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DEPARTAMENTO DE CIÊNCIAS DA VIDA

FACULDADE DE CIÊNCIAS E TECNOLOGIA
UNIVERSIDADE DE COIMBRA

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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 Hugo Paiva Rodrigues (Instituto do Mar da Universidade de Coimbra) e do Professor Doutor Jaime Albino Ramos (Universidade de Coimbra)

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Abstract

Changes in marine productivity have been correlated with fluctuations in large scale atmospheric conditions driven by global indices such as the North Atlantic Oscillation (NAO). During the winter of 2009/2010 the second lowest NAO index was recorded leading to detrimental conditions that affected productivity levels in the Northeast Atlantic. The Cory's Shearwater *Calonectris borealis* is a plastic pelagic top predator which due to its status as sentinel of the marine environment can indicate qualitative changes at various levels of the food web. During the chick-rearing seasons of 2011, 2012 and 2014 we examined the at-sea foraging behavior of Cory's Shearwaters breeding in two islands of the Northeast Atlantic with contrasting productivity patterns: Berlengas, located on the rich upwelling area of the Portuguese shelf, and Cima Islet located in a poor oceanic environment in the Madeira Archipelago. During a year of low productivity Kernel estimations demonstrated that whereas Cima Islet's birds expanded their home ranges and core foraging areas to further grounds, Berlengas' birds maintained their distribution near the breeding colony. Under these conditions, birds from both islands increased significantly their foraging effort. MaxEnt modelling showed that once oceanographic conditions ameliorated from 2012-2014, all birds decreased significantly their foraging effort, and oceanic breeders concentrated their activity closer to their breeding grounds every year. Our study confirms that the Cory's Shearwater possess very high flexibility in its foraging tactics, and that neither oceanic nor neritic populations disperse randomly from their breeding colonies to the open ocean even under conditions of environmental stochasticity. Instead, populations breeding in contrasting environments vary in their responses according to their strategies and to the changing levels of marine productivity in their surroundings of their colonies. Under a future scenario of climate change, the ecological impacts of climatic conditions in marine ecosystems should be assessed considering also the vulnerability of seabird predators to extreme climatic events.

Resumo

Alterações na produtividade marinha tem sido correlacionadas com flutuações nas condições atmosféricas de grande escala impulsionada por índices globais, como o Índice do Atlântico Norte (NAO). Durante o inverno de 2009/2010 o índice NAO foi o segundo mais baixo registrado na historia levando a condições ambientais que reduziram significativamente os níveis de produtividade marinha no Nordeste do Atlântico. A cagarra *Calonectris borealis* é um ave marinha pelágica que, devido a seu estatuto como sentinela do meio marinho pode indicar alterações qualitativas em vários níveis da cadeia trófica. Durante as épocas de reprodução de 2011, 2012 e 2014, examinamos o comportamento alimentar no mar de cagarras em reprodução em duas ilhas do Atlântico Nordeste com padrões contrastantes de produtividade: Berlengas, localizado na área de afloramento costeiro da plataforma continental Portuguesa, e o Ilhéu de Cima localizada num ambiente oceânico mais pobre no arquipélago da Madeira. Durante um ano de baixa produtividade as aves do Ilhéu de Cima expandiram as suas áreas vitais e as áreas alimentação, enquanto as aves das Berlengas mantiveram sua distribuição perto da colónia. Em tais condições, as aves de ambas as ilhas aumentaram significativamente o seu esforço de forrageio. Os modelos MaxEnt mostrar que, à medida que as condições oceanográficas melhoraram no periodo de 2012-2014, todas as aves diminuiu significativamente o seu esforço de forrageio e os indivíduos oceânicos concentraram a sua actividade mais perto do seu local de reprodução em cada ano. Este estudo confirma que a cagarra possui uma elevada flexibilidade em termos de táticas de forrageamento, e que, quer as populações de áreas oceânicas, quer as populações de áreas neríticas, não dispersam aleatoriamente desde as suas colonias de reprodução para o oceano aberto, mesmo em condições ambientais adversas. Em vez disso, as populações reprodutoras em ambientes contrastantes variam em suas respostas de acordo com as suas estratégias e com a alteração dos níveis de produtividade marinha em redor das suas colonias. Em um cenário futuro de alterações climáticas, os impactos ecológicos das condições climáticas nos ecossistemas marinhos devem ser avaliados considerando também a vulnerabilidade dos predadores marinhos a eventos climáticos extremos.

Chapter 1.

Introduction



1.1.Productivity cues in the oceanic environment

Over the past two decades the appearance of the modern global observing system and global eddy-permitting circulation models have caused a revolution in physical oceanography (Siedler et al. 2013). Physical processes occurring at various spatial and temporal scales enable a number of biological processes, and scientists have identified several of them as indicators of high biological productivity in the vast oceanic environment. In the large scale, ocean circulation drives the activity of marine ecosystems worldwide. Westerly and trade winds produced by both the rotation of the Earth and the difference in solar heating at different latitudes lead to the formation of major currents and subtropical gyres in each of the four major ocean basins (i.e. North Pacific, South Pacific, North Atlantic and South Atlantic) (Mann & Lazier 2006).

While a gyre's interior is considered as an area of low biological productivity, the peripheries are affected by phenomena at smaller scales that alter the vertical structure of the ocean. For instance, in a typical tropical structure (TTS) of open waters there is a clear separation between a warmer, upper mixed layer (euphotic zone) and a cooler, heavier layer below (zone of highest nutrients concentration) through a thermocline or pycnocline. Changes in this typical composition often trigger productivity, such as the case of seasonality at higher latitudes. During winter in temperate and polar waters the mixed layer moves progressively deeper, and turbulence penetrates into the zone with the highest nutrients to push them up towards the euphotic zone. However, starting in April the sun warming of spring results in a shallower mixed layer, and phytoplankton cells that are held for longer periods in the euphotic zone causing the notorious spring bloom of the North Atlantic (Mann & Lazier 2006). Temporal factors are necessary at every spatial scale to understand and adequately appraise the nature of bio-physical interactions (Embling et al. 2012).

Likewise, upwelling is a phenomenon that affects the vertical structure. It originates with the equatorward winds present in the major ocean basins and moving parallel along their eastern coast. These wind stresses and the action of the Coriolis forces provoke deep waters to upwell and replace surface waters that are moved offshore. Upwelling events vary temporally influenced by the wind seasons and spatially affected by the ocean's topography. Once again, it is this variability the key to the high productivity. The periods of wind stress provide the upwelling of nutrients necessary for the subsequent outburst of

phytoplankton that is retained in calmer periods in the euphotic zone (Mann & Lazier 2006). The most active upwelling occurs in the 10° band of the Benguela, California, Iberia/Canary and Humboldt currents forming major Eastern Boundary Upwelling Ecosystems (EBUE) that spread to much further latitudes in each basin (Chavez & Messié 2009). EBUE are extremely prolific, hosting large fisheries of small pelagic species that represent 20% of the global fish production in less than 3% of the oceans total surface (Fréon et al. 2009). Besides the upwelling zones typical of coastal regions and continental shelves, in the open ocean mesoscale upwelling also occurs and it is usually indicated by pulses of high surface chlorophyll *a* concentration in satellite imagery (Mann & Lazier 2006).

Another significant factor in marine ecosystem dynamics that largely affects coastal regions and continental shelves is freshwater input. Specifically, in the North Atlantic basin the compound of river and estuarine discharges forms a counterclockwise flow of low salinity that moves bordering coastal regions, promoting upwelling and thus enhancing productivity. Out on the continental shelves the arrival of freshwater input assists in the formation of plume fronts known for their abundance of plankton and aggregations of fish. Every year, the summer brings stronger sun radiation that produces stratification but because of the presence of tidal currents some areas remain turbulent mixed. Therefore, additional fronts are also formed at the boundaries of these stratified and mixed layers (Mann & Lazier 2006).

At a smaller scale, tides that are born from the gravitational pull of the moon and the sun are extremely important altering the vertical zonation of waters remote from shore. If sufficiently strong and in areas shallow enough, they are able to mix the water column all year round, providing a continuous supply of nutrients to the euphotic zone. For instance, a high percentage of herring spawning grounds worldwide have been recorded in tidally mixed offshore regions. Moreover, the strong circular flow usually formed around offshore banks works as a retention barrier for fish larvae. After a longer period of time, fish species may be able to recognize these productive waters as a future spawning ground (Mann & Lazier 2006). Therefore, tidal currents strongly influence ecosystems dynamics, dictating prey distribution and ecology (Embling et al. 2012).

Seamounts are also associated with pelagic biodiversity. The seafloor is far from being a uniform environment. In fact, ocean crust features volcanic islands, seamounts, ridges

and platforms ranging from only tens of meters high to large volcanic formations (Steele et al. 2011). Presumably there are over 14,000 seamounts worldwide (McClain 2007). Their interaction with marine currents enhances internal wave generation, eddy formation, and local upwelling (Keating et al. 1987) increasing the vertical flux of nutrients (Morato et al. 2008). In the Azores archipelago species like the Skipjack *Katsuwonus pelamis*, Bigeye Tuna *Thunnus obesus*, Common Dolphin *Delphinus delphis* and Cory's Shearwater *Calonectris borealis* have been found in high aggregations around seamounts within the 400 m isobaths (Morato et al. 2008). Meanwhile, a long term monitoring study in the Western and Central Pacific (1980-2007) allocated the higher species richness to an area of 30-40 km around seamounts summits which may account as important feeding stations (Morato et al. 2010).

1.2. Seabirds: bioindicators of high biological productivity?

Upper trophic level predators encompass a number of pinnipeds, seabirds, cetaceans and large predatory fish which due to their position in the food chain (i.e. beyond secondary consumers) are considered indicators of the status and performance of the marine ecosystems. This approach becomes handy to assess marine ecosystems with the limited resources available for research. Furthermore, the charismatic nature of top predator species is important to raise awareness and financial support. Marine predators also seek resources at similar spatial and temporal scales as those from human activities (e.g. fisheries), thus data collected from them acquires utmost importance, and it can be easily linked with ecosystem management. Nevertheless, special considerations are necessary to confirm the validity of top predators as bioindicators. First, changes on the population or behavior of a species do not automatically reflect changes due to ecosystem management. Second, it appears that appropriate communities of study would be mostly present in temperate and subpolar regions, and even at this scale would be mainly relevant for coastal and shelf areas. Ultimately, top-predator responses are not 100 % predictive and an integrated multispecies approach is suggested to deal with these issues (Boyd et al. 2006).

