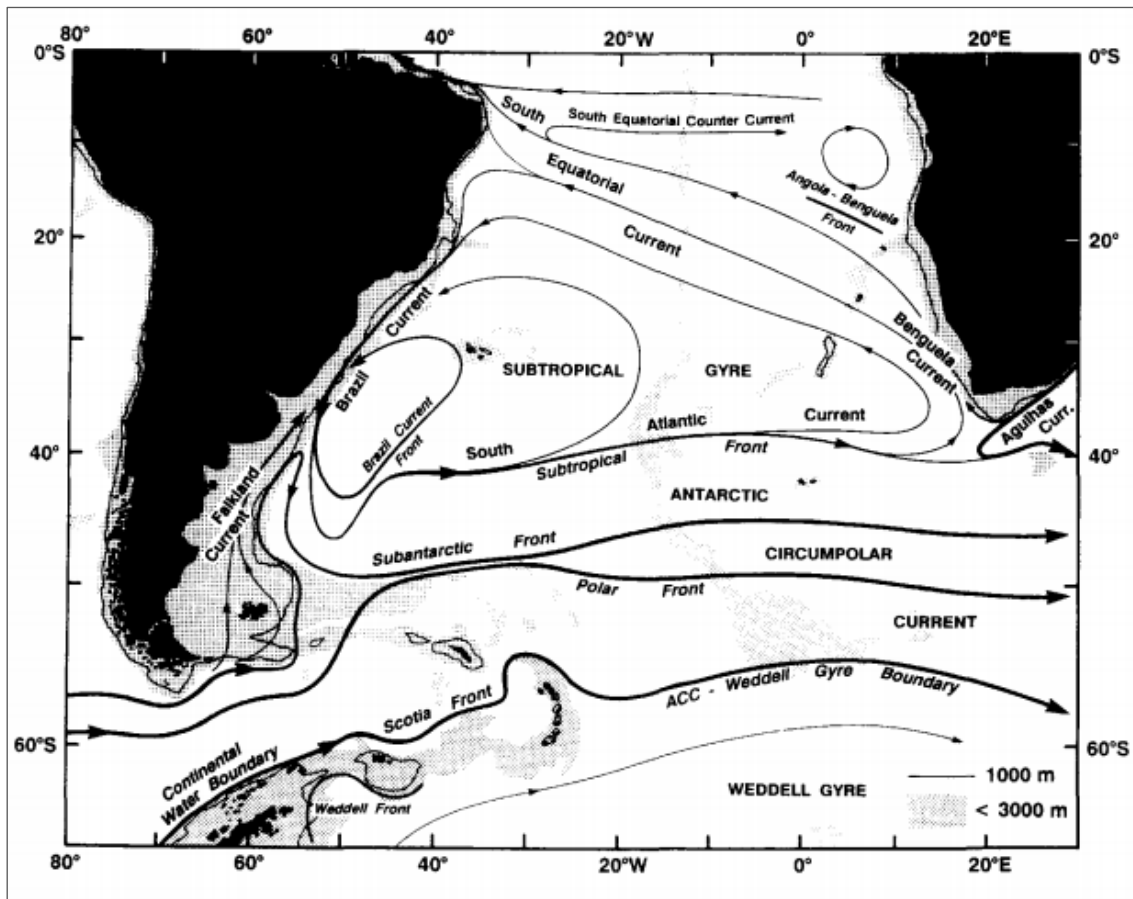
Figure 3 – General near-surface circulation processes of the South Atlantic Ocean. Extracted from Peterson & Stramma (1991).

The deep current flow on the southern Atlantic is fed by waters from the North Atlantic, the Weddell Sea, and from Circumpolar Current through the Drake Passage. The inflow originated from different sources present significant variation in physicochemical and biological parameters like temperature, salinity, nutrients and oxygen. When entering the South Atlantic, these waters are captured by local circulation imposed by the winds and thermohaline processes, creating a stratified profile with layers in various ranges of depth and density (Reid, 1989, Stramma and Peterson, 1989), as shown in Fig. 4.
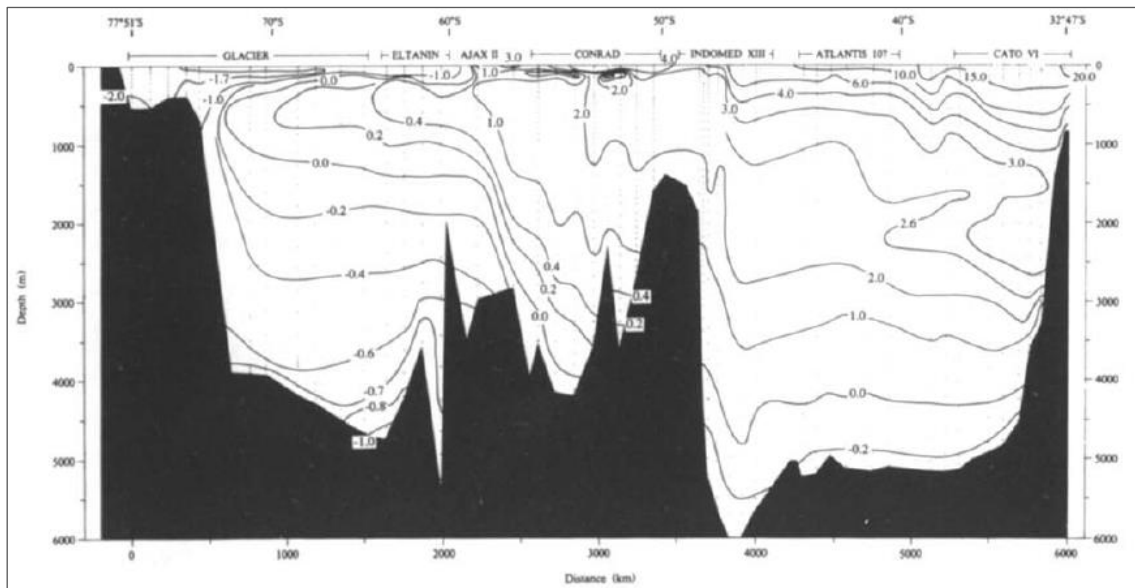
Figure 4 – Example of stratified profile focused on temperature values (°C), following a section from Antarctica (left) to Brazil (right). Extracted from Reid (1989).

2.3   Geolocators and tracking

The devices used in this study were geolocators belonging to the MK5 model (Fig. 5), developed by the British Antarctic Survey (BASTrak), in Cambridge. Each geolocator weights 3.6 g, and is built in hard epoxy to reduce the effects of wear and tear associated with the birds' activity. Geolocators are ideal for this type of study, as they are equipped with very durable batteries (5 years), and are light enough so to not impose physical limits on the birds, especially on long-duration tracking. The weight of the geolocators is a key factor for tracking purposes, as the extra load might impose negative effects on the birds' behaviour, foraging efficiency and breeding success (Phillips et al., 2003). Previous studies showed that leg-mounted geolocators weighting 1.5 – 2% of the animal total body weight exercise little to no short-term effects on Cory's shearwaters (Igual et al., 2005), validating the equipment choice.

Fourteen Cory's Shearwaters were equipped with loggers during the end of the 2011 breeding season (August/September), and were recovered at the end of the following breeding season, in 2012. This provided a 12 months tracking profile of the individuals, with one breeding season, one wintering season, and the migratory routes connecting these two periods (i.e. wintering and breeding migrations). Of the 14 specimens, 8 were males and 6 were females, which were further divided into experienced and inexperienced individuals. The experience level of the birds was determined based on the total number of successful breeding seasons, following similar standards of previous studies (e.g. Haug, 2012). Any individual with 3 or less successful breeding seasons was classified as inexperienced, while any individual with more than 4 successful breeding cycles was classified as experienced (min. = 2 successful breeding cycles, max. = 8 successful breeding cycles).

Information collected from the geolocators consisted of two datasets: 1) Ambient light level readings with reference to time provided twice each day (at local mid-day and midnight), used for geolocation estimates with an average error of 186 ± 114Km (Phillips et al., 2004). 2) Activity record of wet/dry information based on salt-switching technology, used for behavioural analyses.
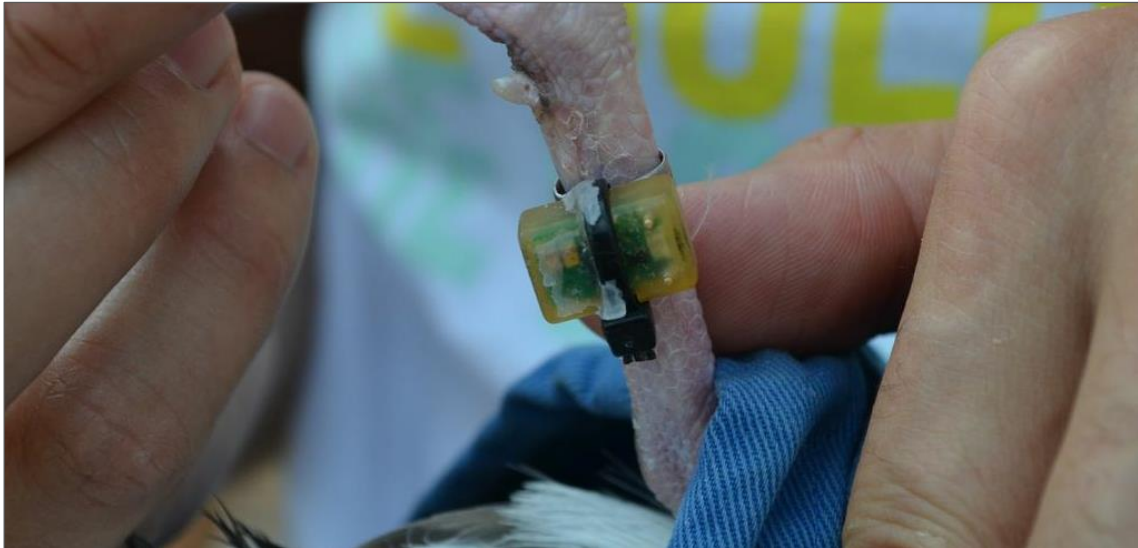
Figure 5 – Geolocator model MK5 attached to a Cory's Shearwater specimen. Photo by Rahel Borrmann (2013).

2.4   Tracking and activity analysis

Information extracted from the trackers was first decompressed with the use of *Decompressor®* software (BASTrak, Cambridge). For geolocation purposes, latitudes were estimated based on the day/night lengths, while the longitude was estimated from the absolute time of local midday/midnight, providing two daily positions for each individual. The light intensity data extracted from the loggers usually present abnormal readings, related to unpredictable shading of the light sensors by the seabird, or by other physical barriers. To remediate this aspect, the light data was processed in *TransEdit2®* software (BASTrak, Cambridge), where such inconsistencies were corrected and a confidence value was attributed to each reading, ranging from 1 (low confidence value) to 9 (high confidence value), depending on the profile and homogeneity of the curves. Light transitions found in the limits of both equinoxes (20th March and 22nd September) were given fixed confidence level values: C.L. = 7 for ± 15 days from the equinox date, C.L. = 5 for ± 10 days and C.L. = 3 for ± 5 days from the each equinox. This decision

reflects the impossibility to determine latitudes with reasonable accuracy during the light period variations associated with the phenomenon (Catry et al., 2011).

