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DEPARTAMENTO DE CIÊNCIAS DA VIDA

FACULDADE DE CIÊNCIAS E TECNOLOGIA
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The role of breeding experience on the foraging specialization of a pelagic marine predator, the Cory's shearwater



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Dissertação apresentada à Universidade de Coimbra para cumprimento dos requisitos necessários à obtenção do grau de Mestre em Ecologia, realizada sob a orientação científica do Doutor Vitor Paiva (Universidade de Coimbra) e do Professor Doutor Jaime Ramos (Universidade de Coimbra)

Fredrik Duvholt Haug

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Abstract

Experience is believed to be an important factor determining the foraging success of animals, but there are still very few studies investigating how foraging abilities develop over time. In this study, the spatial distribution and foraging tactics of inexperienced and experienced individuals of a Procellariiform seabird species, the Cory's shearwater (*Calonectris diomedea borealis*) breeding on the Portuguese continental shelf was compared. Kernel analysis and a multivariate analysis (MADIFA) showed that while the experienced birds were relying on known static features such as the bathymetry of the area, inexperienced birds were using larger areas that were explained by different static and dynamic variables each year. The foraging areas of the two groups overlapped less and less for each year, while stable isotope signatures were becoming more and more similar, as inexperienced birds were foraging on higher trophic prey closer to the coast, like the experienced birds. Linear mixed models comparing home ranges and foraging areas calculated for each group showed that the experienced birds were in general more successful in detecting favourable foraging grounds, except in 2011, when the results showed the opposite. Interestingly, the reproductive success of the inexperienced birds was significantly higher than for experienced birds during that season.

Resumo

A experiência é considerada um factor importante para o sucesso de procura de alimento dos animais, mas há ainda muito poucos estudos que investiguem como as habilidades de procura de alimento se desenvolvem ao longo do tempo. Neste estudo, foi comparada a distribuição espacial e as tácticas de procura de alimento de indivíduos experientes e inexperientes de uma espécie de Procellariiforme, a cagarra (*Calonectris diomedea borealis*), cuja população se reproduz na plataforma continental Portuguesa. A análise de Kernel e uma análise multivariada (MADIFA) mostrou que, enquanto as aves experientes dependiam de variáveis estáticas, tais como a batimetria da área, as aves inexperientes utilizaram áreas mais vastas respondendo em cada ano, a diferentes variáveis estáticas e dinâmicas. Os modelos lineares mistos comparando as características de habitat nas áreas de utilização com as áreas de procura de alimento entre ambos os grupos, mostraram que geralmente as aves experientes têm mais sucesso na detecção de locais de procura de alimento mais favoráveis, excepto em 2011, quando os resultados mostraram o oposto. Curiosamente, o sucesso reproductor das aves inexperientes nesse ano foi superior aquele das aves experientes.

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Chapter 1

Introduction

1.1 – Spatial ecology

One of the central questions in ecology concerns to how animals exploit their environment, namely which food they consume and what habitats they occupy (Johnson 1980). Sound management and conservation of animal populations depends on an understanding of where animals are, why they are there and where else they could be (Aarts et al. 2008). Marine ecosystems are highly heterogeneous environments in which productivity is controlled by physical features and processes (Stommel 1963, Haury et al. 1978). Our knowledge of the major energy fluxes in these systems has been lagging behind compared to that of terrestrial environments (Greenwood 1992, Mann & Lazier 2006), particularly with regards to the upper trophic levels (Larkin 1996). Seabirds are apex predators which feed on prey from several levels of the marine food web (Cury et al. 2011). As in most ecological systems, their prey is distributed in an hierarchical patch structure, in which high density patches at small scales are nested within low-density patches at larger scales (Kotliar & Wiens 1990). This is because oceanographic processes are tied to diel, seasonal and decadal cycles which concentrate prey at a large variety of scales (Weimerskirch 2007, González-Solís & Shaffer 2009). According to optimal foraging theory, there should be a strong evolutionary pressure on animals to adapt foraging tactics to cope with this patchiness (MacArthur & Pianka 1966, Stephens & Krebs 1986). In such a system, a forager should track the spatial distribution of the resource towards the small scale end of the system, until finding a medium-scale patch, then search for small-scale patches by increasing turning rate (Fauchald 1999, Fauchald et al. 2000). For this reason, studies that analyse seabird's interactions with habitats should be conducted at the appropriate scale (Wiens 1989, Fauchald & Tverraa 2003), although this is still often ignored (Ballance et al. 2006). In a review of scale-

Fredrik Haug (2012) Breeding experience and foraging specialization of a marine predator dependent oceanographic processes on seabirds, Hunt & Schneider (1987) suggested that ornithologists should distinguish between macro- (1000s km), meso- (100s of km), course- (1-100km) and fine scale (1-1000m) processes.

1.2 - Seabird ecology

Seabird ecology has historically been investigated from land (Ashmole 1971), as most species breed in colonies and are easily manipulated (Wilson et al. 2002). This is even true for distribution studies, where ranges have been calculated from known flight speeds and periods of absence from the breeding colony (Warham 1996); inferred from ingested prey with known distribution (Skira 1986) or assessed by dye-marking followed by at-sea observations (Weimerskirch et al. 1988). Recordings or surveys on board opportunistic or scientific vessel cruises have also provided insight into the at-sea behaviour and distribution of seabirds (Haney et al. 1985, Veit et al. 1993) and remain a key component of integrative studies today (Tremblay et al. 2009). There are however shortcomings and biases associated with vessel monitoring, including high costs, inability to distinguish breeding status, sex and even species (Grecian et al. 2012), and alteration of birds' normal behaviour due to the presence of the vessel (Tasker et al. 1984, Buckland et al. 1993). An alternative to distant observations became available with the advent of telemetry, and the opportunity to observe animal behaviour instantaneously (Ropert-Coudert & Wilson 2005). There has been a rapid evolution of ever smaller and more precise transmitters, and the early 1990s saw the first deployments of both VHF (Very High Frequency) transmitters (Anderson & Ricklefs 1987) and PTTs (Platform Terminal Transmitters) on seabirds (Strikwerda et al. 1986, Jouventin & Weimerskirch 1990). At this point in time, there are essentially five tracking technologies available, differing considerably in size,

precision and price, and here listed from the least to the most precise: VHF (see above); dead reckoning (Wilson et al. 1991, Benvenuti et al. 1998); GLS (Global Location Service) dataloggers (Wilson et al. 1992, Hill 1994); PTTs (see above) and GPS (Global Positioning System) loggers (Steiner et al. 2000, Weimerskirch et al. 2002). Each system has its use, e.g. dead-reckoning provides detailed data movements under water and is very useful for behavioural studies (Wilson et al. 2007); GLS-loggers are lightweight devices and helpful when studying small seabird species or for long-term attachments, while GPS-loggers with unmatched precision is currently the best technology for identifying key habitat areas. While PTTs provide instant access to the tracking data, at all over higher costs and weight, loggers (GPS, GLS and dead-reckoning) need to be retrieved, and thus involves a risk of losing data (see reviews on seabird telemetry technologies (Wilson et al. 2007, Burger & Shaffer 2008) for extended considerations). All tracking studies should control for adverse effects of the transmitter load and biases as recommended by Burger and Shaffer (2008). As a guideline, it is currently recognized that behavioural and fitness changes can be avoided by keeping the transmitter weight below 3% of the bird's body weight (Phillips et al. 2003), though this rule of thumb has recently been questioned (Barron et al. 2010, Kidawa et al. 2011, Vandenabeele et al. 2011), which further underscores the purpose of performing controls in any study.

1.3 - Biophysical variables

The rapid development within telemetry, coupled with increasing availability of remotely-sensed data, computation power and the sophistication of analytical methods (Ballance et al. 2006, Tremblay et al. 2009) has revolutionized the study of habitat selection (Boyce & McDonald 1999, Fauchald & Tverraa 2003). Evolving from

simple correlation testing between distributions and a few directly measured oceanographic variables, studies today typically incorporate a number of physical or biological 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).

There are a number of oceanographic features and processes known to congregate ocean productivity and seabirds, including upwelling zones associated with continental shelves (Louzao et al. 2006) or seamounts (Morato et al. 2008b); water mass properties like temperature (Paiva et al. 2010b) or salinity (Ainley et al. 2005); mesoscale processes like tidal currents (Becker et al. 1983, Hunt et al. 1998), eddies (Hyrenbach et al. 2006), fronts (Spear et al. 2001, Bost et al. 2009) and thermoclines (Navarro & González-Solís 2009); distance to shore (Briggs et al. 1987) or colony (Hunt Jr. 1997); and wind conditions (Garthe et al. 2009). Within this spectrum of variables it is yet hard to determine which are most important. At first glance it is natural to think that prey distribution need to be the key factor (Tremblay et al. 2009), while correlations with physical variables should be weaker, because they are only indirectly related to seabird abundance through their prey (Ballance et al. 2006). On the other hand, Grémillet et al. (2008) interestingly documented a mismatch between seabirds and their prey in one of the world's major upwelling areas, the Benguela current on the SW coast of Africa. Here seabird distributions matched more with an indirect variable, chlorophyll *a* concentration (chl *a*), than that of their prey: copepods and fish. Indeed, it is concluded by Tremblay et al. (2009) that the relative importance of variables depend on several factors, such as the species considered, sex, breeding status, locality and scale of the study. Most likely, Procellariiform birds take advantage of their dimethyl sulphide (DMS) olfactory

Fredrik Haug (2012) Breeding experience and foraging specialization of a marine predator capabilities in the search for beneficial areas like a frontal system on large scale (Nevitt 1999, Nevitt et al. 2002), then they might use visual cues to identify the edge of a mesoscale eddy, until looking for prey at smaller scales (Tremblay et al. 2009).