Regarding seabirds, their terrestrial breeding system facilitates tracking changes in population sizes (Boyd et al. 2006). Seabirds are also long-lived with many species presenting a high level of philopatry (Prince et al. 1994; Mougin et al. 2001; Gómez-Díaz

et al. 2009; Ramos et al. 2013) which enable permanent monitoring. However, abundance levels of a species alone are not the most reliable indicator because of their late sexual maturity and the variable age when they start attending the colony and breeding (Cook et al. 2014). Instead, parameters used as indicators should reflect the complexity of an ecosystem while managing a simple concept with a direct and cost effective methodology (Dale & Beyeler 2001). As many seabird species are known to be central place foragers during breeding (Onley & Persons 1979; Weimerskirch 2007), the additional energy constrains involved in the processes of incubation and chick rearing challenge individuals to find productive patches inside their foraging ranges (Paiva et al. 2010b). Hence, at sea foraging behavior during reproduction represents a more reliable proxy of productivity in the marine environment because it is closely linked with resource availability inside a species territory.

Examples of the use of seabird predators as indicators of productive hotspots in marine ecosystems are found worldwide. For instance, several studies confirm that the Cory's Shearwater *Calonectris borealis* breeding in remote pelagic environments of the Northeast Atlantic rely on commuting predictable movements to target areas of high productivity in the ocean, and that individuals from different colonies and populations overlap in their foraging areas along certain hotspots which are distinctive for their complex physical processes (Paiva et al. 2010a, 2010b; Ramos et al. 2013; Robert et al. 2014). Similarly, three Procellariiforms as representatives of the pelagic community have been used to identify foraging hotspots over the continental shelf and slope in the Mediterranean Iberian Coast (Arcos et al. 2012). Meanwhile in the Southern Indian Ocean, ten species of seabirds (i.e. albatrosses, petrels and penguins) with diverse habitat requirements have been tracked to assess highly productive areas at an ocean basin scale (Delord et al. 2014).

Another aspect that supports the concept of seabirds as bioindicators is their association with other marine predators. As central place foragers and flock feeders these predators tend to aggregate seasonally around predictable areas (Lascelles et al. 2012). Furthermore, they have been frequently found accompanying other marine subsurface predators during their feeding events, including various species of dolphins and tunas (Hebshi et al. 2008; Santos et al. 2009). An extraordinary example is the multi-species aggregations that occur in central Azores involving several species of dolphins, tunas and seabirds (mostly the Cory's Shearwater) with peak activity at dawn and dusk. Common

dolphins (*Delphinus delphis*) together with spotted dolphins (*Stenella frontalis*) have been observed to encircle fish schools into a compact ball that makes several thousands of fish prey available to other predators close to the surface (Clua & Grosvalet 2001).

1.3.A new era for Seabird Research: GPS tracking and implications for the establishment of Marine Protected Areas (MPAs)

Seabirds are considered the most threatened group of birds worldwide, but traditionally the conservation efforts were focused on threats faced at their breeding grounds (Ramirez et al. 2008). Albeit these actions are beneficial, the quality, location and extent of their feeding grounds have the highest importance for the breeding success and survival of marine top predators (Davis et al. 2005). Consequently, at present seabird scientists around the world are focusing their endeavors on the at-sea foraging behavior using methods such as at-sea surveys, GPS tracking and species-habitat modelling. By targeting areas of high biological productivity and important ecological processes in pelagic environments, seabirds are useful tools to identify candidate MPAs (Paiva et al. 2010e; Lascelles et al. 2012; Le Corre et al. 2012), which makes them ideal surrogate species.

Protection in oceanic environments has lagged behind that of terrestrial ecosystems mainly because of the great challenges involved in marine research. Until the 1990s most of the data was collected at breeding colonies or from vessels. However, the burgeoning of electronic technology caused a revolution in seabird studies, unveiling valuable information about the at-sea foraging behavior and exposure to anthropogenic risks (Burger & Shaffer 2008), essential aspects in conservation management. Since then, there has been an array of tracking devices introduced for different purposes of study. Platform terminal transmitters (PPTs) are an example of modern accurate devices (1-3 km) with solar power enhanced lifespan that do not require recovery for data processing. These characteristics make them ideal for studies of initial dispersion and habitat use of fledging pelagic seabirds. On the other hand, global location sensing (GLS) estimate latitude and longitude based on ambient light levels. Their coarse spatial resolution can be improved with the addition of temperature sensors to record long range movements (Burger & Shaffer 2008). GPS devices are the most precise of all, recording locations up to every second with an accuracy in the range of a few meters. GPS loggers can be as light as 8 g which allows studies of ground speed, micro-movements and area-restricted searching

behavior (ARS) of even relatively small species like kittiwakes (Burger & Shaffer 2008; Kotzerka et al. 2010). This line of research is providing remarkable insights about the behavior of seabirds throughout their entire life cycle, hence at different temporal and spatial scales.

Birdlife International has been continuously identifying Important Birds Areas (IBAs) in terrestrial regions since 1980 as precursors of national and international protected areas. Conversely, a system of marine IBAs has been developing more recently supported in data gathered from tracking devices (Ramirez et al. 2008). Biotelemetry has proved essential to monitor movement ecology and design conservation units at a large scale (Grémillet et al. 2014). Portugal and its archipelagos are an important center for seabird activity, and Azores and Madeira have been identified as areas with priority of conservation. In fact, 20 out of 332 species of seabirds recorded worldwide breed in Portugal and many others frequent its territorial waters. At least ten of these species hold some category of threat status. Hence, SPEA – the Birdlife partner in Portugal – has played a major role in introducing a standard methodology to design marine IBAs proposals (Ramirez et al. 2008). As studies on the at sea behavior and foraging of seabird species continue increasing, delimitation of IBAs and marine protected areas (MPAs) will become more realistic specially when considering highly profitable areas at the meta-population scale (Ramos et al. 2013) and a multi-species approach (Lascelles et al. 2012). The identification of IBAs and MPAs has been accompanied by additional campaigns (i.e. bycatch mitigation, eradication of invasive species, collaboration with regional fisheries management) all enclosed inside the Global Seabird Programme (Birdlife International 2010).

1.4. Behavioral Plasticity in Seabirds and Influence of climate stochasticity

The ability of seabirds to detect hotspots in the open ocean is providing enormous benefits to conservation, thus it is important to comprehend the mechanisms that they rely on to find upwelling areas, fronts or seamounts. Predictable oceanographic parameters are continuously associated with the foraging ecology of seabird predators. This is the case for the Cory's Shearwater, a very widely distributed representative of the Northeast Atlantic, which has been extensively monitored over the last decade in a variety of breeding phases and marine environments. During incubation and chick-rearing, the

feeding areas of this species are characterized by high chlorophyll *a* concentration, low sea surface temperature and low depth (Paiva et al. 2010b), with bathymetry maintaining a high importance across different populations, habitats and spatial scales (Paiva et al. 2010a). The Black-browed Albatross *Thalassarche melanophris* breeding in the Falkland Islands also has a tendency to feed in shallow areas and steep seafloor (Catry et al. 2013). Likewise, in the endangered Monteiro's Storm Petrel of Azores *Oceanodroma monteiroi* the average breeding success was found strongly correlated to oceanic conditions (i.e. Chl-a) (Robert et al. 2014). Other environmental parameters that have been associated with the foraging grounds of seabird predators include: distance to land, oceanographic fronts, salinity, wind speed, among others (Louzao et al. 2009; Tremblay et al. 2009).

The diversity of physical features in the Northeast Atlantic creates a highly heterogeneous environment with two distinctive gradients: productivity increases north from the warmer subtropical waters of Selvagens to the colder waters of Azores and beyond, and oceanic environments are expected to be less profitable than the Portuguese and African coasts and shelves (Paiva et al. 2010c). Therefore, species like the Cory's Shearwater with numerous colonies and populations constrained by divergent environmental conditions, need a high level of plasticity that would be reflected in the at-sea foraging behavior. Because of the additional constraints of the chick-rearing period, populations breeding in low productive oceanic areas (i.e. Madeira and Azores archipelagos) are expected to adopt a bimodal strategy consisting of: short trips for food provisioning to their chicks, and long trips to recover depleted energy reserves (Granadeiro et al. 1998). Conversely, a population breeding in Berlenga next to the Portuguese coast and over the productive continental shelf reports a unimodal strategy of short trips. Furthermore, oceanic populations record higher foraging effort, longer home ranges and foraging areas, adaptations that allow them to cope with the low productivity of the surroundings but at a considerable cost: i.e. lower chick growth and breeding success than in Berlenga (Paiva et al. 2010b, 2010c).

The dual foraging strategy, first discovered in Blue Petrels *Halobaena caerulea* (Chaurand & Weimerskirch 1994) and later documented it in several Procellariiform species (i.e. albatrosses, shearwaters and petrels) (Baduini & Hyrenbach 2003) is seen as an alternative to cope with the issue of distant, unpredictable food resources (Warham 1990). As central place foragers which often breed in remote islands, seabirds are constrained to return to the colony from their feeding grounds (Navarro & González-Solís

2009). Breeding success is highly dependent on foraging effort (Weimerskirch et al. 2000, 2005a), thus flight efficiency is one of the most important adaptations and provides seabirds a certain degree of plasticity to adopt different foraging tactics. Specifically in procellariiforms, species often use wind-shear soaring (i.e. choose flight directions to exploit ambient wind by climbing and descending across the thin wind shear layers) to gain up to 80-90% of the energy required for sustained soaring from the same environment (Paiva et al. 2010d; Richardson 2011). The ability of seabird predators to use the wind fields makes long foraging trips highly profitable, enabling them to recover the energy depleted during chick provisioning (Weimerskirch et al. 2003).

Even though seabirds may be resilient to the natural fluctuations of the environment, human induced climate change is affecting marine ecosystems worldwide. The association between global warming and an increase in the frequency and intensity of extreme heat (Meehl et al. 2000) and extreme weather events (Alley et al. 2003) has been established long ago. Due to future warming strong changes are projected in EBUE regarding intensity, timing and spatial structure (Wang et al. 2015). Moreover, the consequences would be greater at higher latitudes (Crawford et al. 2015). The additional constraints imposed by climate change will cause all taxonomic groups to face a higher risk of extinction (Urban 2015). Naturally, the effects start at lower trophic levels, and deeply impact marine top predators in a bottom-up manner (Grémillet & Boulinier 2009). In the eastern Bering Sea the dearth of resilience in the zooplankton community to variations in ice cover is having detrimental consequences in the production at higher trophic levels (Eisner et al. 2014). Likewise, in Southern Benguela climate induced changes have altered the distribution of fish prey provoking opposing reactions among seabird predators. While Cape Gannets *Morus capensis* and Swift Terns *Thalasseus bergii* have increased their proportion in the seabird community, African Penguins *Spheniscus demersus* and Cape Cormorants *Phalacrocorax capensis* have decreased it by about 50 % and 40 % respectively probably due to their behavioral inertia (Crawford et al. 2015).