The data generated after the *TransEdit2®* processing was then arranged into a general positioning table for the 14 birds. This table was used to determine 4 crucial dates for the behavioural analysis of each bird: (1) departure from breeding colony (end of breeding season), (2) arrival date on wintering area, (3) departure date from wintering area and (4) arrival on breeding colony (next reproductive cycle. The *ArcGIS 10* software was utilized in this process, and the following criteria were adopted:

-        Departure date from colony was extracted from the first position outside of Berlengas as part of a continuous outward migration to the wintering area. Departure from wintering area followed the same reasoning.

-        Arrival dates were established as the first position to appear in the area of interest (breeding colony or wintering area), following the migration route.

The activity data provided by the loggers was based in salt-switching technology, and showed when the bird was in contact with seawater, and for how long. The nature of the "wet activity" could not be determined, however, and is considered to encompass any non-flying at-sea behaviour performed by the bird, such as foraging or resting on the water surface. Data collected from the loggers was processed in *R Software* version 2.14.1 with the *R Studio* IDE (integrated development environment) version 0.97.332, used to calculate the proportion of time spent in water in a specific date, and the average of time spent in water per month.

2.5   Stable isotope analysis

Along with direct tracking techniques, the analysis of stable isotopes (S.I.A.) is considered as a valuable tool for modern ecologists, and has been used in research of aspects like habitat selection, dietary preference and foraging strategies. Stable isotopes do not decay over time (unlike their unstable radiogenic counter-parts, therefore the name), varying in mass, and among several biologically important elements like Hydrogen (H), Carbon (C), Nitrogen (N), Oxygen (O) and Sulfur (O) (Inger and Bearhop, 2008). The very small differences in mass presented by these isotopes are responsible for subtle changes in their behaviour during the chemical reactions involved in the formation of different tissues of birds, making the isotopic ratio of these elements found in blood, feathers, and other tissues, an excellent indicator of diet, distribution and behavioural patterns of seabirds.

It is important to note that different tissues are synthesized and replaced at different rates, making crucial the proper knowledge of biological traits and life history of the animal in question. For example, avian blood plasma can turn over very quickly, providing an isotopic signature of few days prior to sampling. On the other side, the synthesis and replacement process of tissues like feathers or claws can extend from weeks to months, providing information on feeding habits and spatial distribution over a wider period of time.

For this study, Stable Isotope Analysis (S.I.A.) of $\delta^{15}N$ ($^{15}N/^{14}N$) and $\delta^{13}C$ ($^{13}C/^{12}C$) were performed. The ratios of nitrogen (N) are used to determine the trophic positioning of the animal. The reason for this is that during the assimilation of dietary proteins, the ^{14}N is lost to nitrogenous waste products, while ^{15}N is assimilated into consumer tissues in higher quantity (Inger and Bearhop, 2008). Carbon (C) ratios are

used to determine the foraging habitat of the consumer, as the δ^{13}C follows a gradient from high to low values from the coast to more pelagic areas. This happens due to the organic enrichment present in coastal zones, which is gradually diluted in offshore waters (Inger and Bearhop, 2008, Paiva et al., 2010b, Haug, 2012).

Isotopic signatures were determined from collected feathers of 14 individuals. The utilization of feathers for S.I.A. is based on the long-duration aspect of this study, as the isotopic signatures found in these samples reflect the feeding habits of each individual during the moulting phase. During this time, the new feathers are irrigated with blood, and keep an isotopic imprint that can be used for analysis months later. Since events of breeding, migration and moult are time-exclusives in Procellariiformes birds, with no overlaps between them (Warham, 1996), the S.I.A. of the feathers of Cory's Shearwaters is expected to indicate aspects of their foraging behaviour at-sea, during the wintering period.

The feathers collected for S.I.A. were the P1 and S8 – representatives of the preceding summer (breeding) and wintering seasons, respectively – and breast feathers as an overall diet picture for the all-year period (Ramos et al., 2011, Ceia et al., 2013). Prior to S.I.A., the feathers were cleansed of any surface contaminants with successive rinses of a 2:1 chloroform-methanol solution, dried at 60°C for 24 h and then homogenized. The carbon and nitrogen isotopic composition of the samples were determined using a *Flash EA1112 Series* elemental analyser coupled on-line via *Finningan conflo II* interface to a *Thermo Delta VS* mass spectrometer. Isotope ratios are presented in the usual δ notation based on the PeeDee Belemnite (PDB) for carbon and atmospheric N2 (AIR) for nitrogen, and expressed as ‰. δ^{13}C or δ^{15}N = [(Rsample/Rstandard) − 1] × 1000, where R = ^{13}C/^{12}C or ^{15}N/^{14}N, respectively.

Replicate measurements of internal laboratory standards (acetanilide) indicate precision $< 0.2‰$ for both $\delta^{13}C$ and $\delta^{15}N$.

To compare stable isotope results between groups of different experience level, we utilized a Multivariate Analysis of Variance (MANOVA) test for each sample type (P1, S8 and breast), further pooling the results into different time periods (breeding, wintering and all year). Furthermore, we adopted the Stable Isotopes Bayesian Ellipses in R (S.I.B.E.R.) framework. This technique allows for easier visualization and comparison between different sample sizes, and helped us determine differences in niche positioning between groups, along with eventual interaction. The area of the standard ellipse (SEAc, an ellipse that has 95% probability of containing a subsequently sampled datum) was adopted to compare the niche segregation between experienced and inexperienced birds, including any possible overlaps. All metrics were calculated utilizing *R Software* version 2.14.1, with addition of *SIAR* package and *SIBER* functions contained within the platform.

2.6   Kernel utilization distribution

The Kernel Utilization Distribution (K.U.D.) is a technique widely employed in ecological studies to estimate the home range of groups of birds (or other animals), based on the probability density over each observation point in a sample (Worton, 1989, Seaman and Powell, 1996). In this study, the K.U.D. was calculated using the processed tracking data from each bird, to determine the respective distribution throughout the non-breeding season, and any possible differences between experienced and inexperienced birds. To achieve these results, *R Software* version 2.14.1 was utilized, along with the *adehabitat* and *adehabitatHR* packages, all under the *R Studio* I.D.E. version 0.97.332.

The *smoothing factor* (*h*) is an important parameter to be considered when making use of Kernel estimation methods, as it determines the detail level of the data plotted, and can alter the general shape of the distribution, influencing posterior analysis (Seaman and Powell, 1996, Kappes et al., 2011, Haug, 2012). Considering the large-scale tracking profile provided by each bird as they crossed oceans or even hemispheres, a smoothing factor (*h*) = 1° (i.e. 111Km) was decided to be ideal, showing better representation of the distribution and falling into accord with the average error of the loggers (185 ± 115Km). The possible overlapping of kernels was also calculated for the wintering season among experienced and inexperienced birds, and between the groups. For this, the function *kerneloverlap* of the *adehabitat* package was utilized in the *R* environment, and allowed the analysis of spatial segregation between birds with different levels of experience. All kernels were expressed in standard home range distributions (Worton, 1989), considering the utilization distributions of 95% (UD95, home range) and 50% (UD50, foraging area).

2.7   Environmental predictors

To model seabird species occurrence, we used 24 environmental variables (Table 1) that are either known, or suspected, to be 'usually' correlated with seabird distribution and abundance (e.g. Louzao et al., 2006; Tremblay et al., 2009). Oceanographic data were (mostly) extracted from the Environmental Research Division, Southwest Fisheries Science Center and US National Marine Fisheries Service (http://coastwatch.pfel.noaa.gov/coastwatch/ CWBrowserWW180.jsp).

Physical variables (distance to land, mean bathymetry, and bathymetry gradient) were extracted using the cell value nearest to the centroid of each grid cell and were considered invariant throughout the period of our study. Dynamic oceanographic data

(sea surface temperature, sst; chlorophyll -*a* concentration, chla and wind speed, wspd) were extracted as monthly averages from Aqua MODIS, Pathfinder AVHRR satellite imagery and AVISO QuickSCAT products, and varied among months.

Because seabirds may respond to spatial gradients of oceanographic variables (Louzão et al., 2006, Tremblay et al., 2009, Wakefield et al., 2009), we also calculated spatial sst and chla gradients as (maximum value x minimum value) x 100/maximum value, with maximum being the highest and minimum the lowest seasonal mean sst or chla value over a moving 3 x 3 grid cell window. This dimensionless metric expresses the magnitude of change in each habitat variable, scaled to the maximum value. The spatial gradients of chlorophyll a (gchla) and sea surface temperature (gsst) indicate the presence of frontal systems, whereas the gradient of bathymetry (gbat) reflects the presence of topographic features (e.g. shelf break or seamount).

All remaining environmental predictors hosted at the World Ocean Database (see WOD variables at Table 1; Boyer et al., 2009) were extracted and processed to match the spatial extent of the former predictos and temporally extended until 2012 (Tyberghein et al., 2009). All former environmental predictors were interpolated and aggregated to fit a 1º grid mask for habitat modelling.

2.8   Species distribution modelling

2.8.1 Data processing and exploratory analysis

All geolocations were binned into a spatial grid with cell size 1º to match the spatial resolution of remotely sensed environmental data. Every grid cell received an additional binary detection/non-detection value of '1' (hereafter referred to as 'presence'), whereas grid cells that were surveyed but, where no target seabird species were observed were coded as '0' (hereafter referred to as 'absence'). Our models used

latitude and longitude as predictor variables (Table 1) and therefore implicitly included some spatial structure and 'correct' for possible autocorrelation.

2.8.2 Model construction

Model construction, training and testing was performed with Maximum Entropy (MaxEnt) modelling based on presence-only data (version 3.3.3 (http://www.cs. princeton.edu/~schapire/maxent/ [accessed 18 October 2012]). MaxEnt is a general-purpose method for characterizing probability distributions from incomplete information. In estimating the probability distribution defining a species' distribution across a study area, MaxEnt formalizes the principle that the estimated distribution must agree with everything that is known (or inferred from the environmental conditions where the species has been observed) but should avoid making any assumptions that are not supported by the data. The approach is thus to find the probability distribution of maximum entropy (the distribution that is most spread-out or closest to uniform) subject to constraints imposed by the information available regarding the observed distribution of the species and environmental conditions across the study area.

The MaxEnt method does not require absence data for the species being modeled; instead it uses background environmental data for the entire study area. The method can utilize both continuous and categorical variables and the output is a continuous prediction (i.e. a cumulative probability ranging from 0 to 1 that indicates relative suitability). MaxEnt has been shown to perform well in comparison with alternative methods (Elith et al., 2006, Pearson et al., 2006, Phillips et al., 2006, Oppel et al., 2012).

Two MaxEnt models were executed, one for each category of experience. In each model, environmental variables were firstly subjected to a cross-correlation analysis, in order to avoid problems with parameter estimations (Zuur et al., 2007). One of each pairwise highly correlated variables (i.e. rs > 0.7; Tabachnick and Fidell, 1996) was excluded from the model.

2.8.3 Model evaluation and calibration

We divided the tracking data into training and test data by randomly setting aside approximately 30% of the geolocations for spatial evaluation of the models (Araújo and Guisan, 2006, Austin, 2007). We ran MaxEnt on the presence-only positions 100 times. We calculated the mean of the 100 MaxEnt predictions to obtain an average prediction and coefficient of variation of predictions (Édren et al., 2010). The settings of the MaxEnt program were logistic output format, resulting in values between 0 and 1 for each grid cell, where higher values indicate more similar climatic conditions, duplicates removed, and 100 replicate runs of random (bootstrap) subsamples with 30 as random test percentage. The results were summarized as the average of the 100 models.