1.4 – Conservation impact

The marine environment is facing a variety of pressures from human activities such as fisheries, shipping, petroleum industry and development of marine renewables (Halpern et al. 2008, Thaxter et al. 2012). Overexploitation of fisheries precedes all other pervasive disturbances and has fundamentally altered much of our seas (Jackson et al. 2001, Game et al. 2009), including some of the most important coastal upwelling systems in the world (Coll et al. 2008). This realization stands in sharp contrast to the optimistic view on fisheries just two decades ago, where pollution was understood as the main concern in the oceans (Roberts et al. 2005). The increasing awareness of the current pressure has given rise to a collective effort among coastal nations and conservation bodies to develop a network of Marine Protected Areas (MPAs), which is intended to promote the recovery of collapsed stocks, but yet more importantly stop the loss of biodiversity (Kelleher 1999). The dynamic character of oceans poses a challenge for, and debate around, marine conservation. Thus, biological hot spots (Reid 1998) with concentrations of organisms are of particular interest in this conservation effort (Palacios et al. 2006, Trebilco et al. 2008).

Procellariiform seabirds occur in all oceans, are easy to monitor and highly sensitive components of the marine ecosystem (Weimerskirch et al. 2003), thus they are especially suited as bioindicators in this new process (Louzao et al. 2011). Guidelines for determining Marine Important Bird Areas (marine IBAs) have been established (Thaxter et al. 2012), and the IBAs are highly relevant areas for

Fredrik Haug (2012) Breeding experience and foraging specialization of a marine predator establishment of MPAs (Pedersen et al. 2009). In this context, intensive research effort have been carried out to determine key foraging areas of Cory's shearwaters in the Mediterranean and North Atlantic (Paiva et al. 2010c, Arcos et al. 2012), an umbrella species of the region with wide range and niche (Zacharias & Roff 2001).

1.5 - The foraging efficiency of experienced and inexperienced individuals

Although there has been a burst of studies focusing on seabirds during the last decades, the vast majority of this work has been focused on breeding individuals (Votier et al. 2011). This is both because breeders represent an important part of the population and are more likely to return to the colony, increasing the chances for logger retrieval. Thus, there is only sparse information available on habitat use and foraging behaviour of juveniles, immature birds and less-successful breeders (i.e. inexperienced birds; Wong et al. 2008). Seabirds are classic k-strategists with long life spans and an extensive period of immaturity (Burger & Shaffer 2008). As a result, the non-breeding part of the populations may comprise of up to 50 % of the adults (Klomp & Furness 1992), which make them important to consider for a number of reasons (Votier et al. 2011). Firstly, although they generally attend the colonies along with the breeders for most of the breeding season, inexperienced and failed breeders are not necessarily constrained as central place foragers with regular duties at the nest. Thus they may adapt a more explorative foraging tactic at sea and rely on different areas than the rest of the population. It is crucial to understand these intra-population differences better because less experienced birds, as future breeders, are important for population persistence (Votier et al. 2008). Typically, immature individuals also show higher dispersal rates compared with breeders (Huyvaert & Anderson 2004), and should have higher adaptive capacity towards climatic changes (Parmesan & Yohe

2003, IPCC 2007), because seabirds tend to breed in large numbers at relatively few and widely spaced locations (Kokko & López-Sepulcre 2006).

It is generally believed that the lower breeding success of younger birds is at least partially associated to lower foraging success (Forsslund & Pärt 1995), but there are very few studies which compare the foraging efficiency of experienced and inexperienced individuals (Weimerskirch et al. 2005). Some exceptions include the aforementioned study, which found that young, inexperienced wandering albatrosses (*Diomedae exulans*) actually had similar foraging success to that of experienced adults, but differed in their strategies. Inexperienced birds foraged more intensively and found more prey during the night. In another study by Bunce et al. (2005) on Australasian gannets (*Morus serrator*), it was interestingly found that inexperienced breeders had lower breeding success only when food availability was scarce, though this was not evident in a later and perhaps more detailed work on the same species (Pyk et al. 2007). In yet another study on gannets (*Morus bassanus*) breeding on the British Isles, Votier et al. (2011) found that immature birds can disperse widely, potentially exploring other colonies, but mainly acted as central place foragers performing commuting and looping trips. In contrast to the studies on *M. serrator*, they found a difference in diet between experienced and inexperienced *M. bassanus*, as indicated by results from stable isotope analysis.

In addition to identifying individual differences in foraging behaviour and habitat use, annual and inter-annual variation are current priority areas for research. Therefore, studies like that of Yamamoto et al. (2011) on streaked shearwaters (*Calonectris leucomelas*) breeding on islands in Japanese waters, which combine both individual and temporal variation, are very interesting. They revealed a seasonal shift

Fredrik Haug (2012) Breeding experience and foraging specialization of a marine predator in core feeding areas in association with a gradual increase in sea surface temperature (SST) and northward migration of the key prey items, but only by female birds.

1.6 – Study rationale

In this study we tracked Cory's shearwaters (*Calonectris diomedea borealis*) breeding on the Berlengas Islands in the North Atlantic, through three consecutive pre-breeding seasons, and analysed how at-sea distribution and behaviour of inexperienced breeders differ from that of experienced breeders. To my best knowledge, this is the most integrative study on the distribution of a pelagic seabird in the North Atlantic, incorporating both experienced and inexperienced breeders, along with several years of tracking data. Monitoring and research of seabirds at Berlengas is comparably extensive, and in this study we benefit from a completely ringed population and almost a decade-long recording of breeding success. The study aim was to test the following predictions: 1) inexperienced breeders exploit other areas at sea, and track environmental variables less efficiently than experienced breeders. This is expected because inexperienced individuals could have less knowledge of predictable foraging grounds, and perhaps also less ability to track environmental and biological clues. 2) Inexperienced breeders develop their foraging abilities over time and thus should demonstrate increasingly similar foraging patterns and trophic ecology to that of experienced breeders. More specifically, we defined home ranges and key foraging areas through kernel density estimation and assessed the degree of overlap between experienced and inexperienced birds. The affinity for environmental variables was estimated through a multi-model approach and analysed against reproductive success over time, to reveal potential individual progress. Only foraging behaviour of males during the pre-breeding season was used for the analysis. This

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should be ideal, because their foraging behaviour should not be dictated by egg-laying requisite, but solely for building their own energetic reserves in order to undertake the upcoming incubation shifts. Thus it was expected that their foraging choices and success should be dictated by their experience.

Finally, findings of this study may contribute to justify the Portuguese marine IBAs, by either confirming or revising the borders of the identified areas in the waters off the archipelago of Berlengas (Ramirez et al. 2008). It also may comment on the existing guidelines of the marine IBA inventory (Birdlife 2010). Therefore, these results should provide further insight for the recently legislated Special Protection Area (SPA) for the Berlengas region by the Portuguese government.



Cory's shearwater (*Calonectris diomedea boralis*) in flight.

Chapter 2

Methods

2.1 - Sampling design

Fieldwork was conducted on Berlenga Island (39°12'40''49N, 009°30'29''W), Portugal, during the pre-breeding period of Cory's shearwaters (April-May) along 2010, 2011 and 2012. Berlenga Island is the largest island (78.8 ha) of an archipelago that also comprises two groups of smaller islets, "Farilhões" and "Estelas". There are about 300 breeding pairs of Cory's shearwaters on the island (Lecoq 2010) along with immature birds and failed breeders. This study benefited from a long-term database of the breeding population, such that minimum age, sex and previous breeding experience were known for most of the individuals (Lecoq 2010). Cory's shearwaters at Berlengas are not wary of humans and were caught by hand at the burrows during night when they attend the colony to rest, socialize and defend their borrow (Warham 1996). Birds with less than two successful breeding attempts during the six year records were considered inexperienced, while the remaining birds were grouped as experienced. This distinction between inexperienced (≤ 2 years of breeding success) and experienced (> 2 successful years) individuals was based on the frequency distribution of the historical breeding success records for Berlenga.

2.2 - Oceanographic characteristics

Marine systems are classified into neritic zones on continental shelves and oceanic zones defined as beyond the 200 m depth isobaths (Hedgepeth 1957, Ladle & Whittaker 2011). The upper 200 m of the water column also defines the epipelagic zone, in the vertical division of the marine habitat (Mann & Lazier 2006). It is only here that primary production by oceanic phytoplankton can occur, as the light intensity is insufficient at further depths. Therefore it is also known as the photic

zone. Seabirds are constricted to prey available in this zone by their diving capabilities, and it must be considered while studying them (Paiva 2009).

The Berlengas archipelago is located on the Portuguese continental shelf, and the oceanography of the surrounding waters is largely influenced by its geographical position on the northern border of the subtropical anticyclone belt and on the eastern margin of a vast oceanic basin, the Atlantic (Queiroga 1996). Here, the wind regime is regulated by a seasonal migration of the subtropical front and the Azores high, whose centre shifts from 27°N in winter, to 33°N in summer (Queiroga 1996). As a result of this, the coast of Portugal typically experiences weak westerlies during winter and stronger northerlies during summer (Queiroga 1996). The increase in the northerly winds, called “the Portuguese trade winds”, induces offshore Ekman transport of near-surface waters, which is compensated by increased flow of bottom water across the shelf. This system, the Western Iberia Upwelling Ecosystem (WIUE), is a classical upwelling situation, and comprises the northern limit of the Canary Current Upwelling System (CanC), which extends further south along the coast of western Africa (Santos et al. 2007). As dictated by the wind seasonality, the upwelling season lasts from April to September, being more active and persistent between June and September (Fiúza 1982). The oceanography of the area is also influenced by considerable freshwater discharge from numerous rivers forming the Western Iberian Buoyant Plume (WIBP), which increases the productivity of the area (Arístegui et al. 2009).