Changes in atmospheric circulation have been correlated with changes in oceanic circulation, and therefore seriously affect biological processes at all levels of the food web across the oceans. In the case of the North Atlantic, these fluctuations are recorded via the North Atlantic Circulation index (NAO). Monitoring of the NAO over the 20th century indicates opposite atmospheric and biological effects for each side of the Atlantic.

For instance, positive NAO values are associated with warm winters in the Northeast Atlantic which results in the northward movement and expansion of southern fish species and improved recruitment. At the same time, cold winters are expected in the Labrador and West Greenland and detrimental environmental conditions for fish stocks (Mann & Lazier 2006). Furthermore, the NAO has been identified as an indicator of extreme upwelling events (Benazzouz et al. 2014) making it an adequate surrogate of climatic conditions and marine productivity in the region (Paiva et al. 2013a, 2013b; Haug et al. 2015), and a useful indicator of more frequent extreme events in a future scenario of climate change. Due to the fact that the NAO is most pronounced during winter and oscillations leave long-lasting effects on sea surface conditions (Paiva et al. 2013a), the extended winter NAO index from Hurrell (1995) is normally considered.

1.5. Justification and aim of the study

During the extreme climatic conditions of the winter 2009-2010, the upwelling events along the Portuguese coast would have been seriously affected as indicated by the second lowest NAO value (-4.64) since 1648 (Paiva et al. 2013a). The low NAO values translate in very low sea surface temperatures and unusually intense upwelling phenomena which usually mean that strong winds cause plankton and fish larvae to move away from the protection of the continental shelf, increasing their mortality and altering the upper levels of the food web in the subsequent months (Santos et al. 2007). The low productivity of 2010 was also evidenced in the record low figure of pelagic fish landings in Peniche (Paiva et al. 2013a). However, since 2011 the NAO suggests a recovery in productivity levels, reaching a positive figure again in 2012 (Haug et al. 2015), but also with high oscillations from year to year until the present. The aim of this study is to compare the changes in the foraging behavior of a widespread, resilient seabird predator of the North Atlantic, the Cory's Shearwater breeding in two islands with contrasting productivity in their surroundings (i.e. Berlengas in a neritic area, and Cima Islet in an oceanic environment near Porto Santo, in the Madeira Archipelago), and during years of recovery from a drastic climatic event (i.e. 2011, 2012 and 2014). The study took place during chick-rearing, considered energetically the most demanding breeding phase for adults, and during which they are most sensitive to variability in food resources (Grémillet et al. 2014). Human induced climate change is likely to increase the frequency of extreme

climatic events (Huber & Gullede 2011), hence it is important to study the diversity in plastic responses of seabird predators to environmental stochasticity. Because of their status as qualitative sentinels of the marine environment, changes in their feeding behavior are expected to reflect changes in ecological processes at a large scale (Gremillet & Charmantier 2010).

Some signs on how this species adapts to fluctuations in productivity levels are given by Paiva et al. (2013b). Females were studied in Berlengas from 2007 to 2011 during their pre-laying exodus, and each year birds ventured further in their pursuit for productive grounds as the environmental conditions deteriorated. Amazingly, their search took them in 2011 in one of the longest pre-laying foraging excursions to the Altair seamount along the Newfoundland coast in Canada, almost 4,000 km away. Males do not need a pre-laying exodus because they are not constrained by the energy demands of egg-laying, still inexperienced males were especially explorative during the same season, deviating considerably from their usual home ranges and foraging areas (Haug et al. 2015). These two studies were performed during the pre-laying season and may not reflect the responses of Berlengas birds during chick-rearing because pre-laying birds are not constrained by the duties of brood-guarding (Catry et al. 2009). On the other hand, the feeding ecology of an oceanic population during years of contrasting environmental conditions has not been assessed thus far. Due to the propensity of oceanic birds to concentrate their foraging activity in larger areas, and to invest more effort during the breeding season than neritic populations (Paiva et al. 2010b; Alonso et al. 2012) we expect Cima Islet birds to show less buffer against poor environmental conditions. Moreover, birds in neritic areas will always be more buffered against strong environmental changes, because the marine productivity in those areas should be less affected than in more pelagic areas (where birds may be often more limited by the disperse and unpredictable foraging resources). Therefore, we made the following predictions: 1) Cima Islet birds' home ranges and foraging areas will be more affected in years of low productivity compared to birds from Berlengas; 2) the rate of increase in foraging effort will be higher in Cima Islet than in Berlengas during these years; and 3) once productivity around the colonies improves, Cima Islet birds will react faster adopting their usual home ranges, foraging areas, and foraging effort parameters.

Chapter 2.

Methods



2.1. Study Area

Broadly speaking our study takes place in the Northeast Atlantic, a region with particular features that influence its spatial productivity patterns. The subtropical gyre of the North Atlantic is born on the warm waters of the western boundary Gulf Stream current, which moves north east bordering the North American coast until it finds the cold rich waters of the Labrador Current (Fig. 1). This collision results in the formation to the east of the North Atlantic current which moves polewards, and the Azores and Canary currents that flow circling Azores and bordering the Portuguese and African coasts respectively (Mann & Lazier 2006). Conditions inside the gyre are in general constantly stratified leading to low productivity in general (Mann & Lazier 2006).

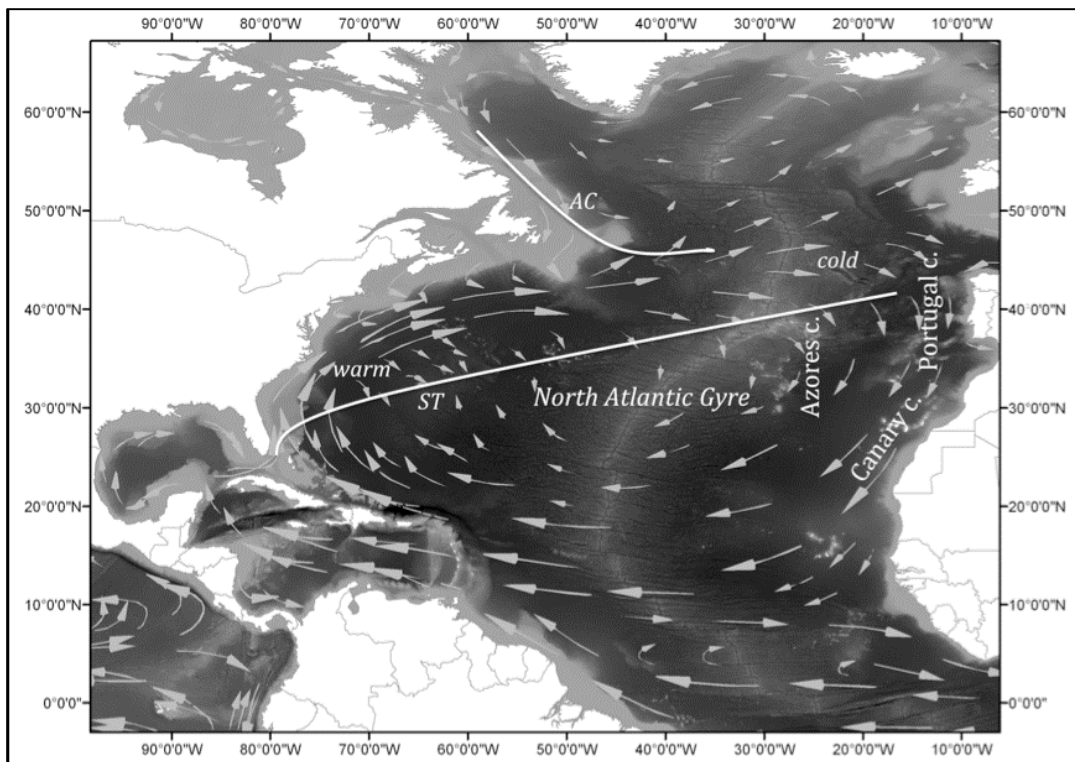


Fig. 1. Main oceanic currents on the North Atlantic region. AC (Arctic convergence), ST (subtropical convergence). The Azores, Portugal and Canary currents are represented (from Paiva 2009)

Conversely, the continental part is under the influence of the highly productive Canary Current upwelling ecosystem (CanC), an enormous marine region that covers an area roughly between the south of Senegal (8°N) and the Iberian Peninsula (43°N), subject to seasonal variations (Arístegui et al. 2009, Benazzouz et al. 2014). Upwelling varies latitudinally as a result of coastal orientation, with the Iberian Peninsula and Morocco

presenting a seasonal and weak pattern that reaches a maximum in summer. Seasonality decreases and upwelling increases further south until becoming semi-continuous at about 10° and 20°N. However, this pattern is interrupted around the Gulf of Cadiz due to the unfavorable topography for coastal upwelling and the exchange of water mass with the Mediterranean Sea (Aristegui et al. 2009a; Chavez & Messié 2009). A clear separation in terms of circulation, physical environment and shelf dynamics divide the CanC into five sub-regions (Fig. 2b): the Galician (SR1 at 42-44°N), Portuguese (SR2 at 37-42°N), Gulf of Cadiz SR3 at 33-37°N), Moroccan (SR4 at 21-33°N), and Mauritanian-Senegalese west coasts (SR5 at 12-21°N). (Aristegui et al. 2009a).

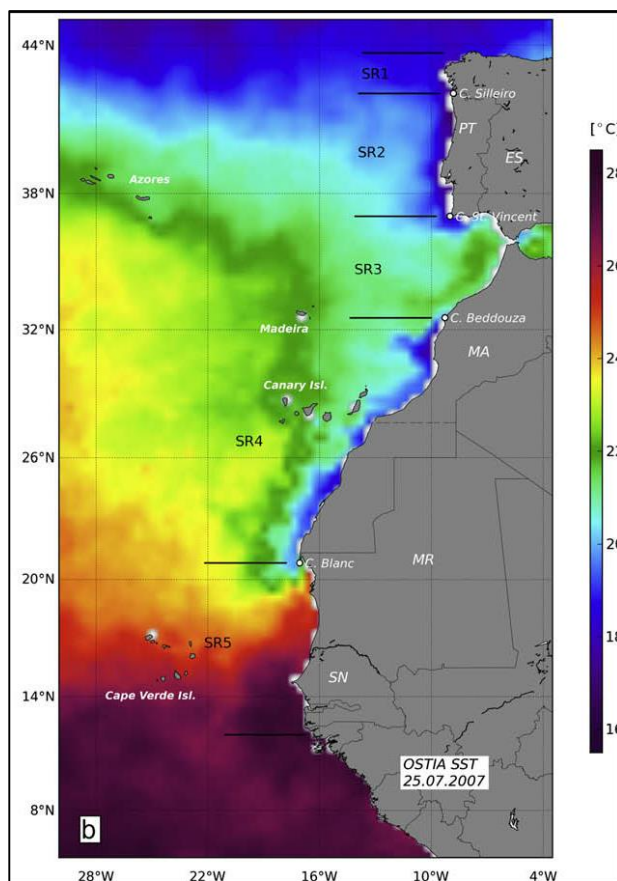


Fig. 2. Map of the five sub-regions form in the CanC: SR1 (Galician), SR2 (Portuguese), SR3 (Gulf of Cadiz) SR4 (Moroccan), SR5 (Mauritanian). PT (Portugal), ES (Spain), Ma (Morocco), MR (Mauritania), SN (Senegal). Sea surface temperature is illustrated in the background (25 July 2007 from OSTIA). Adapted from Aristegui et al. (2009)

More specifically, the entire coast of Portugal (SR2) is located in the northern end of CanC where divergent conditions in the upwelling cycle create a spatial diversity in the shelf systems north and south of Lisbon. The wider north shelf receives higher input of rivers and rainfall causing an early stratification which favors a premature phytoplankton bloom. As the phytoplankton travels offshore there is enough time to develop large populations of zooplankton that can support the typical abundance of pelagic fish in this

region. On the other hand, the southern shelf is narrower and collects a smaller amount of freshwater insufficient for a marked stratification. Phytoplankton bloom then relies on the later surface warming which does not provide enough time for large amounts of zooplankton to grow. Instead the benthic species are benefited, not only by the unconsumed phytoplankton that sinks to the bottom but also by an organic load arriving from the north (Mann & Lazier 2006).