There are three main results of MaxEnt; jackknife chart, Receiver Operating characteristics Curve (ROC) and probability map. Jackknife chart was used to evaluate the contribution of each environmental layer to the final result. The ROC curve measured the model's accuracy, based on 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 (Phillips et al. 2006). Generated models are generally interpreted as excellent for test AUC > 0.90, good for 0.80 < AUC < 0.90, acceptable for 0.70 < AUC < 0.80, bad for 0.60 < AUC < 0.70 and invalid for 0.50 < AUC < 0.60 (Araújo et al.

2005). Finally, the probability map shows the spatial distribution of predicted presence probability.

Two sets of results from the modelling were considered for this study: 1) A species distribution map for the wintering season. 2) The variable contribution table, showing which environmental predictor had greater influence on the results.

To expand the results on the species distribution, another model was made. This model took into account the A2 scenario for global climate change from the Intergovernmental Panel on Climate Change (I.P.C.C., accessible at www.ipcc.ch), a conservative one, predicting an increase of 0.18°C on the sea surface temperature (SST) per decade. Following these predictions, we calculated the possible alterations on species distribution that would occur in the next 10, 50 and 100 years.

Table 1 – Agglomerative clustering of environmental data layers included on the habitat modelling procedures with MaxEnt.

Variable	Code	Derived Metric	Units	Manipulation	Source
Sea Surface Temperature	min_sst	Minimum	°C	Temporal minimum from monthly climatologies (2002-2012)	Aqua-MODIS
Sea Surface Temperature	mean_sst	Mean	°C	Temporal mean from monthly climatologies (2002-2012)	Aqua-MODIS
Sea Surface Temperature	max_sst	Maximum	°C	Temporal maximum from monthly climatologies (2002-2012)	Aqua-MODIS
Sea Surface Temperature	range_sst	Range	°C	Temporal range from monthly climatologies (2002-2012)	Aqua-MODIS
Sea Surface Temperature	winter sst	Mean	°C	Temporal mean from monthly climatologies (December 2011-February 2012)	Aqua-MODIS
Sea Surface Temperature Gradient #	gsst	Mean	%	Temporal gradient from monthly climatologies (December 2011-February 2012)	Aqua-MODIS
Salinity	salinity	Mean	PSS	ArcGIS interpolation of in-situ measurements	WOD 2009*
pH	ph	Mean	-	ArcGIS interpolation of in-situ measurements	WOD 2009*
Dissolved Oxygen	dissox	Mean	ml/l	ArcGIS interpolation of in-situ measurements	WOD 2009*
Silicate	silicate	Mean	µmol/l	ArcGIS interpolation of in-situ measurements	WOD 2009*
Phosphate	phos	Mean	µmol/l	ArcGIS interpolation of in-situ measurements	WOD 2009*
Calcite concentration	calcite	Mean	mol m-3	Temporal mean from seasonal climatologies (2002-2012)	Aqua-MODIS
Chlorophyll a concentration	min_chla	Minimum	mol m-3	Temporal maximum from monthly climatologies (2002-2012)	Aqua-MODIS
Chlorophyll a concentration	mean_chla	Mean	mol m-3	Temporal maximum from monthly climatologies (2002-2012)	Aqua-MODIS
Chlorophyll a concentration	max_chla	Maximum	mol m-3	Temporal maximum from monthly climatologies (2002-2012)	Aqua-MODIS
Chlorophyll a concentration	range_chla	Range	mol m-3	Temporal maximum from monthly climatologies (2002-2012)	Aqua-MODIS
Chlorophyll a concentration	winter chla	Mean	°C	Temporal mean from monthly climatologies (December 2011-February 2012)	Aqua-MODIS
Chlorophyll a concentration Gradient #	gchla	Gradient	%	Temporal gradient from monthly climatologies (December 2011-February 2012)	Aqua-MODIS
Diffuse Attenuation	damax	Maximum	m-1	Temporal maximum from monthly climatologies (2002-2012)	Aqua-MODIS
Diffuse Attenuation	damean	Mean	m-1	Temporal maximum from monthly climatologies (2002-2012)	Aqua-MODIS
Bathymetry	bat	Mean	m	Spatial mean	ETOPO 1
Bathymetry spatial gradient	gbat	Mean	%	Spatial gradient	ETOPO 1
Distance to coastline	dland	Minimum	°	Distance to nearest coastline from centroid of each grid cell	R computed
Wind speed	wspd	Mean	ms-1	Temporal mean from monthly climatologies (December 2011-February 2012)	QuickSCAT AVISO product

* Boyer, T.P., Antonov, J.I., Baranova, O.K., Garcia, H.E., Johnson, D.R., Locarnini, R.A., Mishonov, A.V., O'brien, T.D., Seidov, D., Smolyar, I.V. & Zweng, M.M. (2009). World ocean database 2009. US Government Printing Office, Washington, DC.

 # Calculated over a 3° X 3° moving window as [(maximum value - minimum value)*100]/maximum value, with maximum being the highest mean value in a 3° X 3° moving window.

Chapter 3 – Results
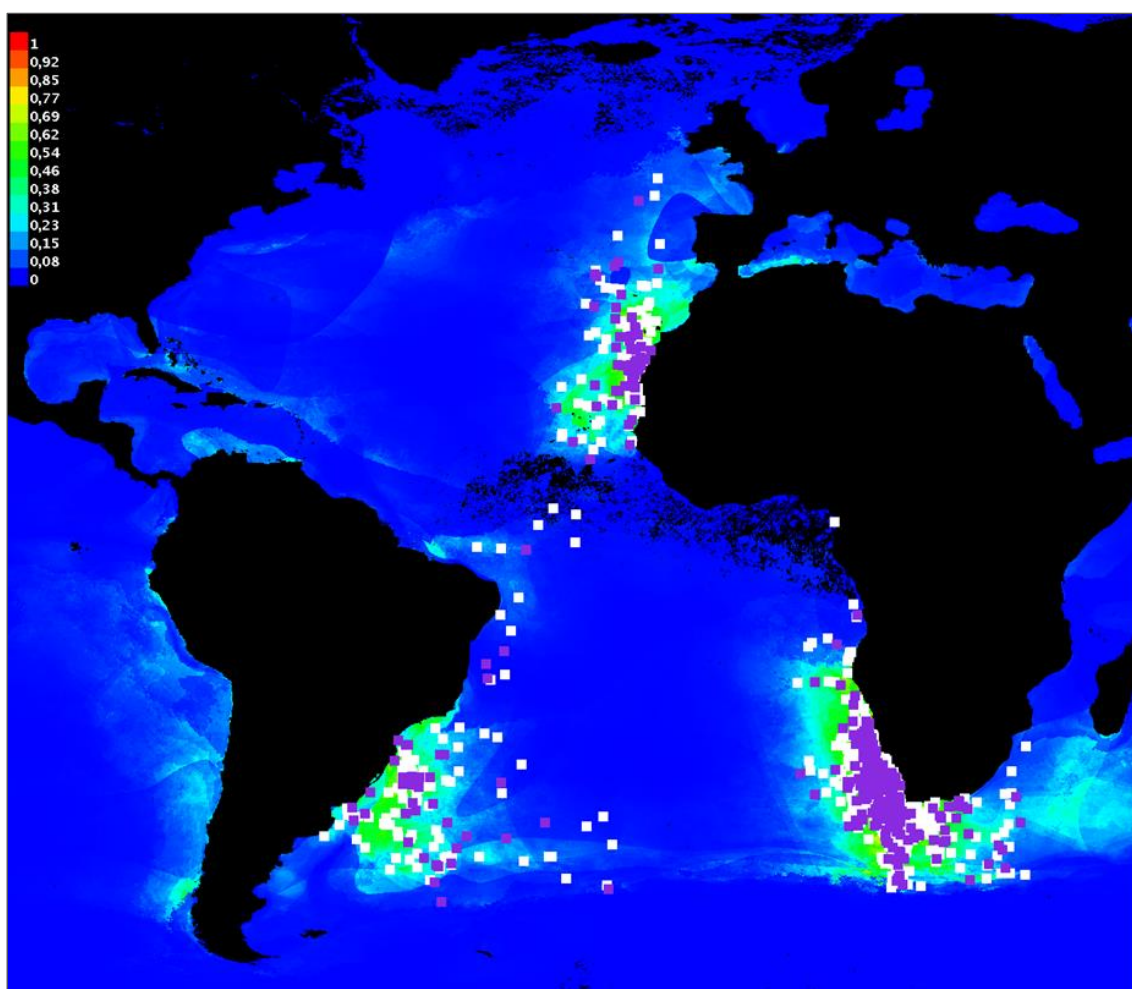
3.1   Migratory profile

Experienced birds showed a more straightforward migratory route, with few or no stopovers (birds 1, 2, 4, 12, 13, 14), while inexperienced birds presented a more diverse migratory profile, with longer paths and one or more stops during the migratory route (birds 5, 6, 7, 9, 10, 11). However, one bird of each group showed a different behavior from the others: bird n°8 (experienced) presented a convoluted migratory path, while bird n°3 (inexperienced) reached the wintering area in a straightforward route. The different strategies employed were also reflected in the travelling time of each individual, which ranged from as little as 3 days (bird n° 6), up to a maximum of 122 days (bird n° 8).
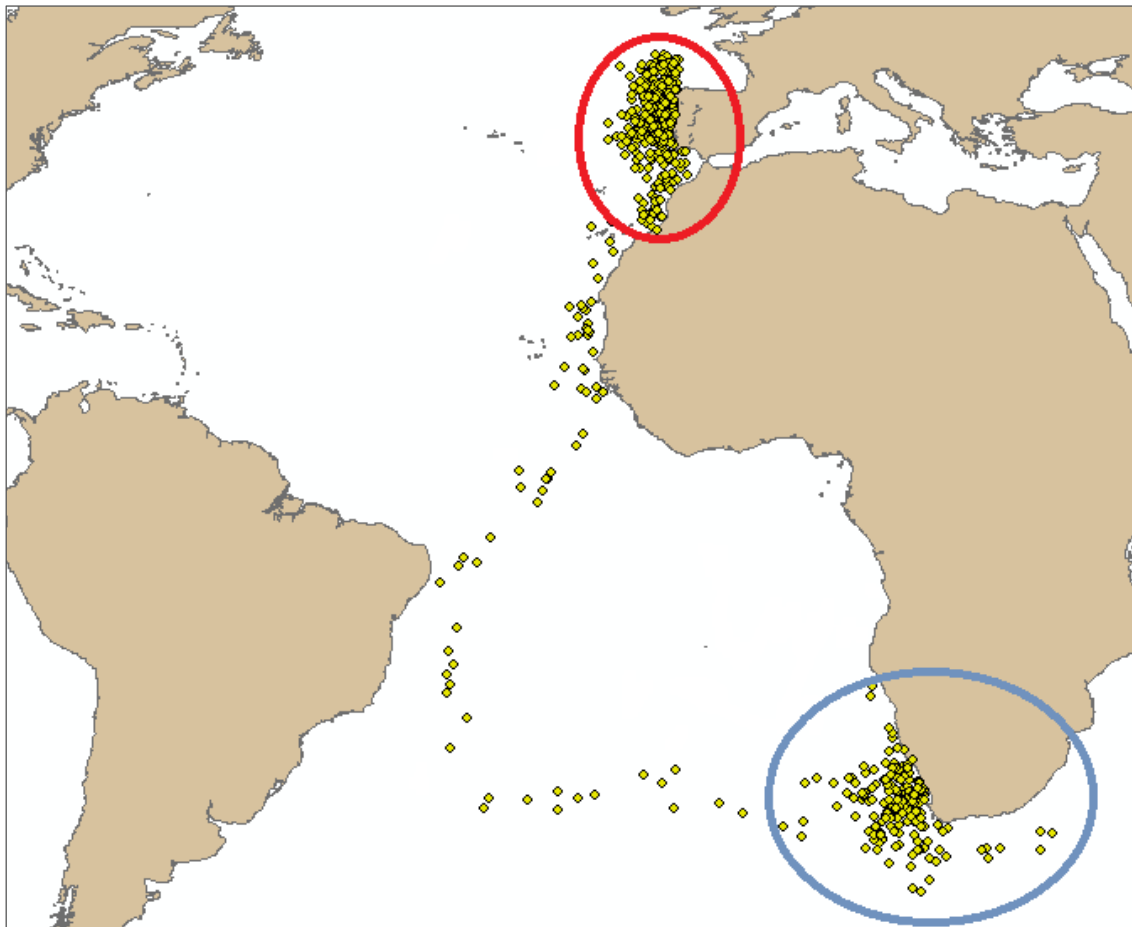
Figure 6 – Example of migratory profile analyzed in ArcGIS (bird 13). Red circle = breeding season distribution. Blue circle = wintering distribution.