The sardine (*Sardina pilchardus*) is the keystone fish species of the entire WIUE and CanC, well adapted to the upwelling regime (Roy et al. 1989) and of great socio-economical importance for Portugal, Morocco, Spain and France (Borges et al.

2003). The sardine spawning occurs during the winter, which normally secures larval retention by minimising the risk of offshore transport by the Ekman transport (Roy et al. 1989). Horse mackerel (*Trachurus trachurus*) is another important species in the region, sharing the same reproductive strategy. Seabirds such as the Cory's shearwater naturally benefit from the productivity as well, with neritic populations showing lower foraging effort compared to populations breeding in oceanic environments such as the Azores (Paiva et al. 2010a). But even though they benefit from the enhanced productivity of the neritic zone, with a foraging range of up to 2000 km, Cory's shearwaters are not constrained to the continental shelf (Paiva et al. 2010b). Individuals of the Berlengas population may explore lucrative feeding areas westwards towards the Azores islands and the Mid-Atlantic Ridge (MAR), attracted to enhanced productivity of fronts, seamounts and underwater ridges (Morato, Varkey, et al. 2008, Amorim et al. 2009). Thus, individuals from the Berlengas may also compete with congeners breeding on the Azores (Paiva et al. 2010c).

2.3 - Loggers: deployment & specifications

Cory's shearwaters were equipped with mini-GPS loggers (25 g; see Steiner et al. 2000 for original design), programmed to collect one location (± 4 m) every 5 min. The GPS loggers are ideal for this kind of study as they provide the greatest accuracy of records and sample positions at a much higher rate than, for instance, PTTs, thus providing high spatial resolution data for the habitat selection analysis (Hamer et al. 2007). The devices were attached to the birds' back feathers, using a small piece of Tesa tape[®] (Figure 1; Wilson et al. 1997). Attachments of tags took less than 10 min and birds were returned immediately to their nest, in order to minimize handling stress. Several studies have reported that there are no deleterious effects for birds

carrying loggers if they do not represent more than 3 % of the bird's body weight (Phillips et al. 2003), including the study species during short-term deployments (Igual et al. 2005). However, there is right to be concerned that this has become a uniform rule of thumb, and it is still important that proper controls are taken in each study (Baron et al. 2012). A thorough assessment of logger effect was performed on the study species at this colony in 2007 (Paiva et al. 2010a). No difference in body mass change or hatching success of birds that were deployed with loggers and a randomly selected subset without loggers was found. In this study, the birds were weighed after retrieval of the devices to continue this evaluation of possible deleterious logger effects. The body mass change is crucial, as the birds should be building up their fat reserves for the incubation period at this time. Birds were weighed in a bag using a Pesola[®] balance (± 20 g). Other biometric measures (wing length, tarsus length, head and bill, culmen, bill height at the gonys and height at the base of the bill) were also collected using dial callipers and a ruler. These measurements were used to determine the sex of birds that did not vocalise by a discriminant function developed by Granadeiro (1993).



Figure 1 – Photos of a GPS-logger deployed on the back feathers of a male Cory's shearwater.

2.4 – Environmental data

Chlorophyll-*a* concentration (CHL) and sea surface temperature (SST) data were downloaded from <http://oceanocolor.gsfc.nasa.gov/>, both downloaded as daily products with a resolution of 0.04° (approx. 4 km) in the SMI-HDF format (Table I). Estimations of SST during night-time was selected over day-time due to lower amplitude of variation of the water temperature and low cloud cover (Paiva et al. 2010b). Bathymetric data (BAT), taken as water depth, was downloaded from the ETOPO2v2 database at a spatial resolution of 0.033° (approx. 3km) and 8-day composites of primary productivity (PP) at a resolution of 0.04° data were both downloaded as ASC-files from the Bloomwatch website: <http://coastwatch.pfel.noaa.gov/coastwatch/CWBrowserWW180.jsp>. In order to work with the most current data from 2012, we downloaded all datasets at the lowest temporal resolution and then constructed monthly composites for the study periods during each of the years. HDF files were converted to raster using the Marine Geospatial Ecology Tools in ArcGIS 9.2, and then to ASCII to create composites. All composites were constructed using the freeware R software (version 2.14, R Development Core Team) and *mosaic* function of the *raster* package. Then the files were converted to raster using the *conversion* tool in ArcGIS 9.2. Spatial gradients of SST, CHL, PP and BAT were obtained by estimating the proportional change (PC) within a surrounding 3 × 3 cell grid using a moving window as follows: $PC = [(maximum\ value - minimum\ value) \times 100 / maximum\ value]$ (Louzao et al. 2006). Gradients of SST, CHL and PP (SSTG, CHLG, PPG) are believed to be good indicators of oceanic fronts, while the BAT gradient (BATG) was used as a proxy for slope. Additionally, three more static variables were generated. Distance to colony

(DCOL) and distance to land (DLAN) was calculated using the *distance* tool in ArcGIS 9.2 spatial analyst, while chlorophyll *a* peak (CHPK) was calculated from binominal layers of CHL concentration in the study period (Apr-May) during the 10 last years (2002-2011). Cells with a CHL concentration $> 1 \text{ mg/m}^2$ were assigned a value of 1 and lower values assigned zeros (Louzao et al. 2012, Suryan et al. 2012).

Table III – Overview of the environmental variables used in the analysis of habitat selection.

Explanatory variables	Satellite	Spatial resolution	Temporal resolution	Range (min-max)	Oceanographic process (description)
<i>Dynamic</i>					
Chlorophyll <i>a</i> (CHL, mg m^{-3})	Aqua MODIS	0.04°	Daily	0.06- 31.7	Ocean productivity
Primary productivity (PP, $\text{mg C m}^{-3} \text{ d}^{-1}$)	BLENDED	0.04°	Daily	293- 7150	Ocean productivity
Sea surface temperature (SST, °C)	Aqua MODIS	0.04°	Daily	13.7- 22.7	Water mass distribution
CHL gradient (CHLG) ^a	Aqua MODIS	0.04°	Daily	0.1- 98.4	Fronts
SST gradient (SSTG) ^a	Aqua MODIS	0.04°	Daily	0.0- 18.2	Fronts
PP gradient (PPG) ^a	Aqua MODIS	0.04°	Daily	0.05- 78.3	Fronts
<i>Static</i>					
Bathymetry (BAT, m)	ETOPO	0.03°	–	1- 5215	Neritic vs. pelagic domains
BAT gradient (BATG) ^a	ETOPO	0.03°	–	0.1- 99.3	Topographic features
Distance to colony (DCOL, km)	–	–	–	0- 276.5	Neritic vs. pelagic domains
Distance to land (DLAN, km)	–	–	–	0- 283.8	Neritic vs. pelagic domains
Chlorophyll peak (CHPK, $\text{CHL} > 1 \text{ mg m}^{-3}$) ^b	Aqua MODIS	–	–	0- 10	Productivity persistence

2.5 – Trip filtering

GPS data were divided into individual foraging excursions by calculating the running distance to colony from GPS position and colony location. Trip duration was calculated and the data divided in short (≤ 1 day) and long (> 1 day) trips by inspecting a frequency histogram of trip duration. Then, the relocations (between consecutive tracking points) were filtered on running flight speed. In attempt to exclude periods where the birds were resting and drifting on the water surface, a lower threshold of 9 km/h (i.e. based on the frequency distribution of speed records;

Guilford et al. 2008) was set for the flight dataset that were used for estimation of home ranges (HR).

In addition to the filtered flight dataset, a dataset of foraging relocations was created to estimate foraging areas (FA). This was done by calculating path sinuosity for all the relocations, defined as the ratio of the actual flight speed given by the GPS receiver to the velocity between every third fix (geographical location). Birds that are circling an area will display a lower calculated speed than the actual GPS speed, and thereby have a higher sinuosity index (Grémillet et al. 2004). A histogram of the sinuosity distribution was used to determine the break-off value for this filtering parameter along with a visual assessment of which relocations were regarded as foraging. The ideal was thought to be a value that included the most foraging relocations, without including sharp turns that are merely alterations in direction. Using these guidelines, a sinuosity index of 1.7 was selected as the sinuosity limit for foraging behaviour, considerably lower than the 3.0 used by Grémillet et al. (2004) for Northern gannets (*Morus serrator*). Finally, following the same approach, a distance-to-colony filter of 2 km was applied in order to remove sinuosity that may be associated with social interaction and particularly while flying over the colony before landing.

2.6 - Kernel estimation

Utilization distribution (UD) kernels were used to characterize the distribution of experienced and inexperienced birds. The UD is a probability density function that quantifies an individual or group's relative use of space (van Winkle 1975). Home ranges (UD95) and foraging areas (UD50) were calculated from the flight-filtered and foraging-filtered datasets, respectively, using UD kernel methods (Worton 1989).

Most of the following analyses require kernels for each individual trip, but home range and foraging area of experienced and inexperienced birds were also calculated collectively. All kernels were estimated using R packages: *adehabitat* and *adehabitatHR* (Calenge 2006). To allow comparison between the two groups and all years, the ad-hoc method was used to find a reasonable smoothing factor (h). The smoothing factor is the most important setting during kernel estimation, determining the detail of the kernels (Kappes et al. 2011). The *ad-hoc* approach requires kernel calculation of a representative subsample setting the h -value as “reference”. The optimal h of the current sample will then be given. Then the mean of those were used to estimate the h for this study. A smoothing factor of 3100 m was used for all the calculated kernels. Trips that were too short and fine-scaled to be estimated at this level were discarded along with those trips with less than 5 relocations of either flight or foraging after the filters in the previous section. This is the minimum number of relocations to estimate a kernel. The overlap between kernels of experienced and inexperienced birds each year was calculated to determine if there was any spatial segregation between the groups. Overlaps were also estimated between each year within the groups to assess the consistency of habitat selection in each group. Both calculations were performed in R with the *kerneloverlap* function of *adehabitat*. Finally the overlaps of the suggested protected area (the marine Important Bird Area; mIBA) and a legal protection area (the Special Protection Area; SPA) with collective kernels of foraging areas (FA) for all years were estimated to validate the protection areas. This was done using a combination of *intersect*, *erase* and *area* tools of the ArcGIS 9.2 toolbox.