The first study colony is located in the Berlenga Island – BER (39°24'49"N, 9°30'29"W), approximately 8 km away from Peniche in the Portuguese coast. BER covers an area of 78.8 ha, and together with the smaller islets of Farilhões and Estelas form the Berlengas archipelago (Faria 2014). Berlenga features the only breeding populations of pelagic seabirds in continental Portugal: the Cory's Shearwater (*Calonectris borealis*), and the Madeira Storm-Petrel (*Oceanodroma castro*), the latter only in Farilhões. Other breeders include: the European Shag (*Phalacrocorax aristotelis*), Lesser Black-backed Gull *Larus fuscus*, or the critically endangered Common Murre *Uria aalga*. The Yellow-legged Gull (*Larus michahellis*) is the most abundant species in the archipelago, and because of its great increase in numbers it has been subject to population control since 1994. Furthermore, the highly productive marine surroundings are important during winter or in the spring and autumn migrations for species such as the Northern Gannet (*Morus bassanus*), with flocks of thousands of individuals frequently observed in these months (Ramirez 2008).

The Madeira archipelago is formed by two main islands: Madeira and Porto Santo. Additionally, five small islets surround Porto Santo (i.e. Fora, Cenouras, Ferro, Baixo and Cima). All islets are uninhabited and thus preserve their characteristic Macaronesian flora and fauna. The second study colony is located in Cima Islet – CIM (33°03'19"N, 16°16'54"W), a rocky formation that reaches 111 m high. Native flora and fauna are still preserved in this area with important seabird breeding species including the Cory's Shearwater (*Calonectris borealis*), Madeira Storm-Petrel, and Bulwer's Petrel (*Bulweria bulwerii*) (Oliveira & Menezes 2004). While Madeira is positioned in an oceanic environment away from the productive continental shelf and the influence of the CanC, sporadic upwelling events still occur. They may be associated to eddies formed from temporal events (Mann & Lazier 2006), or to an island mass effect as a result of the interaction of the tidal currents, dominant trade winds and the interior mountain range. Upwelling is particularly dynamic between Madeira and Desertas Islands (Caldeira et al.

2002). Seamounts in the surrounding oceanic environment such as Ashton, Josephine (Paiva et al. 2010b), Seine and Ampere (Martin & Christiansen 2009) may also promote high biological productivity. Despite the presence of all these factors, low marine productivity is typical of oceanic islands with a short shelf as CIM (Paiva et al. 2010c).

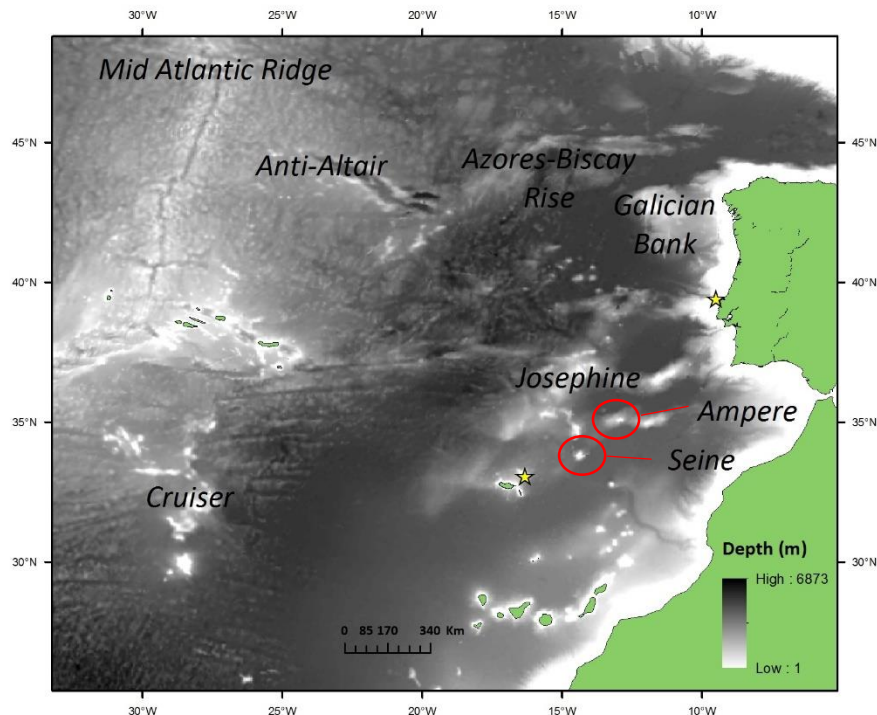


Fig. 3. Seafloor depth (m) in the Northeast Atlantic featuring names and locations of important seamounts of the region. The yellow stars represent the breeding colonies in this study (Berlenga in the north and Cima Islet in the south). Smaller seamounts close to Cima Islet are circled in red.

2.2. Study Species

Procellariiforms are an exceptionally pelagic group of seabirds. Four subfamilies and roughly 80 species form a diverse assemblage of seabirds, the most representative and yet the least known in marine ecosystems (Ramirez et al. 2008, Onley & Scofield 2007). The Cory's Shearwater *Calonectris borealis* is a medium sized representative with an extremely wide distribution, breeding in remote islands and islets of all archipelagos of the Northeast Atlantic except Cape Verde (Onley & Scofield 2007). Taxonomically it was previously known as *Calonectris diomedea borealis* in a complex of two subspecies that also included *Calonectris diomedea diomedea* breeding in the Mediterranean. Since 2014 both races achieved species status following Del Hoyo et al. 2014 (<http://www.birdlife.org/>). *Calonectris borealis* migrates through long trans-equatorial routes from its breeding grounds to reach wintering areas mainly in the coasts of South

America and South Africa, but also in other regions of the north, central and south Atlantic, and the Indian Ocean (González-Solís et al. 2007; Onley & Scofield 2007; Dias et al. 2011).

From the total population (c. 251,100 - 251,300 pairs), 85% breeds in Azores and Madeira, approximately 15% in the Canary Islands (<http://www.birdlife.org/>) and a few individuals in Berlengas (c. 980 - 1070 pairs) (Lecoq et al. 2011). The Cory's Shearwater has a high reproductive investment reflected in its 8 month long breeding cycle that usually starts in early March when adults arrive to their colonies. Nest are placed in natural burrows, cavities and rocky crevices (Navarro et al. 2007). Females are famous for a pre-laying exodus that lasts in average at least 19 days, starts in early May (Jouanin et al. 2001), and is vital to meet the energy demands required to form a large egg. After their return to the colony in late May, females lay a single egg which will be incubated in shifts by the breeding pair during almost two months (Paiva et al. 2010b). Eggs hatch in mid-late July and once again chick rearing responsibilities are shared by both parents alternating duties and provisioning the chicks on a daily basis. As the long three months of chick rearing progress both the frequency of food provisioning and the degree of digestion by the parents decrease (Ramos et al. 2003). By late September the chick stops growing and a reduction in overall body size is compensated with wing growth. This process lasts until late October / early November when chicks finally fledge to start exploring the ocean at night (Warham 1990).

2.3.GPS Loggers: deployment and specifications

GPS loggers were deployed in adult breeders during mid-August 2011, 2012 and 2014 for BER birds; and during September 2011, 2012 and 2014 for CIM birds; corresponding to early and mid chick-rearing period of the study species respectively. Devices consisted of a GPS receiver and logger, antenna, CR2 battery and user interface circuits (see Steiner et al. 2000 for specifications on the original device). Loggers were programmed to record one location (± 4 m) every 5 minutes. The original plastic case was replaced for a long thermo-retractable rubber sleeve to decrease weight and warrant impermeability. Loggers were carefully attached to the bird's back feathers with a small piece of Tesa® tape in a process that took less than ten minutes. Birds were then immediately returned to their nests to minimize handling stress. Logger's weight was recorded below 3% of the bird's

body weight, which has been reported to have no deleterious effects on seabirds, including the study species in BER (Paiva et al. 2010c).

2.4. Trip filtering

Each individual Cory's Shearwater carried a GPS device for a period of several days after which the device was retrieved and data downloaded for multiple foraging trips. Distance-to-colony was determined for each GPS position which allowed us to calculate the number of foraging trips for each bird. We considered that a new trip starts when the distance-to-colony is 0 or close to this value and there is a significant period of time with absence of data (e.g. at least 20 or 30 minutes). Trip duration was also calculated with the time records for each GPS position. Foraging positions were selected after applying several filters, namely: distance-to-colony > 2 km to avoid the influence of activities of birds maneuvering nearby or resting at sea waiting for darkness, speed > 2 km/h to exclude positions of birds resting or drifting at sea; and speed < 15 km/h due to the fact that seabirds usually commute in a direct flight to reach an area of interest, when their speed decreases to forage actively (Louzao et al. 2009). These speed thresholds were confirmed by our own data when inspecting frequency distribution plots of all recorded speeds. The resultant foraging-filtered datasets (one per colony) were used for kernel estimations and species distribution modelling.

2.5. Kernel estimations

Kernel utilization distribution analyses were performed to identify the most relevant foraging areas for the study species at each colony, using the foraging-filtered subsets to calculate Home Ranges (HR) and core foraging areas (FA). The utilization distribution (UD) describes the distribution of geographical positions of an individual or group over a period of time (Van Winkle 1975), providing a probabilistic measure of the animal's relative use of space (Katajisto & Moilanen 2006). Hence, Kernel UD methods (Worton 1989), enable us to transform these location points in polygons that depict higher or lower probability of occurrence (Faria 2014). Kernels were created with the R package *adehabitatHR* (Calenge 2006), assuming UD95 and UD50 to represent HR and FA

respectively based on previous studies of Cory's shearwater in the same study area (Paiva et al. 2010b).