There was considerable variation in the migratory schedule of the tracked birds (Table 2). Departure dates from the breeding colony ranged from late August (bird n° 8, experienced, departed on 29/08/2011) to late November (bird n° 6, inexperienced, departed on 23/11/2011). The birds arrived on the wintering grounds from mid-October (bird n° 12, experienced, arrival on 14/10/2011) to early January (bird n° 11, inexperienced, arrival on 01/01/2012). Departure from wintering grounds showed considerable less variance, encompassing a smaller time-span: the earliest birds began the return trip in late February (birds n° 1 and n° 6, experienced and inexperienced, departed on 22/02/2012) while the latest birds began the return journey in mid-March (bird n° 11, inexperienced, departed on 14/03/2012). The birds arrived on the breeding colony from late February (bird n° 6, inexperienced, arrival on 29/02/2012) to mid-April (bird n° 11, inexperienced, arrival on 10/04/2012). Table 2 shows the migratory schedule for each of the fourteen birds.

The wintering grounds were in both the North and South Atlantic, generally in coastal areas. The coast of South Africa was the wintering location for 5 experienced birds (birds n° 1, 2, 4, 8, 13), with 2 of the group wintering in other areas (bird n° 12, Cape Verde and bird n° 14, South Brazil). The wintering grounds of inexperienced birds varied, with individuals wintering in South Africa (birds n° 5 and n° 9), South Brazil (birds n° 3 and n° 11) and Newfoundland (bird n° 6). Two inexperienced birds presented mixed wintering grounds (bird n° 7 in South Atlantic and South Brazil, and n° 11 in Newfoundland and North Brazil).

Rogério V. Missagia (2013) Spatial segregation of Cory's Shearwater, based on breeding experience.

Table 2 – Tracking summary for 14 Cory's Shearwaters from Berlenga Island, tracked from September – 2011 to September – 2012. The table shows indicators for sex, experience level and wintering grounds, along with relevant dates of the migratory route (departure from breeding colony, arrival to wintering grounds, departure from wintering grounds and return to colony). *South Atl. = South Atlantic, (p) = pelagic, S. Br. = South Brazil, N. Br. = North Brazil.*

Unique ID	Sex	Experience	Deployment	Leave breed	Arrive winter	Leave winter	Arrive breed	Winter Grounds
1	M	Exp	31/08/2011	07/11/2011	28/11/2011	22/02/2012	04/04/2012	South Africa
2	F	Exp	31/08/2011	27/10/2011	30/11/2011	23/02/2012	09/04/2012	South Africa
3	F	Inexp	11/09/2011	29/10/2011	06/12/2011	05/03/2012	04/04/2012	South Brazil
4	M	Exp	02/09/2011	06/11/2011	04/12/2011	01/03/2012	05/04/2012	South Africa
5	M	Inexp	13/09/2011	23/09/2011	14/12/2011	07/03/2012	31/03/2012	South Africa
6	F	Inexp	01/09/2011	23/11/2011	26/11/2011	22/02/2012	29/02/2012	Newfoundland
7	M	Inexp	02/09/2011	30/09/2011	14/12/2011	10/03/2012	05/04/2012	South Atl. (p)+S. Br.
8	F	Exp	21/08/2011	29/08/2011	29/12/2011	08/03/2012	01/04/2012	South Africa
9	M	Inexp	20/08/2011	31/08/2011	24/11/2011	04/03/2012	25/03/2012	South Africa
10	M	Inexp	20/08/2011	08/10/2011	27/10/2011	04/03/2012	30/03/2012	Newfoundland+N. Br.
11	F	Inexp	20/08/2011	21/11/2011	01/01/2012	14/03/2012	10/04/2012	South Brazil
12	M	Exp	21/08/2011	01/09/2011	14/10/2011	26/02/2012	29/03/2012	Cape Verde
13	F	Exp	20/08/2011	05/11/2011	04/12/2011	28/02/2012	04/04/2012	South Africa
14	M	Exp	20/08/2011	18/11/2011	10/01/2012	07/03/2012	04/04/2012	South Brazil

The Kernel utilization distribution for the wintering grounds showed a considerable degree of segregation between experienced and inexperienced birds. Experienced birds tended to winter in coastal areas, especially on South and North Africa, with only one bird wintering in South America. Inexperienced birds wintered in four different areas: Newfoundland, Southern Brazil, South Atlantic and South Africa (Fig. 7). The segregation found during visual analysis was further supported by the overlapping indexes calculated, showing an overlap on the 75% Kernel UD of only 24.2% between the two groups of birds during the wintering period.

The variation in migratory profiles for the inexperienced birds was also supported by an overlap index of 22.5% for the wintering grounds, indicating that inexperienced birds not only present spatial segregation from experienced birds, but also amongst themselves. When compared to their counterparts, experienced birds showed considerable homogeneity in the wintering profile, as the group presented an overlapping rate of 71.8%. As expected, the overlapping rates during the breeding season were high, a reflection of the breeding site fidelity of the species (Table 3).

Rogério V. Missagia (2013) Spatial segregation of Cory's Shearwater, based on breeding experience.
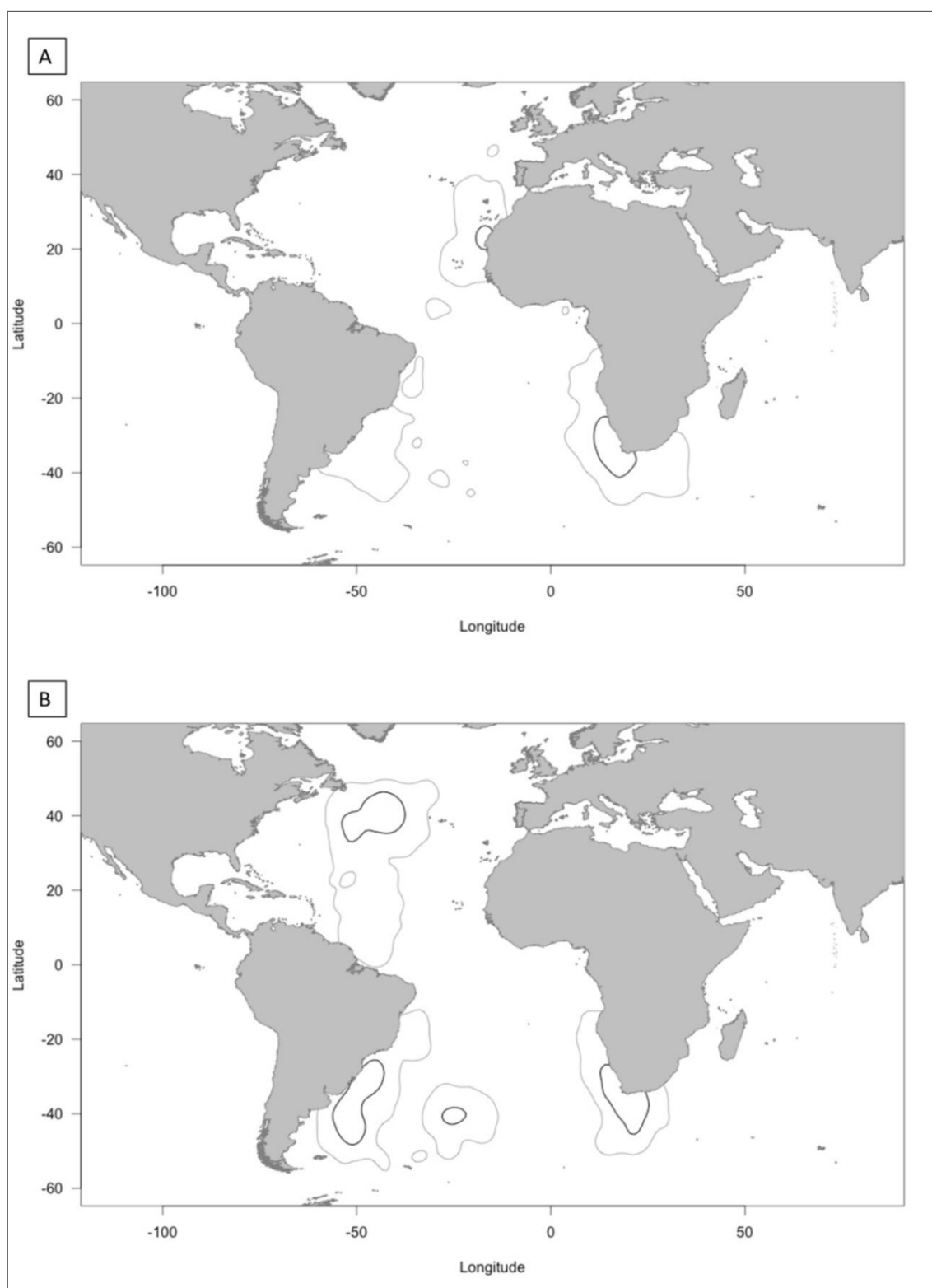

Figure 7 – Kernel utilization distributions for Cory's Shearwaters from September, 2011 to August, 2012. Black contours represent UD50, light gray represents UD95. A) Experienced birds. B) Inexperienced birds.

Table 3 – Percentage of overlap of the 75% Kernel UD for Cory's Shearwaters breeding in Berlenga Island. Numbers are shown in percentual monthly values and seasonal mean for experienced and inexperienced birds, and between groups.