2.7 – Stable isotope analysis (SIA)

Stable Isotope Analysis (SIA) of $\delta^{15}\text{N}$ was performed to investigate the effect of experience on foraging ecology and prey selection, while the $\delta^{13}\text{C}$ analysis offered a validation of the spatial distribution assessed by the kernel analysis. The ratios represent the prey ingested in the past few weeks before the blood sample. The $\delta^{15}\text{N}$ is mainly used to define the trophic position of the consumer, while $\delta^{13}\text{C}$ reflects the foraging habitat of the consumer (Inger & Bearhop 2008, Ceia et al. 2012). There is a gradient of high to low values of $\delta^{13}\text{C}$ from coast to offshore due to the organic enrichment at the coast that is gradually diluted. In SIA analysis it is also possible to take advantage of the differing turnover rates for different tissues, as red blood cells (RBC) is regenerated every 12-22 days while plasma has a turnover rate of about 7 days, they represent prey ingestion in different time scopes: RBC reflects the trophic ecology the last few weeks, and plasma reflects choices made in the last trips before sampling (i.e. around 7 days; Inger & Bearhop 2008).

In order to examine the relation between foraging trips and trophic ecology, blood samples were collected. Each of the tracked birds was sampled upon return from a foraging trip. Blood samples (1 ml) were collected from the tarsal or brachial vein using 25-gauge needles under license. Blood samples were then separated into plasma and red blood cells (hereafter termed RBC) by a centrifugation at 12000 rpm for 15 min, within 2-4 hours of sampling and stored frozen at $-5\text{ }^{\circ}\text{C}$ until preparation for analysis. Successive rinses with a 2:1 chloroform/methanol solution were performed on the plasma samples in order to deplete it for lipids, which may disturb the results (Bearhop et al. 2000, Cherel et al. 2005b). As the lipid content of whole blood (RBC) is typically low, the lipid extraction is typically not required for that

tissue (Cherel et al. 2005a). Samples were dried in an aspirating hood for 48 h at 60°C for the ethanol to evaporate.

Isotope ratios of carbon and nitrogen were then determined through standard methodology (Bearhop et al. 2006, Phillips et al. 2009) by continuous-flow isotope ratio mass spectrometry, using an EA-IRMS (Isoprime, Micromass, UK) at Institute of Marine Research (IMAR), Coimbra, Portugal. Isotopic values are expressed in the δ notation as parts per thousand (‰) deviations from standards (Vienna Pee Dee Belemnite for $\delta^{13}\text{C}$ and N_2 in air for $\delta^{15}\text{N}$) following the formula: $\delta X = [(R_{\text{sample}} / R_{\text{standard}}) - 1] \times 1000$, where X is $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$, and R is the corresponding ratio $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. The analytical precision for the measurement was 0.2‰ for both carbon and nitrogen. All values presented are means \pm 1 SD unless otherwise stated. In this study, the stable isotope analysis was applied to investigate if inexperienced and experienced birds can be segregated along the trophic gradient. Therefore it is assumed that potential intraspecific differences in assimilation efficiency or physiology, does not impact the blood isotope values significantly (Votier et al. 2011).

2.8 - Data analysis

Trip characteristics of all recorded trips ($n=277$) were compared using linear mixed models. For the subsequent analysis we only used short excursions (= 1 day of duration) of male individuals, due to several reasons: 1) The short excursions are more representative of the male Cory's shearwater foraging strategy during the pre-breeding season as most individuals return every night to defend their burrow site (i.e. foraging movements should be rather local). 2) As a result, the long trips are underrepresented and the sample sizes are too small to analyse and interpret

differences between experienced and inexperienced individuals. 3) This study is also aiming to interpret the spatial distribution of experienced and inexperienced males in relation to the recently legislated SPA in the region.

Following, a random subset of the 2010 dataset was selected in order to have a comparable sample size between years. The subset was obtained by two criteria in order to distribute the sample between individuals and over time: 1) Maximum 5 trips by experienced and 4 trips by inexperienced were allowed; 2) every other trip was removed until this criterion was fulfilled. The sample sizes used for the analysis were: $n=52$, $n=41$, and $n=39$, for the respective 2010, 2011, and 2012 seasons.

To understand if there was an effect of experience on habitat selection, environmental characteristics of home ranges and core foraging areas were compared with LME models. Secondly, the characteristics of the home range and the core foraging area for each group was also compared with LME models to assess which variables were important for habitat selection. Mean values of the environmental variables were extracted within home range and foraging areas of all the analysed trips using the *extract* function of the *raster* package in R (Hijmans & van Etten 2012). Then Linear Mixed Effect (LME) models fitted by Restricted Maximum Likelihood (REML) with bird identity as a random effect and trip nested under bird identity to account for pseudoreplication. The LMEs tested primarily the effect of experience on habitat selection, but also habitat selection within each group, by comparing home range and foraging areas.

A Mahalanobis distance factor analysis (MADIFA, Calenge et al. 2008) comparing the environmental characteristics of chosen foraging grounds with that of the available environment, was applied to understand the relative importance of explanatory environmental variables. MADIFA is a multivariate modelling technique

developed to make habitat suitability maps from presence-only data, such as tracking relocations. General Linear Modelling or General Linear Mixed Modelling may also be used on this data, but requires the calculation of pseudo-absences. The MADIFA is a good option for this study because it considers the environmental variability of the area where the niche was sampled, and may therefore be more accurate than other methods (Tsoar et al. 2007). It is also complementary to the commonly applied ecological-niche factor analysis (ENFA), and runs on the freely available software R (Thiebot et al. 2011). The available environment had to be defined for the niche and MADIFA analyses. As only short trips of 1 day or less were kept for the analysis, the maximum daily range was estimated by the following formula: $([\text{mean trip duration} - \text{mean time spent foraging per trip}] * \text{mean flight speed} * 1/2)$. Thus, a daily range of about 240 km was estimated, approximating the 2 degrees in each direction off and along the shore, which was defined as the available habitat (i.e. study area). In order to allow spatial comparison and combined analysis, all environmental variables had to be gathered in a data frame matching the resolution of the coarsest layer. Thus BAT and BATG were simplified to match the other datasets resolution of 0.04° (Figure 2).

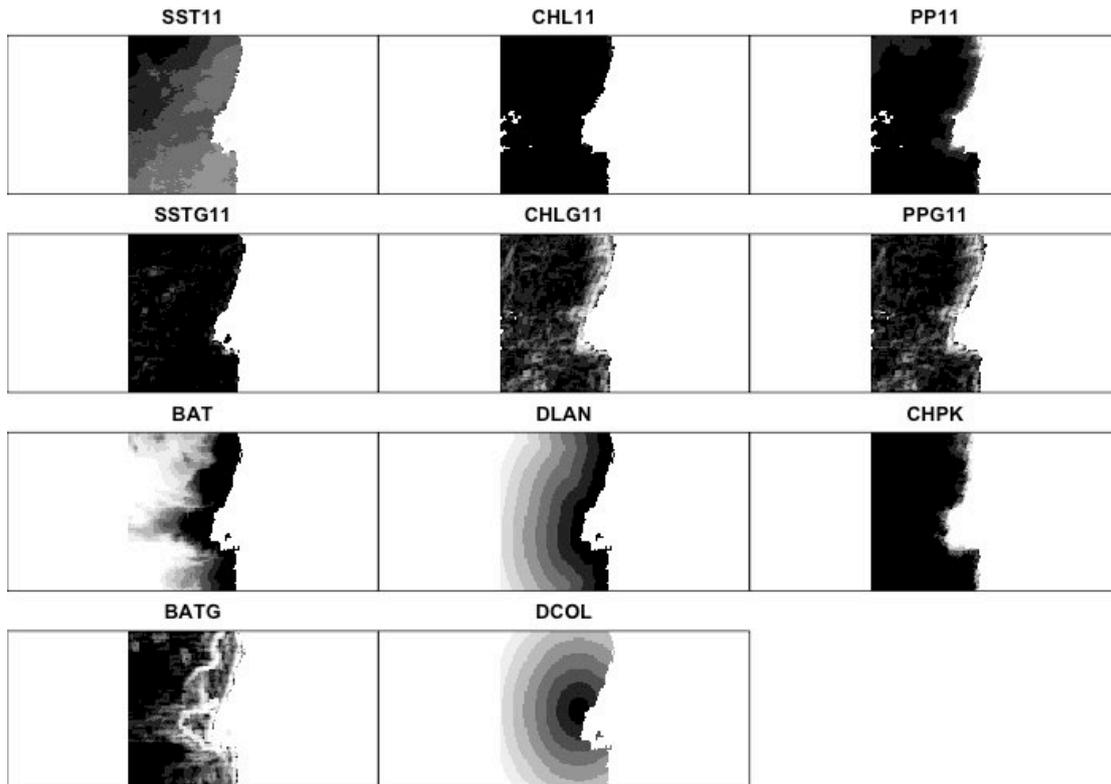


Figure 2 – Graphical representation of the environmental variables used to run MADIFA routines for the 2011 dataset. Gradient of values from darker (lower values) to lighter (higher values). Represented are Sea Surface Temperature (SST; °C), Chlorophyll *a* concentration (CHL; mgm^{-3}), Primary productivity (PP; $\text{mg C m}^{-2} \text{ day}^{-1}$), Bathymetry (BAT; m), Distances to land (DLAN; m) and colony (DCOL; m), Peak of chlorophyll *a* (CHPK) and gradients in SST (SSTG), CHL (CHLG), PP (PPG) and BAT (BATG).