The ad-hoc method was used to compare kernel estimations between different trips and years for each colony. This option of the *kernelUD* function provides an optimal smoothing factor (*h*) that will be applied to all foraging trips and allows comparisons. For this study the values of *h* were determined at 0.1 for BER and 0.3 for CIM. Then, kernel overlaps were performed for each year separately first with trip id as a parameter to compare the consistency of all trips, and second using bird id to estimate the overlap between individuals. Finally, kernel overlaps were calculated for pairs of years and considering all possible combinations (i.e. 2011-2012, 2011-2014 and 2012-2014) in order to assess temporal changes in FA. The function used was *kerneloverlap* of the R package *adehabitatHR*.

2.6.Environmental Data

Environmental predictors were selected from a series of variables that have previously shown important correlations with distribution and abundance of seabirds (Louzao et al. 2009; Tremblay et al. 2009). Included in this study are: sea surface temperature (SST) and chlorophyll-*a* (CHLA) as dynamic variables, and bathymetry (BAT) as static variable. Bathymetry was downloaded from the ETOPO 1 database at ~2 km spatial resolution (0.0167°) as ASC files from the BloomWatch website: <http://coastwatch.pfeg.noaa.gov/coastwatch/CWBrowserWW180.jsp>. Night-time SST was selected because of the lower amplitude of variation in water temperature than during daytime (Paiva et al. 2010b). We also considered anomalies and gradients of SST (ASST and GSST) and CHLA (ACHLA and GCHLA) to account for small scale variability, gradient of BAT (GBAT) which relates to the presence of topographic features (Louzao et al. 2009), and CHLA peak (CHLA_PK) for productivity persistence (Haug et al. 2015) (see Table 1 for details). CHLA_PEAK was computed from binominal layers of CHLA in the study period (March-August) during the 13 last years (2002–2014). Cells with a CHL concentration >1 mg m⁻³ were assigned a value of 1 and lower values assigned zeros (Louzao et al. 2012; Suryan et al. 2012; Afán et al. 2014). Environmental variables (i.e. CHLA and SST) were downloaded as monthly composites, from Aqua MODIS standard mapped image (SMI-HDF format) at ~4 km spatial resolution from

<http://oceancolor.gsfc.nasa.gov/cgi/13>. All HDF files were subsequently transformed to rasters with the Marine Geospatial Ecology Tools (MGET) toolbox package of ArcGis 10.0. Dynamic variables were aggregated in periods of three month composites corresponding to the two seasons prior to the fieldwork each year: spring (SPR: March, April and May) and summer (SUM: June, July and August). Additionally, distance-to-colony (DCOL) and distance-to-land (DLAN) were calculated with the Spatial Analyst toolbox of ArcGis 10.0. As the Cory's Shearwater becomes a central place forager during chick-rearing, returning frequently to the colony is an important constraint (Orians & Pearsons 1979).

2.7. Species Distribution Modelling (SDM)

The environmental variables previously described were used to perform a habitat niche model or Species Distribution Model (SDM) with MaxEnt 3.3.3k software. Multiple methods are available to assess the relationship between species data and environmental parameters at sites, but an important difference lies in the type of data they use. Formal biological surveys usually provide presence/absence data or abundance of species. In these cases, regression methods (i.e. GLMs, GAMs, BRT) have been the most widely used for SDM (Elith et al. 2011). However, in this study (as it happens often in natural sciences) the database represents presence-only records. MaxEnt is able to model species distribution based on presence-only data and maintain a predictive performance at the same level of the highest rated methods (Elith et al. 2006).

At the beginning of the process, tracking data was rescaled into a spatial grid with cell size of 4x4 km (0.0417°) to match the spatial resolution of the environmental data. Then, each grid was coded and assigned a value of 1 if actively foraging or 0 if traveling. Preliminary models were run for BER and CIM for each year, including all environmental variables and 5 replicates. A threshold of 1% was established to evaluate percentage of contribution and permutation importance, thus variables under this value were excluded from the final models. The process was repeated in order to discard variables with only minimal contribution to the models performance. At the end, the final MaxEnt models were run only with the selected variables for each colony and each year with the following settings: logistic output format, duplicates removed, 30% random test percentage, 50 replicates of random (bootstrap) subsamples. Results are summarized as the mean of the

50 models. The outputs also include a jackknife test result chart, a predicted presence probability map, response curves, percentage of contribution, and a graphic of the receiver operating characteristic (ROC) curve which appraises the predictive performance of the model with the Area Under the receiver operating characteristic Curve (AUC). The AUC value ranges from 0 to 1, with 0.5 indicating model performance equal to that of a random prediction. Other values can be interpreted as follows: $AUC > 0.90$ excellent; if $0.80 < AUC < 0.90$ good; if $0.70 < AUC < 0.80$ reasonable; if $0.60 < AUC < 0.70$ poor; and if $0.50 < AUC < 0.60$ unsuccessful (Araujo et al. 2005).

2.8.Data analysis

R software was used in all statistical analyses, including several R packages and functions (e.g. *MASS*, *maptools*, *adehabitatHR*) and custom-built functions. Quantile-quantile plots and Cleveland dotplots were designed for all variables to check for normality and homoscedasticity respectively (Zuur et al. 2009), and when necessary logarithmic transformations were adopted. Inter-annual differences on foraging trips parameters (e.g. maximum distance-to-colony, total distance, UD95, UD50 and others) were tested with generalized linear mixed models GLMMs. Trip identity was nested within the individual as a random term to avoid potential pseudo-replication problems, since all individual birds performed multiple trips. R packages used in the GLMMs were *lme4* (Bates et al. 2014) and *lmerTest* (Kuznetsova et al. 2014). Results are expressed in means \pm SD and are considered significant at $p < 0.05$.

Table 1. Summary of environmental variables used in the species distribution modelling analysis of Cory's Shearwater tracked in Berlenga and Cima Islet colonies. Dynamic variables were calculated for 2011, 2012 and 2014

Environmental Variables / code	Derived Metric	Manipulation / Oceanographic process	Source
<i>Dynamic</i>			
Sea surface temperature / SST_SPR, SST_SUM (°C)	mean	Temporal mean from monthly climatologies for spring and summer of each year of study / water mass distribution	Aqua-MODIS
Sea surface temperature anomaly / ASST_SPR, ASST_SUM (°C)	mean	Temporal deviation of sea surface temperature compared to a 20 year average of sea surface temperature for spring and summer of each year of study / oceanic fronts	Aqua-MODIS
Sea surface temperature gradient / GSST_SPR, GSST_SUM (%)	gradient	Temporal gradient from monthly climatologies for spring and summer of each year of study / oceanic fronts	Aqua-MODIS
Sea surface temperature range / SST_RANGE (°C)	range	Temporal range from monthly climatologies (2002-2014)	Aqua-MODIS
Chlorophyll-a concentration / CHLA_SPR, CHLA_SUM (mg m ⁻³)	mean	Temporal mean from monthly climatologies for spring and summer of each year of study / ocean productivity	Aqua-MODIS
Chlorophyll-a anomaly / ACHLA_SPR, ACHLA_SUM (mg m ⁻³)	mean	Temporal deviation of Chlorophyll-a concentration compared to a 20 year average of Chlorophyll-a concentration for spring and summer of each year of study / oceanic fronts	Aqua-MODIS
Chlorophyll-a gradient / GCHLA_SPR, GCHLA_SUM (%)	gradient	Temporal gradient from monthly climatologies for spring and summer of each year of study / oceanic fronts	Aqua-MODIS
Chlorophyll-a range / CHLA_RANGE (mg m ⁻³)	range	Temporal range from monthly climatologies (2002-2014)	Aqua-MODIS
Chlorophyll-a peak / CHLA_PK (mg m ⁻³)	maximum	Maximum concentration / productivity persistence	Aqua-MODIS
<i>Static</i>			
Bathymetry / BAT (m)	mean	Spatial mean / neritic vs pelagic environments	ETOPO 1
Bathymetry gradient / GBAT (%)	gradient	Spatial gradient / slope (shelf-break, seamounts)	ETOPO 1
Distance-to-colony / DCOL (km)	minimum	Minimum distance to the breeding colony / central place foraging effects	ArcGis
Distance-to-land / DLAN (km)	minimum	Distance to the nearest coastline / neritic vs pelagic domains	ArcGis

Chapter 3.

Results



3.1. Inter-annual environmental stochasticity in the North Atlantic

The extended winter NAO index (December-March) indicated high oscillations in atmospheric conditions in the North Atlantic throughout the entire study period (Table 2). Years 2011 and 2013 recorded negative indices (-1.6 and -2.0 respectively), but were followed by positive values the subsequent year. Even though the NAO in 2014 was slightly lower than in 2012, there was a higher amplitude of variation in the transition from 2013 to 2014 than from 2011 to 2012 (Table 2), suggesting a higher recovery in productivity. The summer NAO index (June-August) corresponding to the season of field work showed an identical pattern, with negative years significantly different than positive years (Table 3). The lowest winter and summer NAO indices of the study period were registered the same year (2013) (Table 2).

Spring (March-May) and summer (June-August) composites of SST and CHLA confirmed strong oceanographic changes in our study area (Northeast Atlantic) during 2011-2014 (Fig. 4, 5, 6, and 7). A warming pattern was detected in the spring sea surface temperature (SST_SPR) over the Portuguese and African coasts in 2011. Specifically, SST_SPR south of Lisbon and a small narrow band over the North African shelf were under the influence of a warmer isotherm (17-19 °C) in contrast to what was observed during years of high productivity (i.e. 2012 and 2014). The central-east part of the Canaries seemed also affected by the warming phenomena of 2011. Conversely, cooler SST_SPR was observed south of Azores (Fig. 4). Concerning the summer sea surface temperature (SST_SUM) in 2011, composites suggested cooler values east of Madeira and Canaries, and again warmer temperatures in the small band adjacent to North Africa (Fig. 5). Regarding Chlorophyll-*a* (CHLA) composites, they indicated higher concentrations during spring than summer (Fig. 6 and 7). Surprisingly, CHLA in spring 2011 seemed to have the highest phytoplankton blooms at least in the oceanic regions of the north (Fig. 6).

Inter-annual changes in oceanographic parameters within the surroundings of BER and CIM were corroborated statistically. The year with the highest SST_SUM was 2011 for Berlenga (BER) and Cima Islet (CIM). Around both islands, SST_SUM was significantly higher in 2011 and 2013 than in the other two years (Table 3). On the contrary, BER and CIM registered lower mean values of CHLA in 2011 and 2013 but without significant

differences between years. Comparing islands, BER recorded significantly lower SST and significantly higher CHLA than CIM (Tables 2 and 3).