MONTHLY	Overlapping (%)		
	Exp x Inexp	Experienced	Inexperienced
January-2012	10.1	69.3	10.4
February-2012	11.2	70.3	12.8
March-2012	13.4	72.8	21.9
April-2012	34.9	71.9	31.4
May-2012	42.1	74.8	39.5
June-2012	55.8	84.9	46.9
July-2012	67.5	89.4	61.1
August-2012	92.8	92.4	72.1
September-2011	81.6	86.1	64.2
October-2011	61.7	76.3	47.2
November-2011	33.1	70.8	28.4
December-2011	16.0	71.2	11.3
SEASONAL			
Breeding	62.4	82.8	52.5
Non-breeding	24.2	71.8	22.5

3.2   Activity analysis

Considering both experienced and inexperienced individuals, there was a higher amount of time spent in water (i.e. lower activity levels) by the birds from October, 2011 to February, 2012. An increase in activity started in March, 2012 and extended through the breeding season, with the lowest proportion of time spent in water (i.e. highest activity levels) during the months of June and July (2012). There were also distinguishable variations between the birds' activity during light and dark periods: daytime activity was higher than nocturnal activity during the non-breeding season, but considerably lower during the breeding season. The group activity summary is depicted below (Fig. 8).
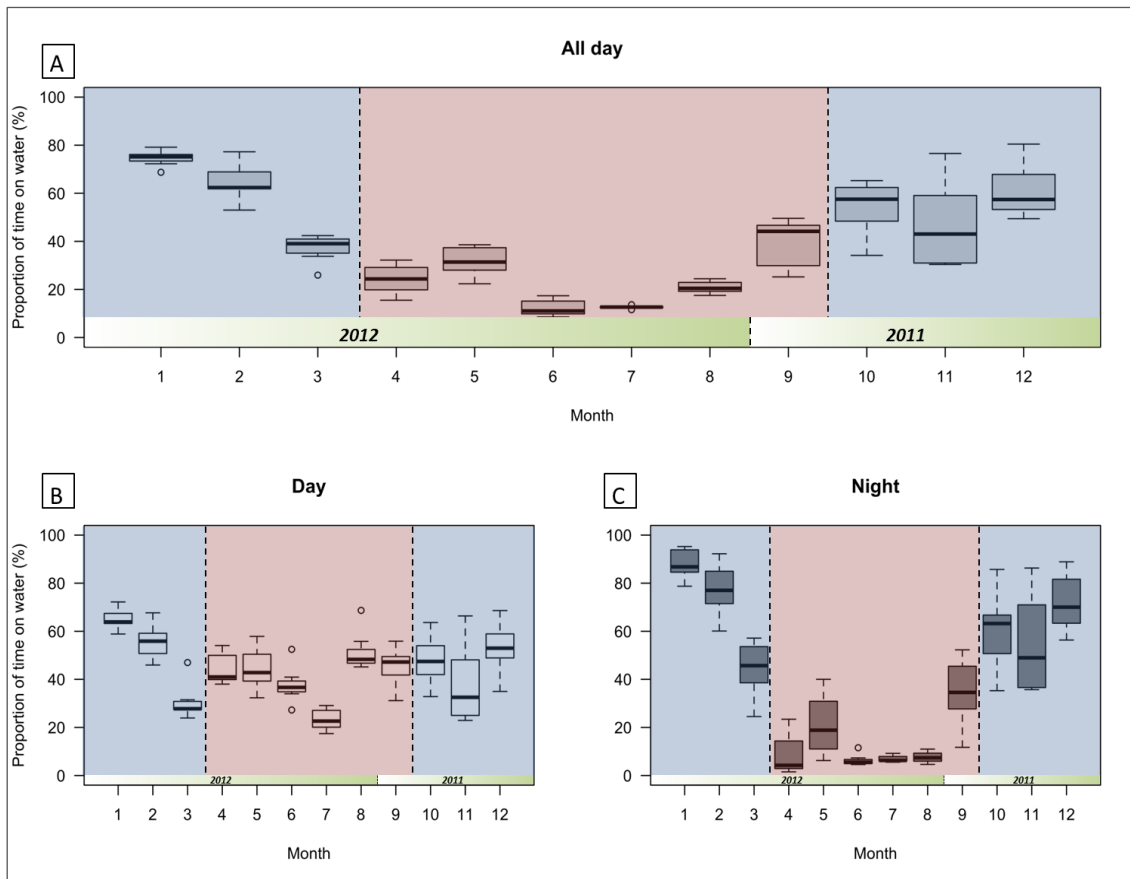
Figure 8 – Monthly (A), daily (24h), (B) daytime and (C) night-time activity profile for 14 Cory's Shearwaters from Berlenga Island, expressed through proportion of time spent in water. Blue shading represents non-breeding period, while red shading represents the breeding season.

Results from the comparative activity analysis between the two groups showed a considerable degree of variation between experienced and inexperienced birds throughout the year (Fig. 9). Overall, experienced birds presented lower activity levels than inexperienced ones, spending more time in water, either feeding or resting. Inexperienced individuals showed a considerable degree of activity, spending less time in idle behaviour. During March and November, however, the activity levels of were inverted, and inexperienced birds were less active than experienced individuals.
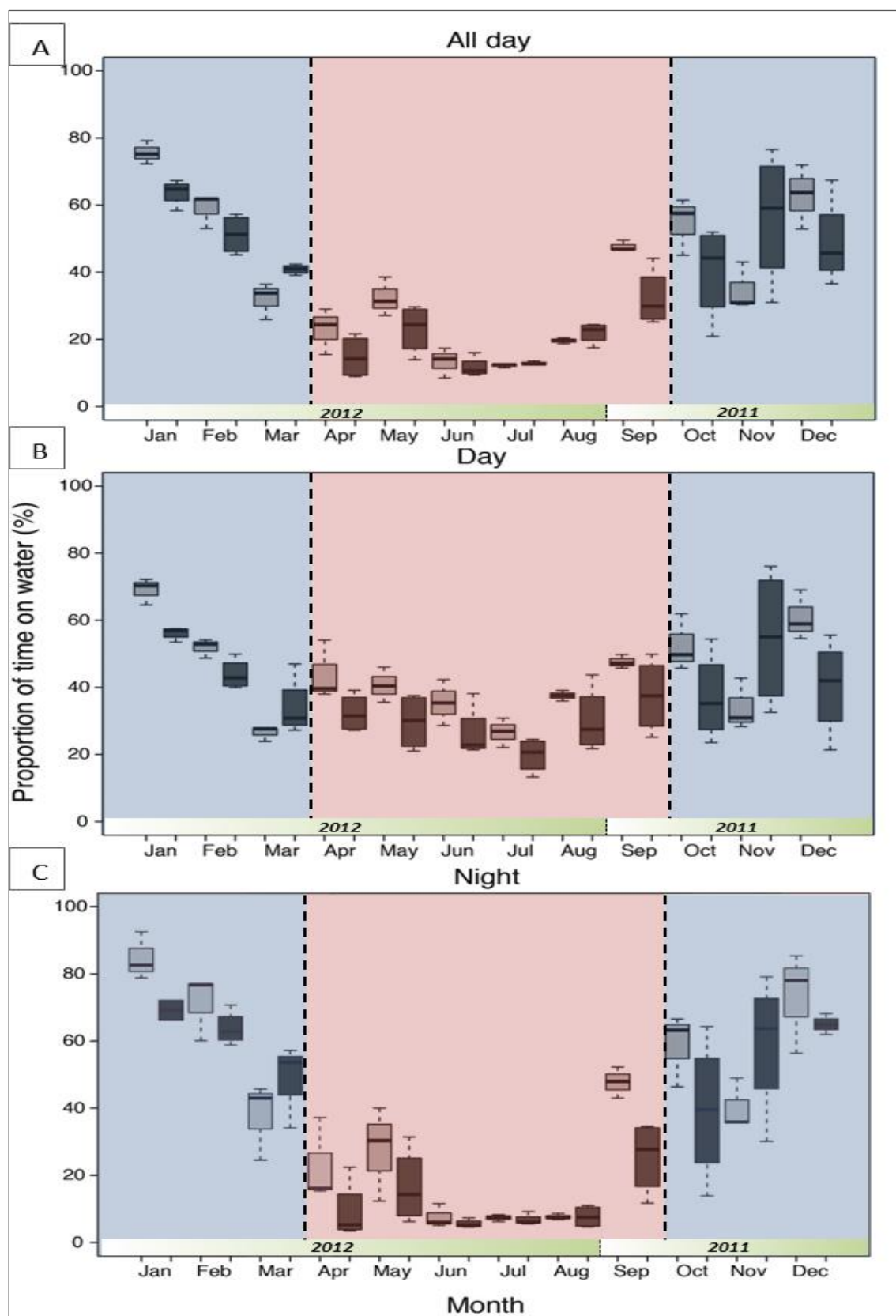
Figure 9 – Differences in proportion of time spent in water (A), daily (24h), (B) daytime and (C) night-time between experienced (light grey) and inexperienced (dark grey) Cory's Shearwaters. Blue shading represents non-breeding period, while red shading represents the breeding season.

3.3   Stable isotope analysis

Results from stable isotope analysis for $\delta^{15}C$ (Fig. 10) showed that significant differences in foraging location between Cory's shearwaters with different experience levels occurred during the wintering period (S8: $F_{1,12} = 6.7$, $P = 0.02$). During the breeding season, there was no evident differences in isotopic signatures between experienced and inexperienced individuals (P1: $F_{1,12} = 2.3$, $P = 0.15$). There was also a significant difference in the isotopic signatures representing the overall picture for the non-breeding period (Breast: $F_{1,12} = 9.74$, $P = 0.008$).

Figure 10 – Stable isotope analysis for $\delta^{15}C$ in sampled feathers of Cory's Shearwaters from Berlenga Island. The plots show the result variation between experienced and inexperienced birds during breeding season, wintering period and as an overall non-breeding picture.