The SIA results were analysed applying a MANOVA (Wilk's lambda statistics), followed by Two-way ANOVAs with biological tissue (plasma and RBC) and year (2010-2012) as independent factors. All data are presented as mean \pm 1 SD, unless otherwise stated. Results were considered significant at $p \leq 0.05$.

Chapter 3

Results

3.1 – Foraging patterns

Both experienced and inexperienced birds demonstrated a dual foraging strategy alternating between daily trips in the colony surroundings and long excursions as far as the Labrador Current off the east coast of Canada (**Figure 3**). From a total of $n = 277$ recorded trips, only $n = 32$ were long (>1 d.) and were not inspected in the analysis of habitat usage.

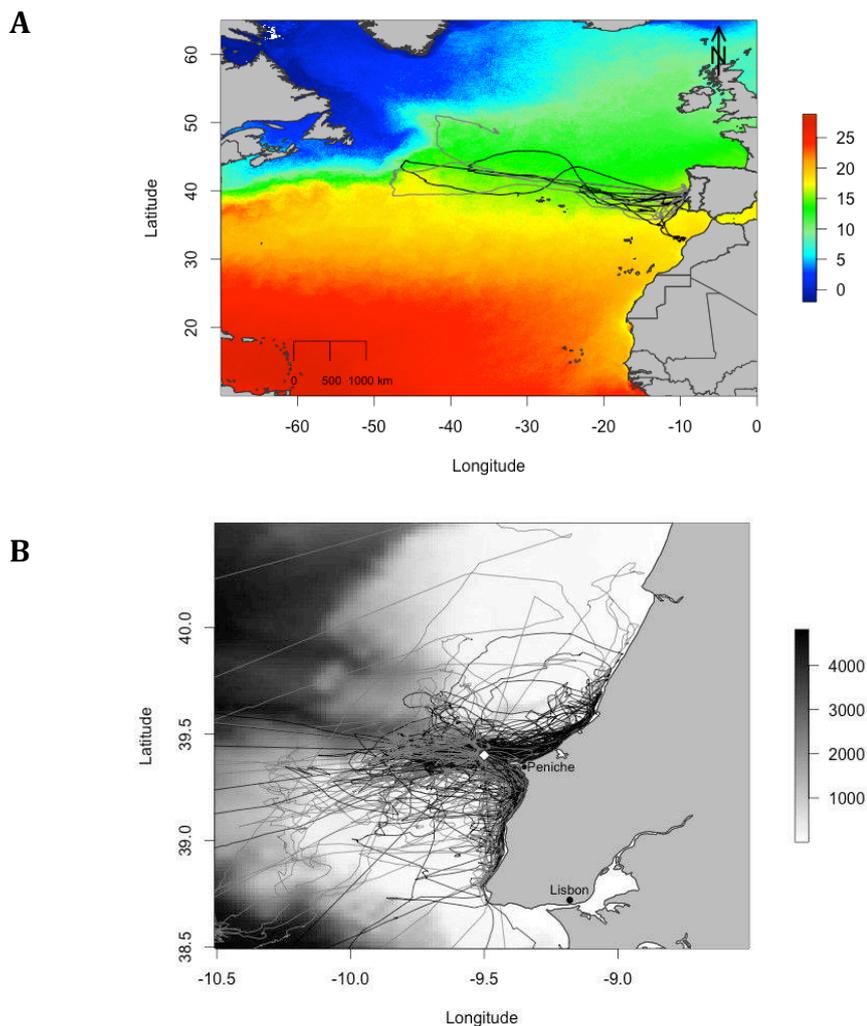


Figure 3 – All long (A; > 1 day) and short (B; = 1 day) excursions of experienced (black) and inexperienced (grey) Cory's shearwaters tracked in April 2010, May 2011 and May 2012, plotted on a mean composite of sea surface temperature (SST) (in $^{\circ}\text{C}$) of those months (A) and over the bathymetric relief (B).

The foraging parameters were similar in experienced and inexperienced birds (Table II) There was a consistent tendency towards longer trips in both time and distance for inexperienced, which was further reflected in larger home ranges and core feeding areas, but there were no significant differences ($F < 1.43$, $p > 0.14$, LME).

The breeding success of inexperienced birds also increased significantly during the study period from 18% in 2010 to 64% in 2011 ($\chi^2 = 4.54$, $df = 1$, $p = 0.03$), though their breeding success in 2012 is yet unknown.

Table IV – Trip characteristics of short and long trips made by experienced and inexperienced male Cory’s shearwaters in all the study seasons, given as: mean \pm SD (sample size).

	Experienced	Inexperienced
Short trips		
Trip duration (h)	14.6 \pm 2.7 (156)	15.2 \pm 1.0 (99)
Maximum foraging range (km)	25.6 \pm 14.9 (99)	31.8 \pm 20.4 (99)
Distance covered (km)	111.8 \pm 58.4 (156)	132.6 \pm 89.7 (99)
Home Range (HR, km ²)	756.1 \pm 399.1 (117)	900.5 \pm 553.1 (79)
Core feeding area (FA, km ²)	126.1 \pm 57.8 (117)	130.1 \pm 59.5 (79)
Long trips		
Trip duration (h)	81.7 \pm 82.1 (20)	159.4 \pm 138.6 (12)
Maximum foraging range (km)	556.2 \pm 1003.2 (20)	642.8 \pm 894.9 (12)
Distance covered (km)	1223.7 \pm 1882.2 (20)	2157.2 \pm 2084.1 (12)

3.3 – Spatial segregation

Spatial segregation was assessed with regards to overlap of UD95 (home range) and UD50 (core foraging area) kernels between experienced and inexperienced individuals (Figure 4). There was an average of 24% overlap between the core

foraging areas of the compared groups, while the home ranges overlapped 55% on average. The core foraging areas overlapped less and less with passing years: 32% (2010), 25% (2011) and 16% (2012).

The inter-annual consistency of habitat usage within each group was also assessed through kernel overlaps (Figure 4). There was an average of 65% overlap between the core foraging areas of experienced individuals between years (2010x2011: 67%; 2011x2012: 65%; 2010x2012: 61%), while inexperienced had an average of 28% overlap between years (2010x2011: 48%; 2011x2012: 7%; 2010x2012: 29%).

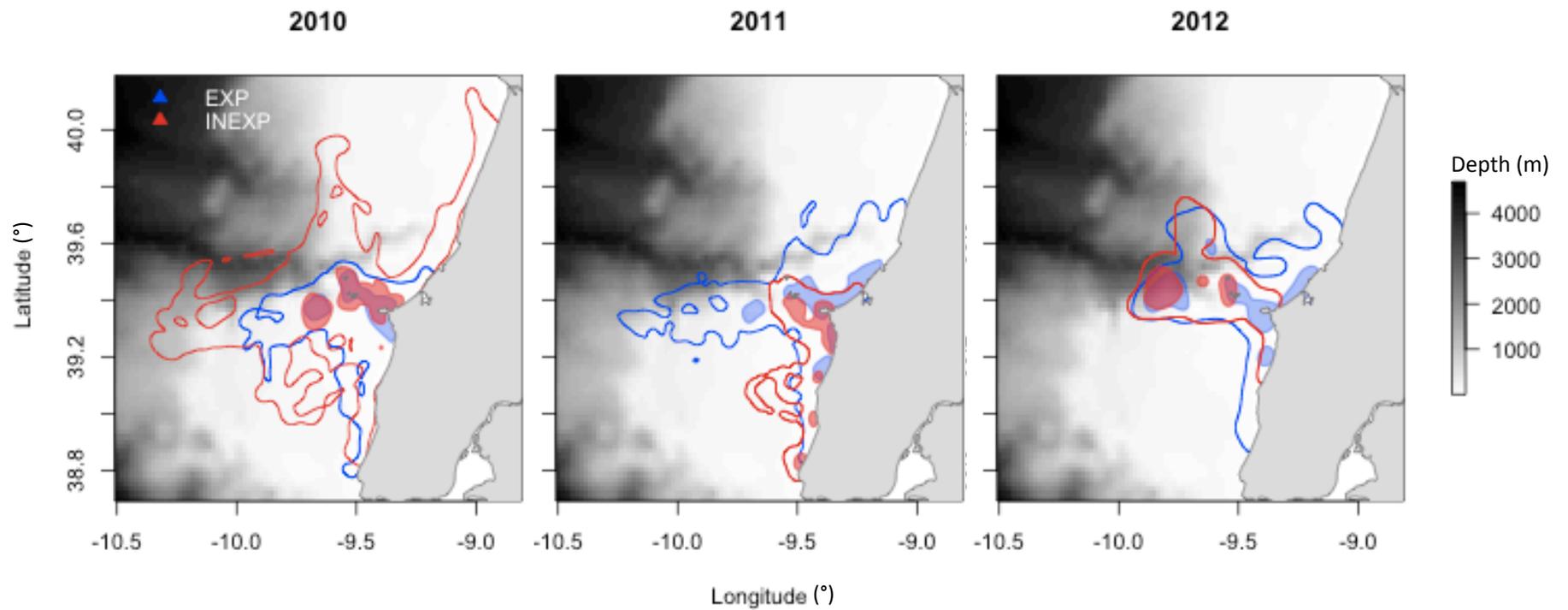


Figure 4 – Home range (UD95) and core foraging areas (UD50) of experienced (blue) and inexperienced (red) estimated for each year and plotted on bathymetry.