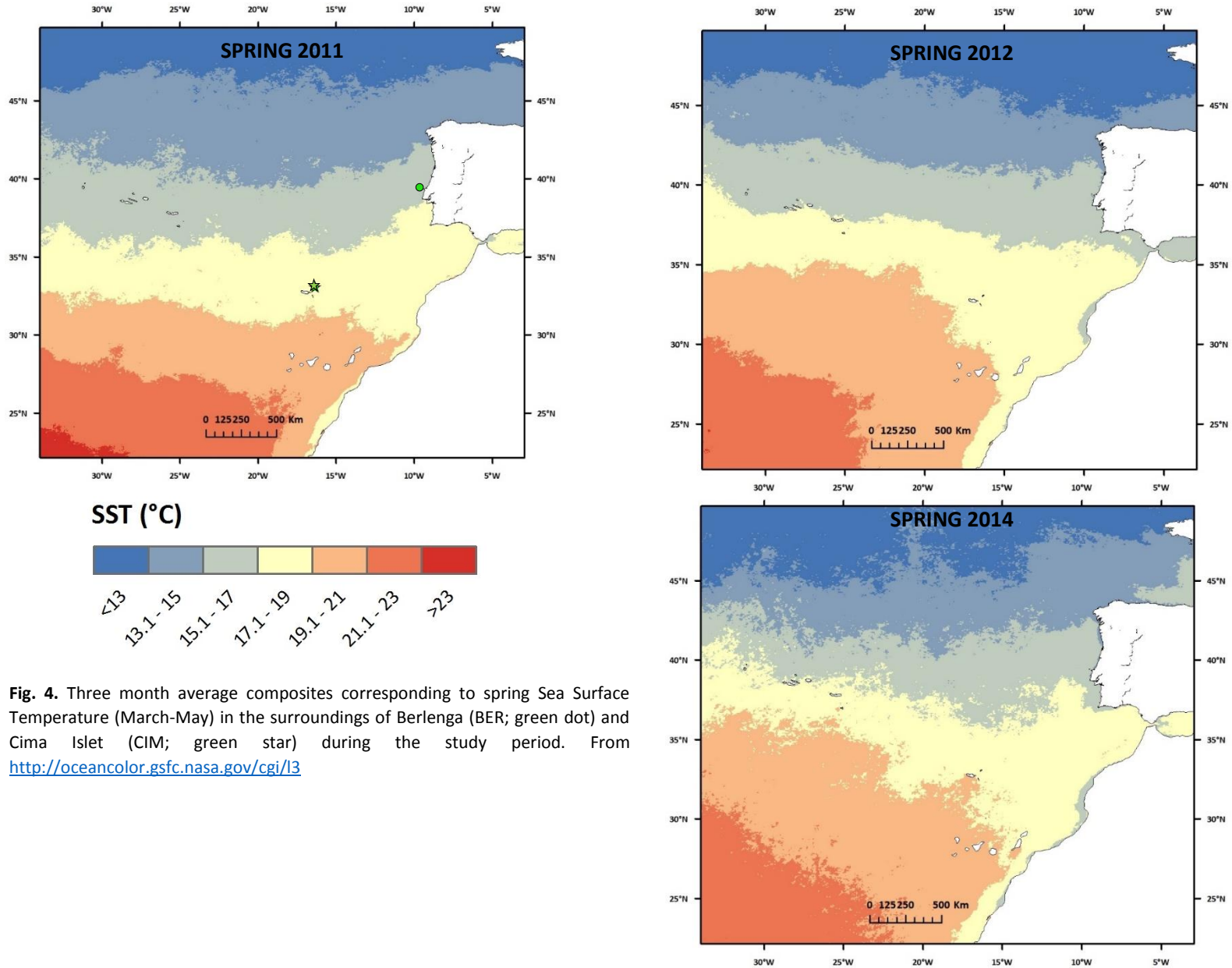
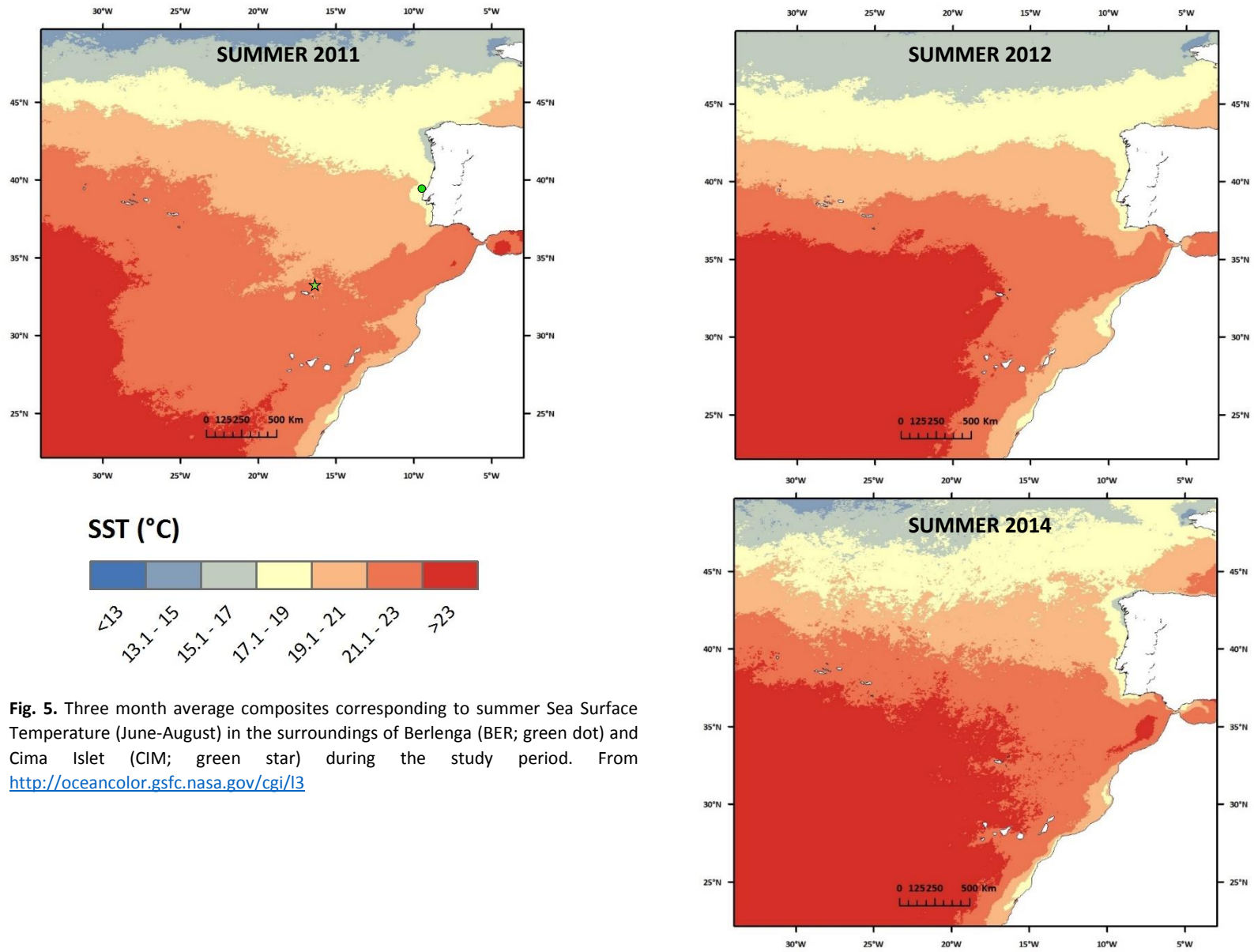


Fig. 4. Three month average composites corresponding to spring Sea Surface Temperature (March-May) in the surroundings of Berlenga (BER; green dot) and Cima Islet (CIM; green star) during the study period. From <http://oceancolor.gsfc.nasa.gov/cgi/l3>



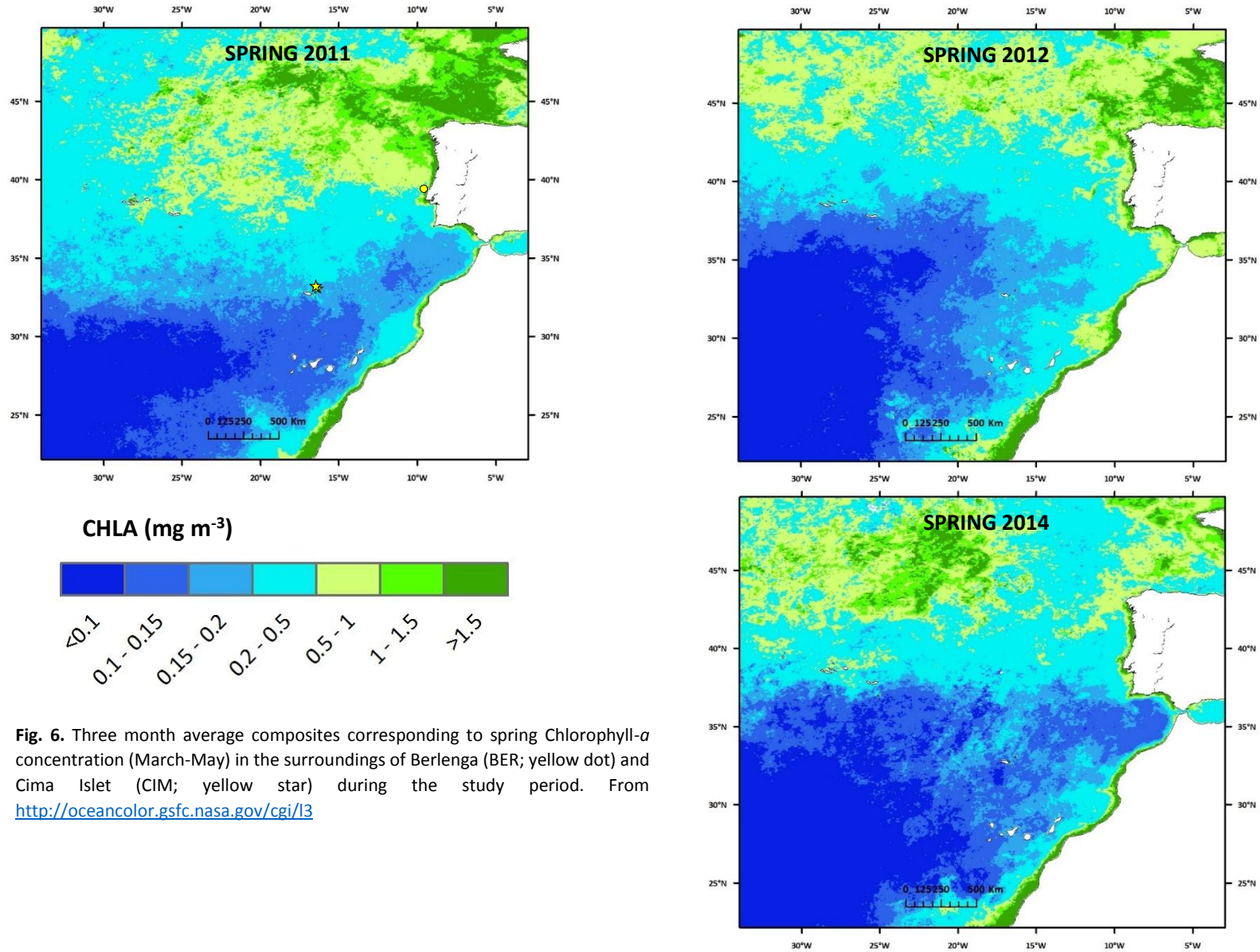


Fig. 6. Three month average composites corresponding to spring Chlorophyll-*a* concentration (March-May) in the surroundings of Berenga (BER; yellow dot) and Cima Islet (CIM; yellow star) during the study period. From <http://oceancolor.gsfc.nasa.gov/cgi/l3>