The analysis of δ^{15}N isotopic signature (Fig. 11) showed significant differences in trophic ecology between experienced and inexperienced birds during both breeding and wintering seasons (P1: $F_{1,12} = 11.9$, $P = 0.004$ and S8: $F_{1,12} = 6.22$, $P = 0.028$, respectively). No significant differences were found in the δ^{15}N isotopic signature representing the overall picture for the non-breeding period (Breast: $F_{1,12} = 2.54$, $P = 0.13$).
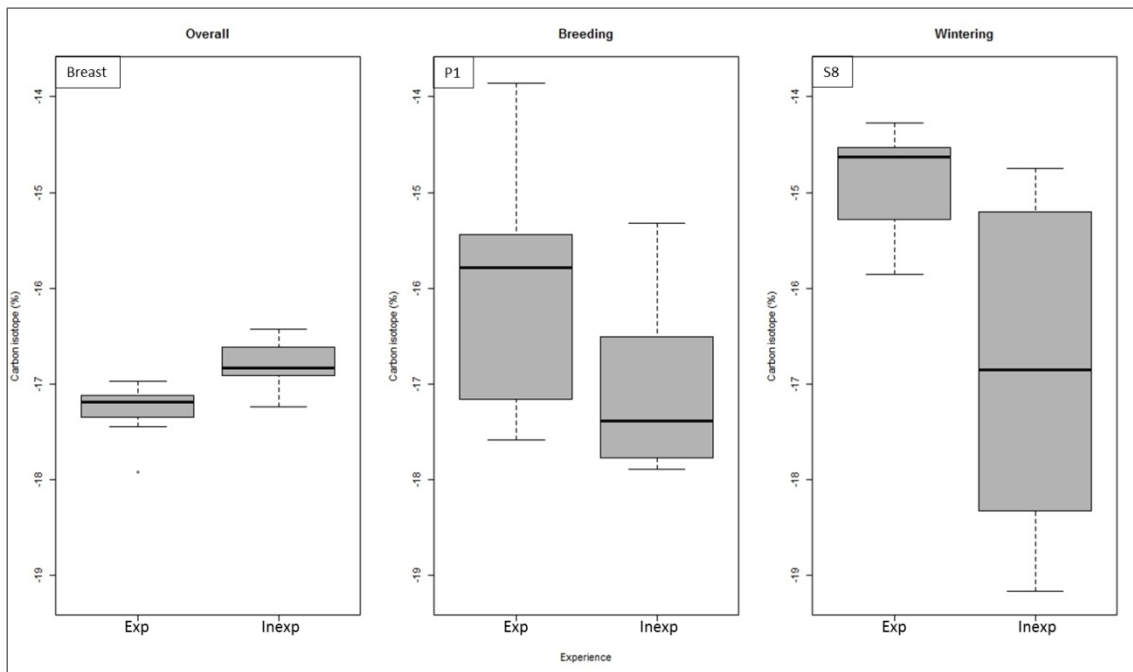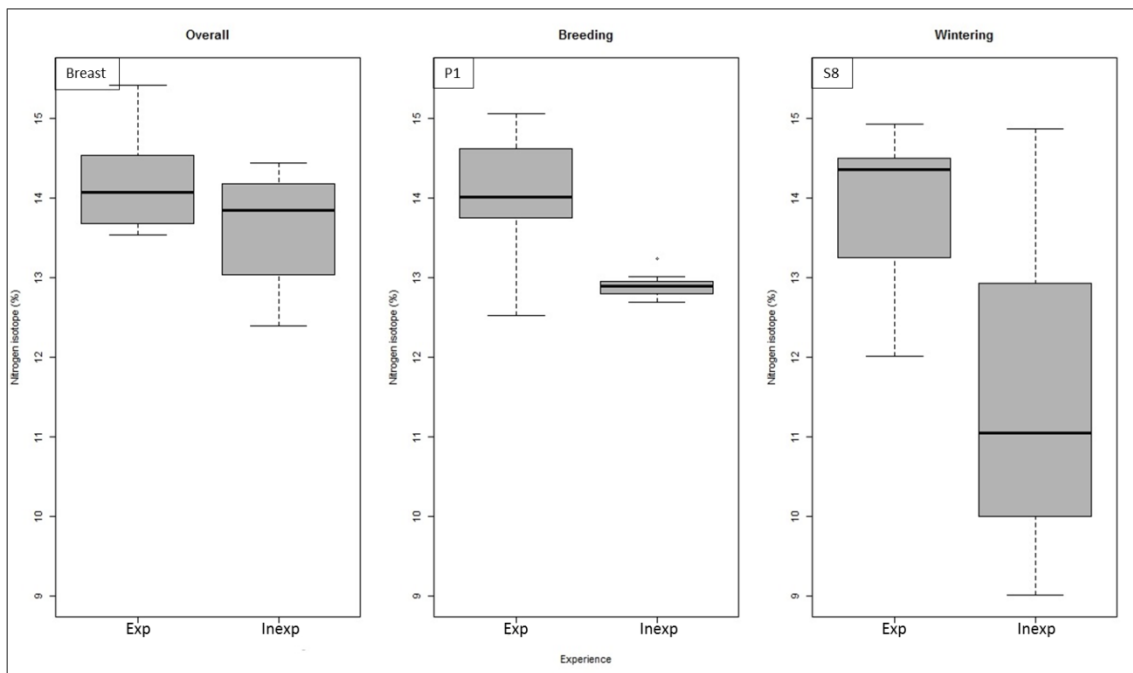

Figure 11 – Stable isotope analysis for δ^{15}N in sampled feathers from Cory's Shearwaters from Berlenga Island. The plots show the results variation between experienced and inexperienced birds during breeding season, wintering period and as an overall non-breeding picture.

Results from the Stable Isotope Bayesian Ellipses (S.I.B.E.R.) showed a considerable variation between seasons (Fig. 12). During the breeding period (P1), experienced birds occupied a higher trophic niche when compared with inexperienced ones, and were also marginally less pelagic regarding foraging range (i.e. lower carbon isotope value). The isotopic niche area did not overlap and the Standard Ellipse Area (SEAc) indicates a significantly higher niche area for experienced birds (SEAc = 4.14), than inexperienced ones (SEAc = 0.67). Results of the wintering season analysis (S8) indicate the permanence of experienced birds in a higher isotopic niche, while presenting even lower pelagic activity. However, the isotopic niche area of the same group was significantly smaller (SEAc = 2.07) when compared with inexperienced birds (SEAc = 15.12), with a small overlap between them. The overall analysis (Breast) showed a similar trophic niche area for both groups (Experienced: SEAc = 0.59, Inexperienced: SEAc = 0.75), and a pelagic profile more insinuated for experienced birds.

Figure 12 – A) Isotopic niches for different experience levels of Cory's Shearwaters from Berlenga Island (Inexp = inexperienced, Exp = experienced), represented in Bayesian Ellipses for overall non-breeding period (Breast), breeding season (P1) and wintering (S8). B) Standard ellipse areas (SEAc) for corresponding periods.
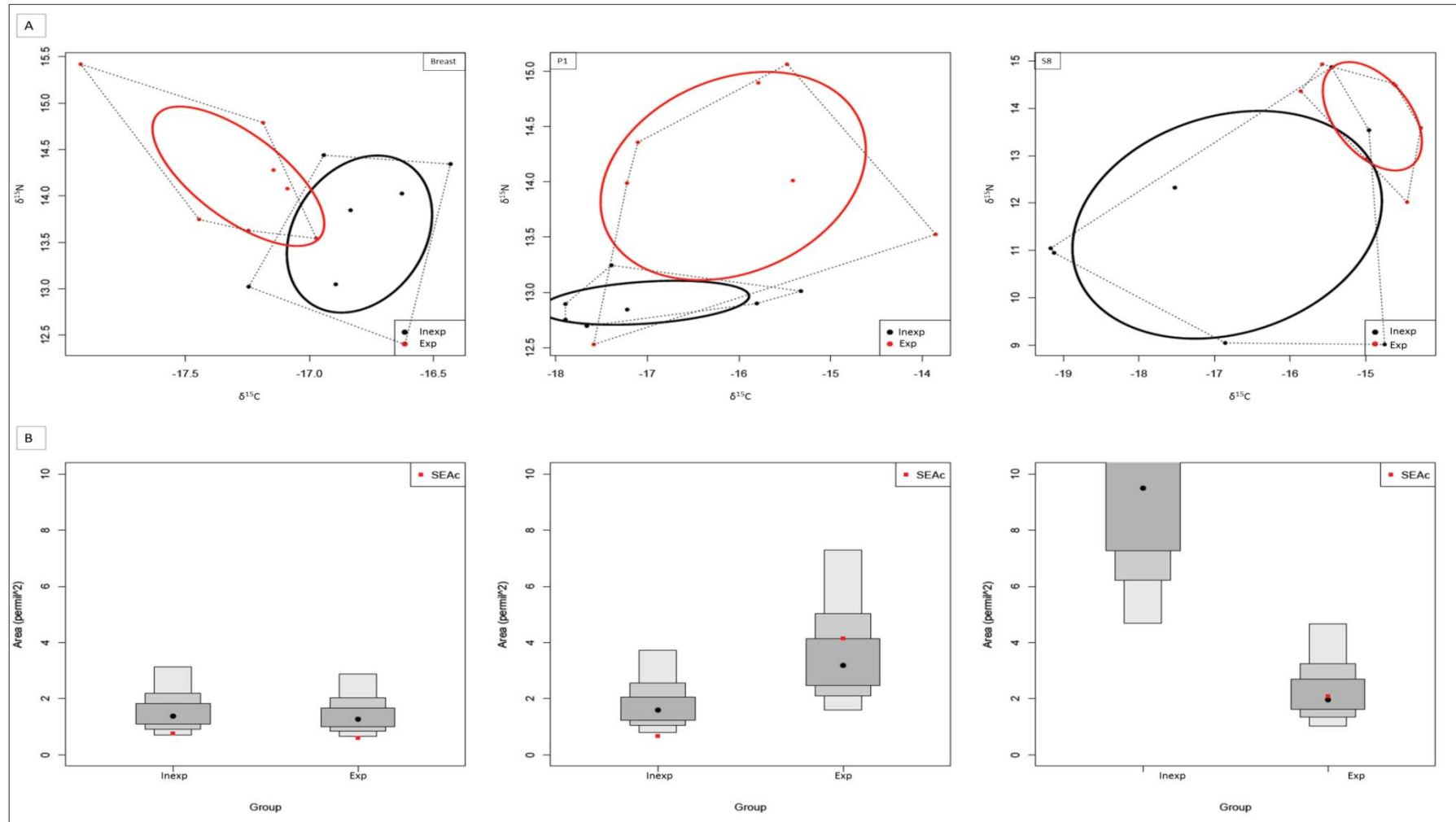
3.4   Species distribution modelling

MaxEnt results showed a well fitted model for both groups of birds, reaching high values of confidence expressed by AUC values (Experienced: AUC = 0.933, Inexperienced: AUC = 0.885). Distance to land and sea surface temperature (SST-winter) were the most important variables differentiating between the distribution of experienced and inexperienced birds, supporting respectively the coastal foraging and trophic niche suggested by stable isotope analysis. Maximum photosynthetically available radiation (PAR-max) also showed considerable influence on the model, but with a reduced permutation importance value. The distribution of inexperienced birds was mainly influenced by wind direction and speed (Wind-winter), sea surface temperature (SST-winter) and dissolved O_2.

Experienced			Inexperienced		
Variable	Contr. (%)	Perm. Importance (%)	Variable	Contr. (%)	Perm. Importance (%)
Dist. Land	17.5	33	Wind-winter	16.6	11.4
PAR-max	16.4	6.1	SST-winter	15.2	11.3
SST-winter	11.7	21.4	Dissolved O_2	12.4	4.6
Silicate	11	11.1	Cloud Fr-mean	7.9	7.4
Dissolved O_2	10.8	0.6	Chlo A-range	7.8	1.2
Salinity	9.8	7.1	pH	6.6	3.9
SST-range	4.6	2.6	Nitrate	5.9	8.6
SST-min	3.6	3.1	PAR-max	4.8	12.7
Wind-winter	3.1	1.4	PAR-mean	4.2	13.3
PAR-mean	2.9	2.2	Silicate	4	8.1
Chlo A-min	2.8	0	Dist. Land	3.2	2.4
Cloud Fr-max	1.9	2.5	Cloud Fr-min	2.7	2.6
Nitrate	0.9	1.2	Salinity	2.4	3.2
pH	0.8	0.8	SST-range	1.6	0.6
SST-mean	0.8	1.8	Chlo A-min	1	2.8

Table 4 – Relative contribution and permutation importance of environmental variables applied to MaxEnt model for experienced (left) and inexperienced birds (right). The table is color-coded as it follows: White = <5%, Green = 5 – 10%, Yellow = 10 – 20%, Orange = 20 – 30%, Red = >30%.