3.4 – Habitat selection

The LME models demonstrated that all significant differences between HR and FA, here interpreted as habitat selection, was selection towards productivity proxies. Secondly there were a higher rate of selection towards static variables like bathymetry (BAT), distance to colony (DCOL) and areas with persistently high chlorophyll levels (CHPK), than towards dynamic variables (e.g. gradient in SST, SSTG). Experienced individuals were generally selecting more productive areas (e.g. Primary Productivity – PP – of 2012) than inexperienced, and they were exploiting areas closer to land (lower DLAN). During 2011 there were some contradictory results to the general patterns, as inexperienced were foraging in more productive waters (i.e. higher values of CHPK) (Table III).

Table III - Comparison of the environmental conditions within home range (HR) and foraging areas (FA) of experienced vs inexperienced individuals and within each group: a comparison of environmental conditions inside that groups' HR and FA. This table lists the dynamic variables.

	2010				2011				2012						
	n	HR	n	FA	LME	n	HR	n	FA	LME	n	HR	n	FA	LME
SST (°C)															
EXP	26	15.47 ± 0.07	26	15.47 ± 0.09	F=0.00 p=0.89	32	16.75 ± 0.12	30	16.7 ± 0.13	F=48.30 p=0.003	16	15.56 ± 0.19	16	15.5 ± 0.37	F=1.23 p=0.29
INEXP	26	15.51 ± 0.08	26	15.51 ± 0.13	F=0.20 p=0.63	9	16.69 ± 0.06	8	16.62 ± 0.09	F=19.9 p=0.003	13	15.67 ± 0.09	13	15.75 ± 0.22	F=3.89 p=0.07
LMM		F=3.60 p=0.06		F=1.50 p=0.23			F=1.7 p=0.20		F=2.80 p=0.10			F=3.42 p=0.08		F=4.66 p=0.04	
SSTG (%)															
EXP	26	1.91 ± 0.35	26	1.93 ± 0.66	F=0.03 p=0.87	32	1.91 ± 0.35	32	2.22 ± 0.79	F=9.81 p=0.004	16	3.63 ± 0.61	16	4.38 ± 1.72	F=5.61 p=0.03
INEXP	26	1.79 ± 0.25	26	1.76 ± 0.36	F=0.55 p=0.47	9	1.68 ± 0.35	9	1.86 ± 0.59	F=3.55 p=0.10	13	3.09 ± 0.58	13	2.64 ± 1.13	F=5.86 p=0.03
LMM		F=2.03 p=0.16		F=1.42 p=0.24			F=3.11 p=0.09		F=1.6 p=0.21			F=5.89 p=0.02		F=9.85 p=0.004	
CHL (mg/m³)															
EXP	26	1.71 ± 0.64	21	1.72 ± 1.06	F=0.58 p=0.46	32	0.94 ± 0.33	22	1.12 ± 0.9	F=1.87 p=0.19	16	0.74 ± 0.6	11	0.49 ± 0.29	F=0.08 p=0.79
INEXP	26	1.39 ± 0.59	26	1.32 ± 0.67	F=1.12 p=0.30	9	0.83 ± 0.2	5	0.74 ± 0.19	F=0.20 p=0.68	13	0.49 ± 0.13	12	0.39 ± 0.04	F=32.32 p=1e-04
LMM		F=3.46 p=0.07		F=2.46 p=0.12			F=0.96 p=0.33		F=0.87 p=0.36			F=2.24 p=0.15		F=1.62 p=0.22	
CHLG (%)															
EXP	26	49.63 ± 13.2	26	53.07 ± 22.53	F=1.89 p=0.18	32	59.36 ± 10.06	32	59 ± 15.54	F=0.03 p=0.86	16	48.48 ± 9.55	16	44.54 ± 17	F=1.99 p=0.18
INEXP	26	40.45 ± 10.78	26	39.46 ± 15.49	F=0.43 p=0.52	9	56.05 ± 5.84	9	57.24 ± 7.98	F=0.14 p=0.71	13	40.67 ± 6.29	12	29.87 ± 6.77	F=28.75 p=2e-04
LMM		F=7.54 p=0.01		F=6.44 p=0.01			F=0.88 p=0.35		F=0.11 p=0.75			F=6.42 p=0.02		F=7.93 p=0.01	
PP (g C m⁻² d⁻¹)^c															
EXP	26	3.04 ± 0.42	24	3.13 ± 0.68	F=2.31 p=0.14	32	2.20 ± 0.57	21	2.43 ± 1.39	F=1.85 p=0.19	16	1.15 ± 0.16	15	1.30 ± 0.45	F=2.55 p=0.13
INEXP	26	2.74 ± 0.54	26	2.67 ± 0.71	F=0.87 p=0.36	9	2.04 ± 0.40	5	1.96 ± 0.40	F=0.13 p=0.74	13	1.03 ± 0.13	12	0.99 ± 0.032	F=0.35 p=0.57
LMM		F=5.31 p=0.03		F=5.56 p=0.02			F=0.61 p=0.44		F=0.54 p=0.47			F=4.54 p=0.04		F=4.81 p=0.04	
PPG (%)															
EXP	26	29.74 ± 5.52	26	28.05 ± 7.35	F=4.44 p=0.05	32	44.84 ± 8.13	32	44.93 ± 13.05	F=0 p=0.96	16	30.85 ± 6.84	16	28.81 ± 10.48	F=2.42 p=0.14
INEXP	26	25.9 ± 5.13	26	24.5 ± 6.89	F=2.82 p=0.11	9	42.43 ± 4.67	9	43.62 ± 6.26	F=0.23 p=0.64	13	25.07 ± 5.18	13	20.95 ± 6.79	F=13.47 p=0.003
LMM		F=6.72 p=0.01		F=3.23 p=0.08			F=0.72 p=0.4		F=0.08 p=0.77			F=6.31 p=0.02		F=5.44 p=0.03	

HR: Kernels encompassing 95% of all flight relocations; FA: Kernels encompassing 50% of foraging relocations. Values are means ± SD. LME: Linear Mixed Models with trips as the unit nested under individuals. Significant values are shown in bold.

Table III - (continued for static environmental variables)

	2010						2011						2012					
	n	HR	n	FA	LME		n	HR	n	FA	LME		n	HR	n	FA	LMM	
CHPK (mg/m³)																		
EXP	26	5.61 ± 2.03	26	5.60 ± 2.85	F=0.05 p=0.83		32	6.33 ± 1.93	28	6.53 ± 2.54	F=3.53 p=0.07		16	4.42 ± 2.42	15	4.27 ± 4.01		F=2.55 p=0.93
INEXP	26	4.32 ± 2.37	26	4.16 ± 2.87	F=0.41 p=0.53		9	8.01 ± 0.87	7	9.12 ± 1.00	F=13.67 p=0.01		13	2.77 ± 1.63	12	1 ± 0.86		F=29.06 p=2e-04
LMM		F=4.45 p=0.04		F=3.22 p=0.08			F=6.37 p=0.02		F=6.87 p=0.01			F=4.40 p=0.05		F=7.66 p=0.01				
BAT (m)																		
EXP	26	140 ± 101	26	117 ± 113	F=1.64 p=0.21		32	144 ± 177	30	120 ± 188	F=5.2 p=0.03		16	412 ± 276	15	453 ± 375		F=0.53 p=0.48
INEXP	26	317 ± 317	26	270 ± 396	F=1.71 p=0.2		9	57 ± 23	8	37 ± 17	F=11.75 p=0.01		13	641 ± 272	12	951 ± 275		F=20.10 p=0.001
LMM		F=7.39 p=0.01		F=3.57 p=0.06			F=2.14 p=0.15		F=1.54 p=0.22			F=4.99 p=0.03		F=14.78 p=7e-04				
BATG (%)																		
EXP	26	79.79 ± 7.08	26	84.72 ± 8.5	F=19.38 p=2e-04		32	79.83 ± 4.96	32	83.31 ± 6.36	F=12.9 p=0.001		16	81.6 ± 2.56	16	83.06 ± 6.53		F=1.18 p=0.29
INEXP	26	75.65 ± 10.14	26	79.31 ± 15.2	F=4.07 p=0.05		9	77.81 ± 5.63	9	84.37 ± 5.31	F=9.5 p=0.02		13	80.96 ± 4.82	13	81.9 ± 5.99		F=0.65 p=0.44
LMM		F=2.92 p=0.09		F=2.51 p=0.12			F=1.1 p=0.30		F=0.21 p=0.65			F=0.21 p=0.65		F=0.25 p=0.62				
DLAN (km)																		
EXP	26	18.02 ± 8.7	26	17.48 ± 12.05	F=0.24 p=0.63		32	15.23 ± 10.93	32	13.84 ± 14.5	F=2.88 p=0.10		16	22.25 ± 9.66	15	24.26 ± 15.98		F=1.43 p=0.25
INEXP	26	25.93 ± 13.54	26	27.91 ± 20.33	F=1.06 p=0.31		9	10.23 ± 3.32	8	6.67 ± 4.82	F=11.32 p=0.01		13	30.58 ± 7.3	13	40.36 ± 13.30		F=24.27 p=3e-04
LMM		F=6.27 p=0.02		F=5.05 p=0.03			F=1.80 p=0.19		F=1.87 p=0.18			F=6.59 p=0.02		F=8.24 p=0.01				
DCOL (km)																		
EXP	26	14.03 ± 5.61	26	15.56 ± 6.64	F=4.48 p=0.04		32	18.91 ± 7.24	30	23.99 ± 12.57	F=9.70 p=0.004		16	17.51 ± 4.72	15	24.14 ± 9.76		F=17.50 p=9e-04
INEXP	26	20.22 ± 10.7	26	22.91 ± 17.11	F=1.84 p=0.19		9	16.11 ± 7.29	8	20.46 ± 11.53	F=2.16 p=0.19		13	18.96 ± 4.1	13	28.08 ± 8.32		F=36.32 p=1e-04
LMM		F=6.84 p=0.01		F=4.17 p=0.05			F=1.05 p=0.31		F=0.52 p=0.48			F=0.77 p=0.39		F=1.30 p=0.27				

HR kernels encompassing 95% of all flight relocations; FA kernels encompassing 50% of foraging relocations. Values are means ± SD. LME Linear Mixed Models with trips as the unit nested under individuals. Significant values are shown in bold.