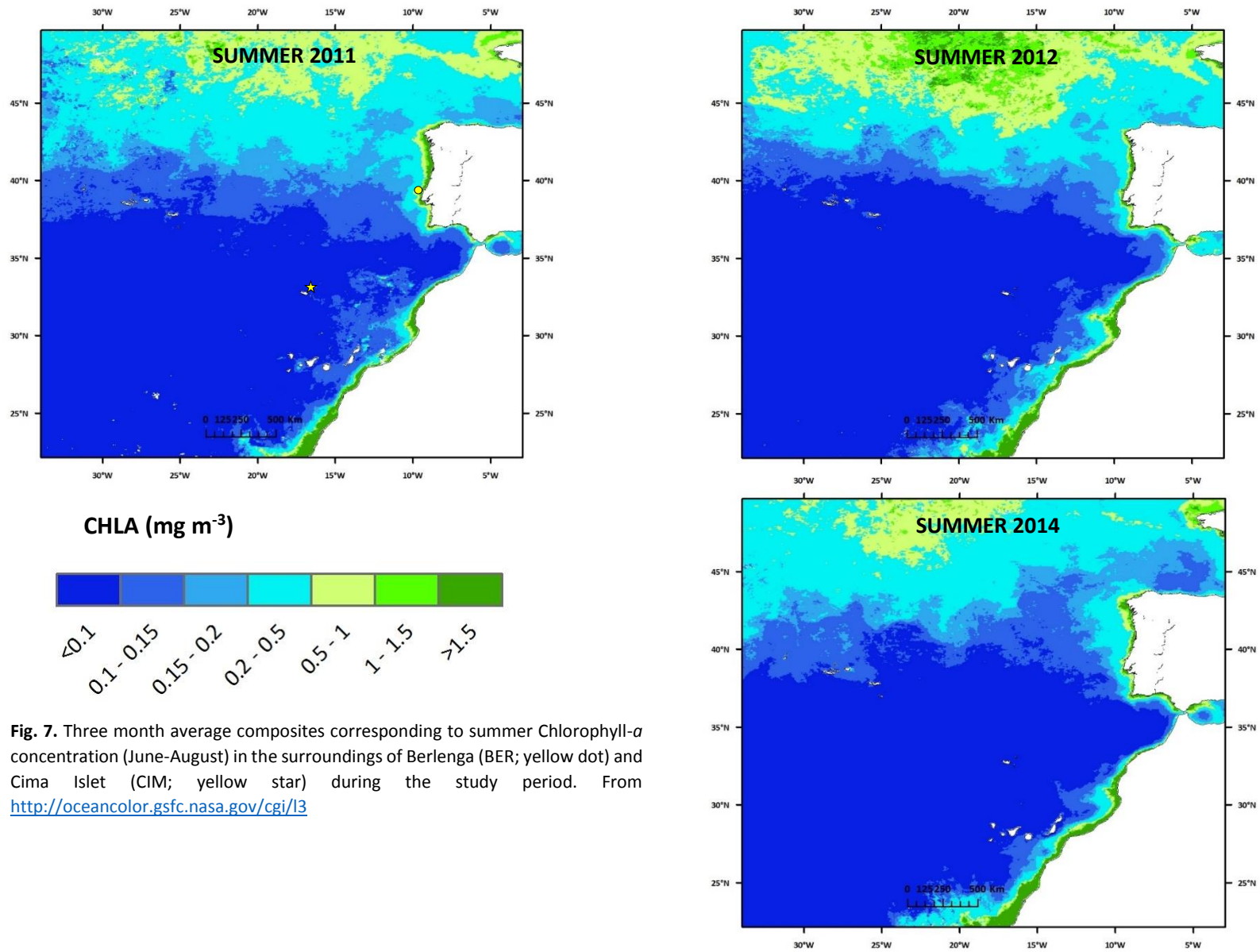


Fig. 7. Three month average composites corresponding to summer Chlorophyll-*a* concentration (June-August) in the surroundings of Berlenga (BER; yellow dot) and Cima Islet (CIM; yellow star) during the study period. From <http://oceancolor.gsfc.nasa.gov/cgi/l3>

Table 2. Mean (\pm SD) regional and local environmental predictors in the colony surroundings of Cory's shearwaters from Cima Islet (CIM) and Berlenga (BER) between 2011 and 2014; foraging habitat and trip characteristics and spatial ecology and fitness parameters of both populations. FA – core Foraging Area; 50% Kernel Utilization Distribution (50 UD). Environmental predictors are for summer (June-August) of each year, unless otherwise stated.

Variables	2011		2012		2013		2014	
	CIM	BER	CIM	BER	CIM	BER	CIM	BER
Regional environmental predictors								
Extended winter NAO index (December - March)	-1.6		3.2		-2.0		3.1	
NAO index (Jun - Aug)	-1.1 \pm 0.4		1.75 \pm 0.3		-1.6 \pm 0.8		1.4 \pm 0.5	
Local environmental predictors (within 60 km)								
Chlorophyll <i>a</i> concentration (CHL; mg m ⁻³)	0.3 \pm 0.7	1.7 \pm 0.3	1.0 \pm 0.2	2.1 \pm 0.1	0.5 \pm 0.2	1.3 \pm 0.5	1.5 \pm 0.2	2.3 \pm 0.3
Sea Surface Temperature (SST; °C)	24.5 \pm 1.3	20.0 \pm 1.5	20.2 \pm 1.2	17.2 \pm 1.8	23.2 \pm 1.2	19.2 \pm 1.4	20.3 \pm 1.3	16.9 \pm 1.5
Habitat of foraging areas (within FR)								
Chlorophyll <i>a</i> concentration (CHLA; mg m ⁻³)	0.5 \pm 0.2	1.0 \pm 0.3	1.4 \pm 0.4	1.9 \pm 0.2	—	—	1.7 \pm 0.3	2.0 \pm 0.5
Sea Surface Temperature (SST; °C)	22.0 \pm 0.9	19.0 \pm 0.6	19.2 \pm 1.1	17.0 \pm 1.2	—	—	18.8 \pm 0.6	19.8 \pm 0.9
SST anomaly (ASST)	3.6 \pm 0.5	1.7 \pm 0.2	-1.6 \pm 0.3	-2.2 \pm 0.4			2.1 \pm 0.5	1.6 \pm 0.6
FA kernel UD area (km ²)	3.4 \pm 1.3	2.1 \pm 1.0	2.5 \pm 1.2	1.8 \pm 0.8			2.6 \pm 1.1	1.6 \pm 0.5
Foraging trip characteristics								
N tracks [N birds]	42 [11]	38 [11]	76 [9]	24 [6]	—	—	44 [8]	31 [6]
Trip duration (days)	4.5 \pm 1.7	2.3 \pm 0.6	1.9 \pm 0.2	1.1 \pm 0.7	—	—	2.1 \pm 0.6	1.2 \pm 0.4
Maximum distance from colony (km)	975.4 \pm 63.1	625.1 \pm 54.0	487.0 \pm 47.4	195.4 \pm 44.4	—	—	402.2 \pm 83.2	129.7 \pm 24.0
Time spent flying trip ⁻¹ day ⁻¹ (h)	8.2 \pm 1.5	6.8 \pm 1.8	6.5 \pm 1.3	5.0 \pm 0.6	—	—	6.8 \pm 1.9	5.1 \pm 0.8
% of time spent in foraging areas	48.9 \pm 9.6	38.1 \pm 5.8	33.1 \pm 5.7	20.1 \pm 2.5	—	—	32.3 \pm 8.4	19.4 \pm 3.6
Fitness parameter								
Adult's body condition index (BCI)	-1.1 \pm 0.5	-0.9 \pm 0.3	0.6 \pm 0.2	0.8 \pm 0.3	—	—	0.5 \pm 0.2	1.0 \pm 0.4

Table 3. Generalized Linear Mixed Effect Models (GLMMs) testing the effect of the interaction between year (2011, 2012 and 2014) and Island (CIMma Islet, CI vs Berlenga, BER) on regional and local environmental predictors in the colony surroundings (60km around the breeding colony), foraging habitat and trip characteristics and spatial ecology and fitness parameters shown in Table 1. The individual was used as a random effect to avoid pseudo-replication issues. Significant results in **bold**. Effect was evaluated with Post-hoc multiple comparisons with Bonferroni correction.