Future predictions of spatial distribution of Cory's Shearwaters were made considering variations restricted to the sea surface temperature (SST), with scaling based on the A2 scenario from IPCC. The resulting model suggests the occurrence of a poleward shift caused by the proposed increase on sea surface temperature, and shows the consequent differences in the spatial distribution of experienced and inexperienced birds (Fig. 13).

Within the first 10 years, populations would move away from their known habitats and into previously unexplored, more pelagic areas. Experienced birds would start to make use of South Atlantic pelagic areas, while inexperienced birds would spread towards the Arctic Circle. In 50 years, experienced birds would reach the both the Arctic and Antarctic Circle, while inexperienced birds would essentially be distributed throughout the whole North and South Atlantic oceans, including both Polar Circles and the Mediterranean Sea. From this point, up to 100 years in the future, the variations on spatial distribution shift would continue to be intensified.
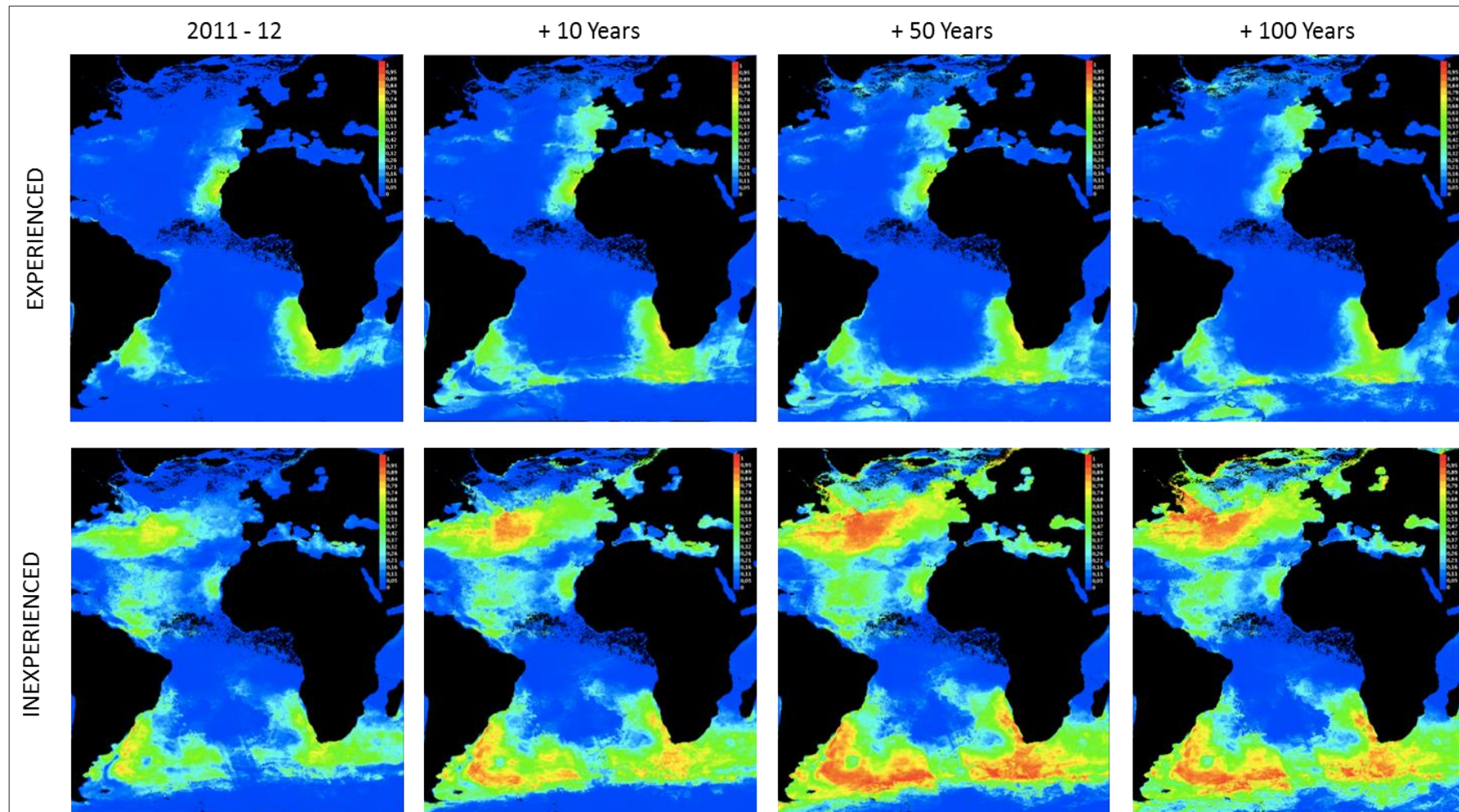
Figure 13 – Present and future foraging distribution of Cory's Shearwaters from Berlenga Island, based on the A2 scenario from the International Panel on Climate Change.

Chapter 4 – Discussion

4.1   Migratory profile of experienced and inexperienced birds

There was a clear difference on the migratory profile presented by experienced and inexperienced birds regarding their outgoing route and wintering grounds. Inexperienced birds wintering routes were marked by large detours and stopovers in foraging areas located in Newfoundland, North of Brazil and South Atlantic. Following the same tendency, wintering grounds of inexperienced birds also varied, and were sometimes located in different hemispheres (e.g. birds 5 and 6). In comparison, experienced birds showed a considerable uniformity in their migratory profile, with straightforward routes and less variation in their migratory grounds.

Both the flexibility and fidelity of Cory's Shearwaters to wintering areas have been analyzed before (e.g. Dias et al., 2010), showing that individuals can shift their routes, stopover areas and wintering destinations between years. Normally, the areas used as stopovers are of high productivity, and may have been chosen as wintering grounds in previous migrations. However, the relation between wintering flexibility/fidelity and the experience level of the birds has not been fully explored, and the spatial variation encountered between the groups is commonly (and correctly) attributed to differences in environmental predictors such as sea-surface temperature and marine productivity, or even morphological differences between populations separated geographically (e.g. Catry et al., 2011).

Our results indicate the existence of another plausible explanatory factor, related with the experience levels of each bird. It is known that young Cory's Shearwaters (non-breeders) spend most of the time at the sea, as many other species of seabirds (Warham, 1996). During this period, young birds can gather information on the conditions and foraging opportunities of different sites, gradually building a

"knowledge base" for migratory destinations and even establishing one (or several) "preferred" migratory strategies (Dias et al., 2010). Even though the inexperienced birds tracked in this study were already in reproductive age, the suggested learning period is still apparent in their migratory profile, and might continue to exercise influence as they make the transition into experienced breeders.

Previous studies showed that wind parameters may have a significant local-scale influence on foraging strategies of seabirds, as well as on the choice of migratory routes for wintering areas (Weimerskirch et al., 2005, González-Solís et al., 2009, Paiva et al., 2010d, Soares, 2013). Wind currents flow clockwise in the Northern hemisphere and counter-clockwise in the Southern hemisphere, leading researchers to hypothesize a figure-eight migratory route for other shearwater species (Warham, 1996, González-Solís et al., 2007). This premise can be supported by our study, since some of the tracked individuals presented a migratory route that resembles the proposed eight-figure (birds 1, 3, 11 and 12). The results of habitat modelling (i.e. MaxEnt results) determined the wind speed during winter as the primary environmental predictor influencing the distribution of inexperienced birds, supporting the role of experience level in the migratory profile of Cory's Shearwaters even further, since the effective use of wind currents can enable and/or facilitate the exploratory behavior of birds during their early years and through the first breeding seasons.

As more successful breeders, experienced birds tend to leave the colony at later dates, after the chick-rearing period, while inexperienced – and most likely unsuccessful – breeders leave at early dates. This gives inexperienced birds the extra amount of time to explore different foraging areas, unlike experienced birds, that must adopt direct migratory routes to wintering grounds, essentially compensating for the time invested in a successful breeding. The straightforward migratory profile presented by experienced

birds can also be related to the gradual gathering of information on the conditions and foraging opportunities of different sites. Experienced birds may possess established or "preferred" migratory strategies, chosen based on early exploratory years, and correlated with the overall foraging potential of the wintering grounds in question. Therefore, experienced birds proved to be less exploratory and less pelagic than inexperienced ones, foraging in coastal areas, closer to land. This characteristic was also supported by the habitat modelling analysis, which showed the distance to land as the primary variable determining the distribution of experienced Cory's Shearwaters during wintering period. As expected, wind parameters scored low values for explaining the distribution of experienced birds, when compared with distance to land (3.1% and 17.5%, respectively).

The migratory schedule of the tracked birds covered a large time-span, with timing between individuals ranging from a few days to months of difference in certain occasions. Differences in migratory schedule of seabirds have been found to exist between individuals of a same population and between populations of different breeding colonies (e.g. Kubetzki et al., 2009), with the same phenomenon being also described in Cory's Shearwaters (e.g. Catry et al., 2011). Most of these differences are attributed to factors like geographical location, variations in the morphology and taxonomy of each bird or population. Individual success (or failure) in a given breeding attempt could also act as a determinant, since unsuccessful breeders don't have to provide for their offspring, and can leave the colony at earlier dates. However, no clear correlations between migratory schedule and experience level have been identified in previous studies, and our analysis supports this premise, since, despite individual variance, no significant differences were found on the migratory schedule of experienced and inexperienced individuals.

As mentioned above, the choice of wintering grounds is closely related to the foraging potential of different areas, which can be influenced by certain environmental variables like primary productivity, bathymetry and sea-surface temperature. Despite the high variability on the migratory profiles of inexperienced birds, the general picture showed that two areas were most sought after as wintering grounds by the whole group: South of Brazil, influenced by the Southern branch of the Brazil Current (4 birds) and South Africa, influenced by the Benguela and Agulhas Current (7 birds). These areas are known for being associated with major upwelling phenomena, presenting high chlorophyll -*a* concentrations and high rates of primary production (Longhurst, 1998, Camphuysen and Van der Meer, 2001, González-Solís et al., 2007, Paiva et al., 2010a.), and provide high quality foraging grounds for several seabirds and other marine animals. The fact that none of these areas were exclusive to either experienced or inexperienced individuals indicates that, even though the choice of migratory routes can be affected by different experience levels, its influence on the final destination of each bird is most likely reduced.

The effects of different migratory strategies are a topic of discussion, being generally correlated with resource availability or levels of intra and inter-specific competition (Lewis et al., 2001, Dias et al., 2010, Catry et al., 2011). The results for Kernel utilization distribution showed a clear segregation between experienced and inexperienced birds throughout the year, which fits into a possible scenario where the intra-specific competition in the species would be attenuated. However, the nature of the data collected in this study prevents further analysis on the subject, as any assumptions regarding the reduction of inter-specific competition or the magnitude of such effects require a more detailed and localized monitoring.

4.2   Activity levels

The daily activity levels showed by the fourteen individuals throughout the year follow general predictions of activity for seabirds. This means that, as a whole, the birds spent more time in the water during the non-breeding season (from September to March), when they are free of the highly demanding breeding constraints (e.g. providing for the chicks). The lack of these breeding constraints allows the birds to spend more time resting on the surface of the water, and likely foraging through the 'sit-and-wait' technique (Schreiber and Burger, 2001), essentially recovering from the energetically expensive events that took place in the previous months, such as migration and breeding (in the case of the successful breeders). Recently, a lot of interest has arisen on the possibility that events happening during the non-breeding season could affect the condition and performance of individuals during the breeding period, the "carry-over effect" (Catry et al., 2011). Considering this possibility, the high amount of time spent in the water showed by the experienced birds during the non-breeding season might reflect positively on their reproductive success, since the low activity levels allows them to efficiently replenish any spent nutritional reserves, in preparation for the energetically demanding upcoming months.