In the multivariate analysis, the first principle component analysis (PCA) axis resulting from the MADIFA method, always explained more than 95% of the variation in environmental variability of foraging locations for experienced individuals, while the explanatory power of the first PCA axis was always much lower (max. 70%) for inexperienced individuals (Table IV). There was also a clear pattern in the number of variables that were correlated with the first and second axis. Bathymetry was highly correlated with the first PCA axis in all years and for both groups (Table IV). Distance to land was the only other variable with a correlation higher than 40% with any of the axes for experienced birds, though there were several variables fulfilling this criterion among the inexperienced birds.

Table IV – Principle component analysis (PCA) tables from Mahalanobis distance factor analysis (MADIFA) of experienced and inexperienced birds.

	2010		2011		2012	
Experienced						
Axis	1	2	1	2	1	2
% of variation explained	96%	2%	97%	2%	97%	2%
Bathymetry	-0.99	-0.68	1	-0.68	1	-0.57
Distance to land	0.11	0.69	-0.05	0.72	-0.04	0.79
Distance to colony	-0.01	0.15	-0.01	0.14	-0.03	0.02
Primary Productivity	0.01	0.1	0	-0.01	0	0.15
Chlorophyll <i>a</i> peak	0	0.08	0	0.08	0.01	0.08
Inexperienced						
Axis	1	2	1	2	1	2
% of variation explained	56%	26%	67%	13%	70%	16%
Bathymetry	0.89	-0.07	0.83	-0.14	-0.94	-0.16
Sea Surface Temperature (SST)	0.42	-0.01	-0.31	-0.03	0.19	0.01
Distance to colony	0.09	-0.31	0.25	0.06	-0.21	-0.46
Primary Productivity	0.02	0.01	0.17	-0.06	0.06	0.04
Distance to land	-0.11	-0.57	-0.3	0.08	0.13	0.87
SST Gradient	0.02	0.68	-0.01	-0.26	-0.02	0.02

3.5 – Stable isotope analysis (SIA)

Overall, there were significant differences in carbon and nitrogen isotope ratios of plasma among inexperienced and experienced birds and between years (MANOVA, Wilk's lambda, $F_{2,29} = 7.70$, $p = 0.002$ and $F_{2,29} = 7.99$, $p = 0.002$, respectively). If results from the two isotopes are analysed separately, there was a significant effect of experience, and a significant overall influence of year on $\delta^{15}\text{N}$ (Two-way ANOVA, $F_{1,29} = 12.71$, $p = 0.001$ and $F_{1,29} = 8.68$, $p = 0.001$) and a significant effect of experience but not year on $\delta^{13}\text{C}$ ($F_{1,29} = 10.83$, $p = 0.003$ and $F_{1,29} = 1.11$, $p = 0.30$, respectively). In separate pairwise comparisons with Bonferroni correction applied to p values, mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were significantly lower in inexperienced than in experienced adults during 2010. This trophic segregation diminished and became statistically non-significant during the following study years (Figure 5).

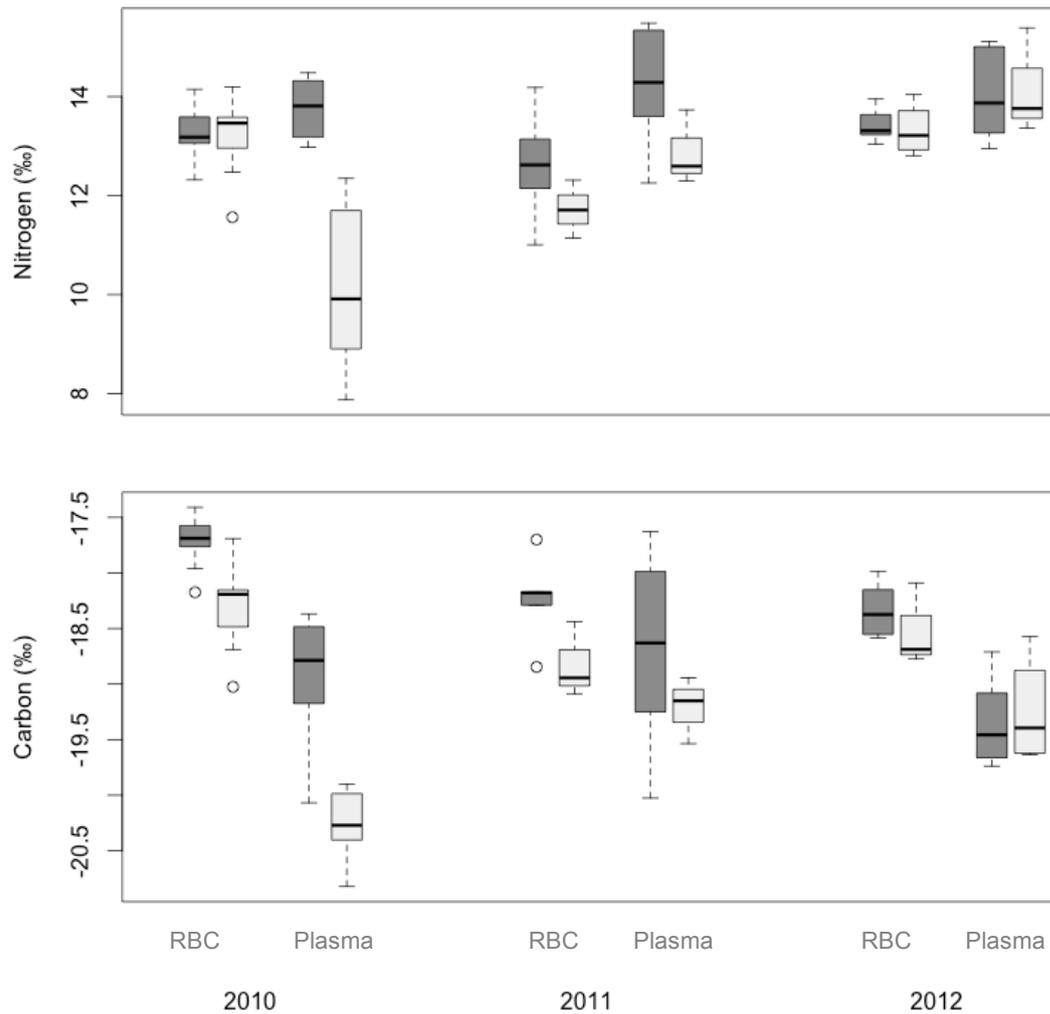


Figure 5 – Isotopic values of $\delta^{15}\text{N}$ (upper pane) and $\delta^{13}\text{C}$ (lower pane) of experienced (dark grey) and inexperienced (light grey) birds plasma and RBC during 2010, 2011 and 2012.

Both carbon and nitrogen isotopic signature of birds' red blood cells (RBC) segregated according to birds experience and study year (MANOVA, Wilk's lambda, $F_{2,29} = 11.21, p < 0.001$ and $F_{2,29} = 29.26, p < 0.001$). There was a significant effect of study year (Two-way ANOVA, $F_{1,29} = 7.05, p = 0.01$) but not of experience ($F_{1,29} = 0.12, p = 0.73$) on $\delta^{15}\text{N}$. $\delta^{13}\text{C}$ segregated by both experience ($F_{1,29} = 13.01, p = 0.001$) and study year ($F_{1,29} = 10.35, p = 0.003$). Pairwise comparisons revealed that only during 2010 and 2011, the carbon signature of inexperienced individuals was

significantly lower than that of experienced birds. With passing years the long-term trophic ecology of individuals seems to become more similar.

3.6 – Conservation aspects

By calculating the overlaps in ArcGIS, it was found that the mIBA covered 81% and 85% of the core foraging areas for experienced and inexperienced birds respectively, while 59% and 66% were covered by the SPA (Figure 6).

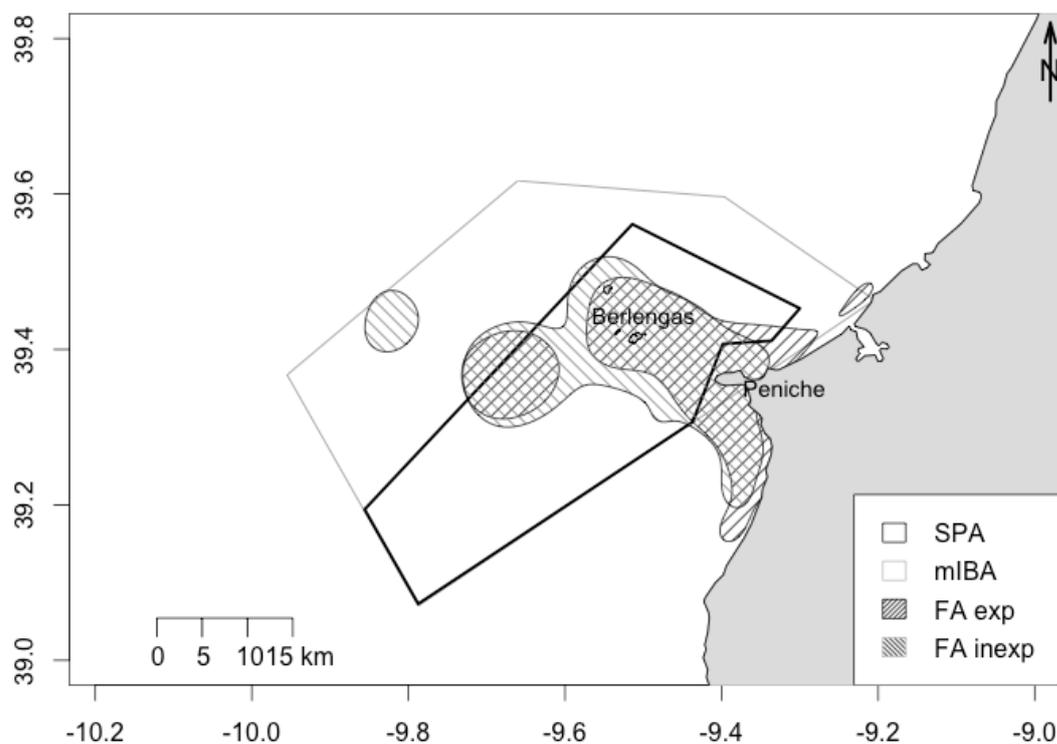


Figure 6 – A comparison of the identified marine Important Bird Area (grey border), the designated Special Protection Area (black border) and persistent core foraging areas (FA) of experienced (45° hatching) and inexperienced (-45° hatching).

Chapter 4

Discussion

4.1 – Spatial segregation

The separation of experienced and inexperienced breeders applied in this study did yield very interesting results regarding intraspecific divergences in spatial distribution, prey selection and development of foraging abilities, but is nevertheless “just” an educated way to distinguish young and old adults, and ideally the age of the birds would have been used for this purpose. Though, unlike other marine predators like fish and mammals whose age can be estimated by otoliths and teeth, there is usually no straightforward way to age seabirds. As emphasized above the Cory’s shearwaters population at Berlengas is a small population of only 300 individuals and carefully monitored for more than a decade, but seabirds are especially long-lived species and even in this case, as many individuals were first ringed as adults, only minimum age is known for many of the birds. It may be argued that a problem with this definition is that breeding experience is derived from breeding success and thus relies on the assumption that experience gives success. On the other hand this assumption is at the worst debated. Secondly, the breeding score is the best method available to separate the groups of this population and correlates well with minimum age, which was another option, and it is also an accepted approach within seabird research (e.g. Weimerskirch et al. 2005).

There were several evidences of niche spatial segregation between experienced and inexperienced individuals. UD kernel analysis showed that the foraging areas (FA’s) of the two groups only overlapped 24 % on average among the study years. This segregation was only well confirmed in 2010 by significant differences in both plasma and RBC carbon isotopic ratios, while there were only differences in the long-term aspect (RBC) in 2011. These are not contradictory

results, but rather indicate that the foraging grounds of the groups were highly separated at similar distances to the coast during 2010. The $\delta^{15}\text{N}$ results also showed that experienced individuals were consistently feeding upon prey items located higher in the trophic chain, although this separation was not significant for the entire study period (RBC) of 2010. This was also the year where the foraging areas overlapped the most (32%), compared to 16% in 2012. Kernel overlaps were also calculated for the FA's of each group between years, and provided very strong evidence for the hypothesis that inexperienced birds are more explorative (Thiebot et al. 2011, Votier et al. 2011). According to this analysis the experienced individuals were more than twice as consistent in their targeted areas (average of 65% overlap of FA's between years) than the inexperienced (28%). This is supported by the trip characteristics which shows that mean trip duration, trip length and habitat size of inexperienced was consistently higher for both short and long trips (though these differences were not significant).

4.2 - Habitat selection

A key question addressed by this study, was if the birds differed in their foraging tactics and habitat selection. There is a general picture documented by the estimation of the FA kernels and supported by the carbon isotopic signatures that experienced rely more on the areas close to the coast, north and south of Peniche, while inexperienced are using larger areas and relying more on small offshore seamounts South-West of Berlengas than the experienced ones. The LME's comparing environmental characteristics of the home range and foraging area estimated for each group, showed clearly, but not without exception that the experienced were more successful in targeting areas believed to be productive. Indeed

there was a general pattern of experienced using shallower habitats with stronger gradients and higher productivity, with the exception of 2011 that showed the opposite trend. Although, the data indicate that inexperienced found these lucrative foraging grounds more by fortune of an experimental searching strategy, than a sudden increase in foraging abilities. The MADIFA strongly indicate that experienced individuals are relying on known features, as the distribution of foraging relocations was almost solely explained by bathymetry. According to the MADIFA analysis bathymetry is also the primary explanatory variable for inexperienced, but they are additionally relying on a number of other static and dynamic variables (e.g. distance to land or SST). The foraging grounds of inexperienced overlapped much less between years than that of experienced, supporting the results of the MADIFA. Together the MADIFA and the kernel overlaps provide an understanding why inexperienced could be more successful than experienced birds in periods of strong environmental stochasticity.

4.3 - Foraging efficiency

The first and primary purpose of the LMEs was to compare the foraging efficiency between experienced and inexperienced birds. To my best knowledge this study is the most complete investigation of the hypothesis that inexperienced birds are less efficient foragers than experienced ones, due to large sample sizes, high accuracy of the GPS and the multiple years of investigation. Although three years is a relatively short period in the life of a seabird, inexperienced individuals clearly demonstrated a development in foraging efficiency through the study period by their trophic signatures which gradually increased from significantly lower than the inexperienced in 2010 to similar in 2012. Among few studies focusing on the development of

foraging abilities in seabirds, Weimerskirch et al. (2005) found that in Wandering Albatrosses (*Diomedae exulans*) inexperienced differed from experienced in their foraging strategy, but not in their efficiency, while studies on Australasian Gannets (*Morus serrator*) by Bunce et al. (2005) and Pyk et al. (2007) showed that differences in foraging success between immature and adult birds may be enhanced in periods of low prey availability.

The gradual development of inexperienced birds towards more efficient foragers is not immediately reflected in the results of the LME models, which showed that experienced individuals were targeting shallower and more productive areas with stronger gradients in 2010 and 2012, while in 2011 the inexperienced were finding the better foraging grounds. Considering the much more explorative behaviour of inexperienced birds, the 2011 may be considered a particularly fortunate season for this group. Interestingly the inexperienced birds were more than twice as successful as the experienced during that year, 64% breeding success compared to 25%. The use of remotely sensed data to predict foraging behaviour of marine top predators has been debated as the temporal relation between the marine productivity proxies and actual productivity is uncertain (Balance et al. 2006). Moreover it has been suggested that the current rapid climate change (IPCC, 2007) may result in spatial or temporal mismatch between foragers and their prey in many ecological systems (Worm and Tittensor 2011), as organisms respond differently to these changes, e.g. Grémillet et al. (2008) documented a spatial mismatch between copepods and pelagic fish as well as between pelagic fish and seabirds in the Benguela upwelling system, consequently seabirds were found in areas of high planktonic activity but with low availability of their prey, pelagic fish species. Opposite to the results by Grémillet et al. (2008), this

study demonstrates the usefulness of satellite-derived data for studying the spatial distribution of marine top predators.

4.4 – Conservation issues

The multi-year kernels of FA's overlapped largely (81% for experienced; 88% for inexperienced; 85% on average) with the mIBA identified in 2008 (Ramirez et al. 2008), while the designated SPA overlapped much less (59% for experienced; 66% for inexperienced; 63% on average). Thus, the results of this study justify the borders of the current mIBA, and suggest that making a protected area with static borders is a sensible option in this region. The foraging areas identified demonstrate that the current protected area (SPA) fails to include important foraging areas along the coast, north and south of Peniche, and therefore just includes 63% of the most important foraging areas. Although the Berlengas population of Cory's shearwaters have been slightly increasing during the last two decades (Lecoq 2012), this should be a great concern as there has been a negative trend for the pelagic fish species of the area since the late 1960s (Borges et al. 2003). Although the effect of fishing effort is challenging to disentangle (Arístegui et al. 2009), it is probable that an increase in northern winds during winter, inducing winter upwelling, has caused a regime shift from high to low productivity (Dickson et al. 1988, Santos et al. 2007), because the larvae of the main pelagic preys, Sardines (*Sardine sp.*) and Horse mackerel (*Trachurus trachurus*) is transported off the coast and dies. The North Atlantic Oscillation (NAO) index, which is a strong predictor of many meteorological patterns across Europe and North America has been in an extensive positive phase during the last decades, and is also correlated with this change in Iberian wind patterns (Borges et al. 2003). Cory's shearwaters breeding on the Berlengas are expected to respond to these fluctuations,

Fredrik Haug (2012) Breeding experience and foraging specialization of a marine predator and as documented by Paiva et al. (in press) very poor Sardine years like the 2010 season forced the birds to significantly increase their foraging range and effort. In that year, exceptionally long distances travelled and large home ranges were also observed for the two groups compared in this study, during the chick-rearing period (early September). The negative trends of these key prey species of marine top predators including the Iberian fisheries strongly emphasize the need for attentiveness and further research.

4.5 – Conclusion

This study documented a clear spatial segregation of experienced versus inexperienced Cory's shearwaters, which increased with each year of the study. The experienced individuals relied heavily on static variables like the bathymetry of the area, while inexperienced individuals were much more explorative, having a different combination and weighting of important variables (i.e. productivity proxies) for each study year. The nitrogen stable isotope ratios indicate that the diet of inexperienced birds was becoming more and more similar to that of experienced ones over the study years in concordance with the hypothesis that the groups should become more and more similar over the years (i.e. in terms of their trophic ecology). However their foraging strategy and targeted areas did not become more similar. The population has been increasing at a rate of about 10% per year the last two decades (Lecoq et al. 2012), and that might explain why they are spatially segregating. In addition, the reduction in concentration of one of their key prey, Sardines, may add a pressure that forces the species to adapt new strategies.

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