Still considering the whole group, results showed clear variation between daily and nocturnal activity levels. During the breeding season, activity levels were lower during the day, when the birds were foraging and providing not only for the chicks, but also for themselves. During the night, the proportion of time spent in the water was very low, which might induce the conclusion of high activity levels. However, these values are in fact the reflection of the nesting behaviour presented by the adults during the night period (Warham, 1996), and do not represent any activity parameters. Interestingly enough, these trends were inverted during the migration and wintering

periods, with birds spending more time in the water during the night. Even though the activity data collected is not detailed enough to specify the type of behaviour performed in the water, the possibilities are not many, being mostly limited to either foraging or resting on the water surface. Previous studies have shown that seabirds tend to fly and hunt for prey during the day, and spend part of the night resting on the sea surface (e.g. Garthe et al., 1999, Weimerskirch and Guionnet, 2002, Catry et al., 2004a), a pattern that should be considered as the most probable for the studied individuals. Nevertheless, nocturnal foraging should not be excluded as a possibility, since some species of petrels and shearwaters are known for hunting prey in the dark, taking advantage of the moonlight and of vertical migration performed by some fish species (Ballance and Pitman, 1999, Mougeot and Bretagnolle, 2000). This is a difficult premise to confirm, however, and any correlations between nocturnal activity and foraging should be handled carefully.

The activity data also showed a considerable difference between the activity levels of experienced and inexperienced birds, with experienced individuals spending more time in the water throughout the day (and night) than inexperienced ones. This trend was found in almost every month (the only exceptions being November and March), happening equally in both breeding and wintering periods. To explain this pattern, it is important to take into account the different migratory strategies of experienced and inexperienced Cory's Shearwaters (section 4.1), which suggests the possibility of an exploratory period occurring during the first years of life of any given bird, adding to the gradual increase of their knowledge regarding the best wintering grounds (i.e. with higher foraging potential). In this case, the differences in activity found between experienced and inexperienced individuals could be explained by the combination of two factors: 1) The already established, high-productivity wintering

grounds and foraging areas of experienced birds, which allows them to spend less time flying and foraging (i.e. essentially out of the water). 2) The increased exploratory behaviour (and consequently, flight time) of inexperienced individuals, which reduces the amount of time spent on the water surface. It is important to highlight that, despite being largely based on the migratory behaviour of each group during the non-breeding period, this reasoning might be also validated during the breeding season. In a previous study, Haug (2012) analyzed the differences on foraging strategies of Cory's Shearwaters belonging to the same colony in Berlenga Island during the breeding period, and reported a general tendency for longer foraging trips performed by inexperienced birds (in both distance and time), while experienced birds tended to forage in more coastal areas, therefore flying for shorter distances. This type of variation could be compared to the one found during the migratory events of the non-breeding period, when experienced birds migrate using straightforward, shorter routes and inexperienced birds migrate following longer paths, with many stopover areas, and allow us to draw a correlation between activity levels and experience, focused in a smaller scale.

Even though results indicate a general correlation between total activity and foraging/migratory behaviour, the data pool used is still small and restricted to a short span of time. The continuous monitoring of the group, along with analysis of future patterns presented by birds with different experience levels might improve the applicability and confidence of such trends.

4.3   Comparison of foraging ecology related to experience

The analysis of different foraging strategies presented by experienced and inexperienced seabirds became more important in recent years, but few studies actually tackled the problem with solid supporting data. In our study, the results found by the stable isotope analysis showed significant differences on the foraging ecology of experienced and inexperienced individuals. When focused into a specific time period, results from the Carbon isotope analysis indicates that experienced birds forage closer to land during both breeding and wintering seasons, while inexperienced birds tend to forage in more pelagic areas. These results support the conclusions made based on tracking and activity patterns, and fall into accord with data from isotopic analyses realized during the breeding season of Cory's Shearwaters in Berlenga Island by Haug (2012).

As showed above, the role of experience on the migratory behaviour and activity of Cory's Shearwaters was significant, making it easy to establish a connection between isotopic profile and experience levels. However, other factors might influence the segregation found within the group, such as environmental conditions and the individual history of each bird. Previous research on Black Browed Albatrosses (*Talassarche melanophrys*) showed that environmental variations may mask any age or experience-related differences in demographic traits, shifting the spatial distribution and even causing fluctuations on the survival rates and breeding success of both experienced and inexperienced birds (Nevaux et al., 2007), with similar patterns being found in other species of seabirds like Great Skuas (*Catharacta skua*, Ratcliffe et al., 1998) and Blue Petrels (*Halobaena caerulea*, Barbraud and Weimerskirch, 2005). Results from the habitat modelling analysis (MaxEnt) performed during this study are correlated to this premise, showing that environmental variables affected the distribution of the tracked

birds during the year (see Table 4). Therefore, even though our results from the isotopic analyses may support the experience-related foraging segregation in Cory's Shearwaters, they should not be considered an exclusive influencing factor, but part of much more complex group of variables.

Considering the Carbon signatures, an interesting variation was expressed in breast feathers, which showed an inversion of the foraging pattern found in the signature of other sampled tissues, and classified experienced birds as being more pelagic than inexperienced ones. The reasoning for the analysis of breast feathers is based on the fact that, since moulting happens continuously during the non-breeding season, these feathers may be considered a more homogeneous sample, showing an overall picture of the foraging behaviour during the period, instead of focusing on a specific time (Ceia et al., 2013). However, the results of this analysis contradict the premises regarding the experience-related foraging differences on the species, and might indicate that, under this context, breast feathers are not as effective as a tissue sample for Carbon isotope analyses when compared with primary or secondary feathers (which isotopic signature can be more accurately delimited in time). The continuity of this type of monitoring could help elucidate the validity of breast feathers as sampling tissue in studies comparing the behavioural differences between experienced and inexperienced birds.

Results from Nitrogen stable isotope analysis indicate that experienced birds forage on higher trophic level prey than inexperienced ones during both breeding and wintering seasons, while the latter hunted for prey located on lower levels of the food chain. Similar results were found by Haug (2012), but were focused on the breeding season of individuals breeding in the same colony were this study was carried out, not showing any data on the non-breeding period. Still on the same study, Haug suggests

that the diet of inexperienced individuals can become gradually similar to those presented by experienced birds in consecutive seasons, hinting at the possible learning process suggested by Dias (2010).

The S.I.B.E.R. analysis also showed interesting results regarding the isotopic niche areas for birds of different experience levels. During the breeding season, experienced birds possessed a much larger niche area than inexperienced ones, while during the wintering period, the situation was reversed. This phenomenon might be related to the different migratory profiles presented by the groups, since, for being significantly more exploratory and pelagic during the non-breeding season (refer to section 4.1), inexperienced birds would have the opportunity to forage in several different areas, sometimes separated by thousands of kilometers, and inhabited by different kinds of prey. The breeding site fidelity presented by the species would mitigate this situation, overlapping the foraging area of experienced and inexperienced birds into a much more restricted area, where the constant variety of prey might benefit individuals with more developed foraging strategies (i.e. experience) and effectively reducing the isotopic niche area of inexperienced birds.

4.4   Future scenarios

Much has been discussed regarding the impact of climate change on the distribution of seabirds. The general consensus points towards the prejudicial effects and fluctuations of highly influential environmental predictors, like sea surface temperature, dissolved oxygen and productivity rates (Schreiber and Burger, 2001, Irons et al., 2008). To verify this hypothesis, we performed a modelling exercise on the MaxEnt platform, considering a possible temperature increase of 0.18°C per decade for the next 100 years, the A2 scenario proposed by the IPCC (one of the more conservative

scenarios of future climate change). The results suggest that changes in the environment after the first decade should cause an increase on the global spatial distribution of Cory's Shearwaters, with experienced and inexperienced birds foraging in areas previously ignored. In a recent study, Péron (2012) analyzed the foraging distribution of King Penguins (*Aptenodytes patagonicus*), highlighting the influence of increases on sea surface temperature. In this case, temperature increase acted as one of the main drivers of foraging distribution on the species, inducing birds to search for resources in higher latitudes, which characterizes a poleward shift scenario. It is not unreasonable to consider the possibility of a similar scenario occurring in Cory's Shearwaters, since sea surface temperature (SST) was considered one of the three most influential environmental predictors affecting the spatial distribution of both experienced and inexperienced individuals (Table 4).

Considering the inherent differences in distribution and migratory behavior presented by birds with different levels of experience throughout the year, we can also assume that experienced birds would be more affected by shifts in distribution than inexperienced ones, since these birds already engage in migratory events that takes them to more pelagic areas. Therefore, the close relation found between the distribution of experienced birds and distance to land suggests that the expansion of their foraging grounds could greatly affect their foraging success, along with any other consequently related aspect, like survival rates and breeding success. Many reasons could be responsible for this, including: 1) The increase of intra and inter-specific competition for resources, resulting from the probable overlap with foraging grounds typical of other marine animals, especially in the South Atlantic and Arctic and Antarctic Circles. 2) The necessity of feeding in areas with low foraging potential, due to unfavorable environmental conditions or other productivity issues. 3) The increased energetic cost of

longer foraging trips, which would not be effectively compensated due to the low prey availability. 4) The increased distance between the foraging grounds and breeding colony during the breeding period, potentially reducing the breeding success of this population.

It is important to notice that, even though the modelled distribution is based around conservative, albeit solid projections for temperature increase, the final scenario loses reliability proportional to the number of years predicted. Also, previous studies showed that Cory's Shearwaters present a remarkable foraging plasticity, and may be among the species of seabirds better adapted to endure climatic variations (Dias et al., 2010, Paiva et al., 2010a). Because of these factors, and taking into account the nature of data collected in this study, the final distributions projected should be considered mere guidelines for future projects, instead of an established trend for this population. Further monitoring might provide the necessary data to build a more solid model for the species.

4.5   Conclusions

This study provided significant insights regarding the effects of different experience levels on the spatial distribution and foraging ecology of Cory's Shearwaters during both breeding and wintering seasons. Inexperienced individuals presented a much more pelagic behaviour than experienced ones, with an annual spatial distribution marked by long migratory processes, several wintering grounds, and feeding strategy based on prey located on lower trophic levels. Experienced individuals yearly distribution was based mainly around coastal areas, with straightforward migratory routes, few foraging areas, and diet based on higher trophic level prey. Modelling exercises added valuable information to these results, identifying the main environmental variables responsible for the differences found. These factors allow us to conclude that experience plays an important role determining the occurrence of spatial segregation in the species, showing it as a trait that should not be considered by itself, but added to a much bigger pool of influencing factors. Furthermore, this study allowed us a glimpse of what might be the gradual learning of foraging strategies in inexperienced Cory's Shearwaters, along with the supposed effects of this period of foraging behaviour of the group.

Modelling predictions showed us that climate change might have a significant influence on the spatial distribution of the species, exercising greater influence on experienced individuals. Nevertheless, the true effects of such large-scale events cannot be calculated with high precision, making the continuity of populational and environmental studies even more important for the conservation of this and other marine taxa.

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