Variables	Year			Island			Year*Island		
	GLMM	P	Effect	GLMM	P	Effect	GLMM	P	Effect
Regional environmental predictors									
Extended winter NAO index (December - March)	—	—	—	—	—	—	—	—	—
NAO index (Jun - Aug)	$F_{3,8} = 33.46$	0.001	2011,2013 < 2012,2014	—	—	—	—	—	—
Local environmental predictors (within 60 km)									
Chlorophyll <i>a</i> concentration (CHLA; mg m ⁻³)	$F_{7,118} = 1.19$	0.15	—	$F_{7,118} = 3.19$	0.02	CIM < BER	—	—	—
Sea Surface Temperature (SST; °C)	$F_{7,118} = 4.09$	0.01	2011,2013 > 2012,2014	$F_{7,118} = 3.75$	0.02	CIM > BER	—	—	—
Habitat of foraging areas (within FA)									
Chlorophyll <i>a</i> concentration (CHLA; mg m ⁻³)	$F_{5,249} = 4.33$	0.01	2011 < 2012,2014	$F_{5,249} = 2.35$	0.04	CIM < BER	$F_{5,249} = 2.55$	0.05	CIM 2011 < all
Sea Surface Temperature (SST; °C)	$F_{5,249} = 2.98$	0.04	2011 > 2012,2014	$F_{5,249} = 3.98$	0.01	CIM > BER	$F_{5,249} = 2.31$	0.04	CIM 2011 > all
SST anomaly (ASST)	$F_{5,249} = 24.1$	0.001	2011 > 2012,2014	$F_{5,249} = 0.98$	0.12	—	$F_{5,249} = 0.88$	0.15	—
FA kernel UD area (km ²)	$F_{5,249} = 1.10$	0.13	—	$F_{5,249} = 4.02$	0.01	CIM > BER	$F_{5,249} = 0.77$	0.17	—
Foraging trip characteristics									
N tracks [N birds]	—	—	—	—	—	—	—	—	—
Trip duration (days)	$F_{5,249} = 3.87$	0.02	2011 > 2012,2014	$F_{5,249} = 1.01$	0.11	—	$F_{5,249} = 0.37$	0.21	—
Maximum distance from colony (km)	$F_{5,249} = 4.28$	0.01	2011 > 2012,2014	$F_{5,249} = 15.34$	0.001	CIM > BER	$F_{5,249} = 2.67$	0.04	CIM 2011 > all
Time spent flying trip ⁻¹ day ⁻¹ (h)	$F_{5,249} = 1.04$	0.12	—	$F_{5,249} = 0.67$	0.16	—	$F_{5,249} = 0.58$	0.26	—
% of time spent in foraging areas	$F_{5,249} = 2.77$	0.03	2011 > 2012,2014	$F_{5,249} = 0.98$	0.13	—	$F_{5,249} = 0.55$	0.27	—
Fitness parameter									
Adult's body condition index (BCI)	$F_{5,249} = 4.37$	0.01	2011 < 2012,2014	$F_{5,249} = 0.57$	0.17	—	$F_{5,249} = 0.51$	0.18	—

3.2. Differences in the foraging strategies among populations in response to variations in the environment

Overall Cory's Shearwaters had the most exploratory patterns during their foraging trips of 2011, especially CIM birds which targeted fairly distant foraging grounds (FA; 50UD), covering additional territories in various regions the Northeast Atlantic (Fig. 8B). During 2012 and 2014, FA were mostly concentrated in the colony surroundings around Madeira, and over the coast and shelf of north Morocco (Fig. 8D, 8F). These two areas were also frequently targeted in 2011, making them the most exploited regions of the study period for CIM. As far as home ranges (HR; 95UD) are concerned, they were extremely sparse in 2011 when the birds explored most of the Northeast Atlantic. After the improvement of oceanographic conditions in 2012, CIM birds clearly reduced their HR and FA; and in 2014, they were completely restricted among the colony surroundings, the Seine seamount and the north Moroccan coast. On the other hand, BER birds' FA were consistently located over the continental shelf in the colony surroundings during the three study years (Fig. 8A, 8C, 8E). HR of some individuals were identified in more distant areas during 2011 and 2014 but they did not account for the presence of core foraging areas.

Results from kernel overlaps calculations confirmed less consistency in the foraging behavior of Cory's Shearwaters during 2011. Even though the graphical outputs suggested otherwise, BER birds also demonstrated very irregular patterns in 2011 recording their lowest mean overlaps among individuals in HR and FA (54% and 29% respectively). Overlaps were highest in 2012 in this island (Table 4). At CIM, birds showed a gradual increase in kernel overlaps among individuals from 30% in HR, and 18% in FA in 2011 to 62% in both HR and FA overlap in 2014 (Table 4). However, when comparing mean overlaps among years it was possible to deduce that as a whole population, both islands concentrated their foraging efforts in similar regions every year. Mean overlaps between years (i.e. 2011-2012, 2011-2014, and 2012-2014) was always estimated at 70% or higher in BER, and above 60% in CIM (Table 4).

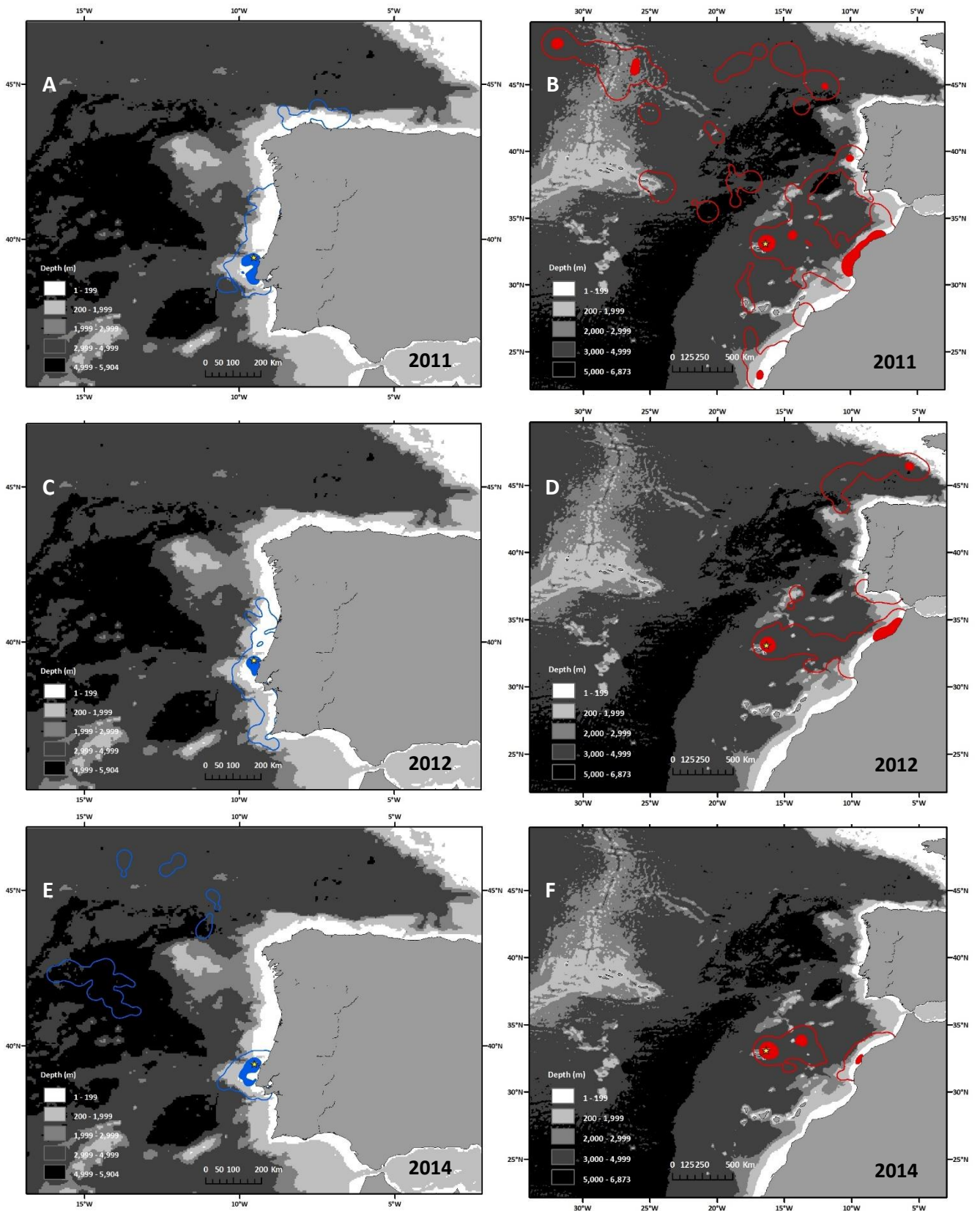


Fig. 8. *Calonectris borealis* kernel utilization distribution plots during the three years of study for Berlenga – BER (blue) and Cima Islet - CIM (red). Stars indicate the breeding colonies. Outer lines represent Home Ranges (UD95) except in (B) where (UD99) was used in the contour; and filled polygons represent core Foraging Areas (UD50). All maps are plotted over bathymetry (m). Note that (B), (D) and (F) which represent kernel UD in CIM are drawn at a different scale due to the higher foraging trip characteristics of birds from this colony

Table 4. Results from kernel overlaps (in %) for the birds of Berlenga (BER) and Cima Islet (CIM). Kernels are compared for all trips, individuals birds, and finally among years of study to assess the consistency in foraging behavior. BER trips 2014 did not produce any results because no five relocations were found. HR 95UD – Home Range 95% kernel Utilization Distribution. FA 50UD – Foraging Area 50% kernel Utilization Distribution

	BER 2011		CIM 2011		AMONG YEARS	
	trips	birds	Trips	birds	BER 2011-2012	CIM 2011-2012
HR 95UD	43	54	44	30	77	64
FA 50UD	15	29	32	18	83	61
	BER 2012		CIM 2012		BER 2011-2014	CIM 2011-2014
HR 95UD	58	69	53	48	70	71
FA 50UD	28	56	33	37	82	64
	BER 2014		CIM 2014		BER 2012-2014	CIM 2012-2014
HR 95UD	58	63	65	62	74	72
FA 50UD	33	36	48	62	76	66
Mean HR	53	62	54	47	73	69
Mean FA	25	40	38	39	80	64

The foraging trip characteristics confirmed the very high foraging effort displayed by Cory's Shearwaters in 2011. Trip duration was significantly higher by more than 1 day in BER, and by more than 2 days in CIM when compared with productive years. Birds also travelled to significantly further distances (over 400 km in both islands), and spent more time in foraging areas (15-18% extra) during that year. As a result, FA in 2011 were slightly larger but the differences were not significant. Another parameter that was affected and recorded particularly low values in 2011 was Body Condition Index (BCI) of individual breeders (Tables 2 and 3). Comparing islands, only maximum distance from the colony was significantly higher in CIM birds than in BER birds (Table 3).

Relating environmental parameters in the proximity of BER and CIM with those found in core foraging areas, BER birds did not necessarily target areas with lower SST and/or higher CHLA. In fact, SST was on average 2.9°C higher in 2014, and CHLA records were lower every year inside FA compared to the island surroundings. On the other hand, CIM birds indicated each year a strong preference to exploit FAs with considerably lower SST and higher CHLA (Table 2).

3.3. Habitat use in response to inter-annual environmental variability

All MaxEnt models featured very high AUC values, indicating excellent predictive performances. The lowest AUC scores were obtained for the models of 2011 (BER; 0.974 and CIM; 0.922). The models of 2012 and 2014 performed even higher with a very small or non-existent standard deviation (Appendix 1 and 2). In the case of BER, DCOL was a predictor that maintained its high importance throughout all the study years, while DLAN was a major contributor only in 2011. Sea surface temperature was the most important environmental variable in 2012, with 56.7% contribution of SST_RANGE and 17% permutation of SST_SPR. Another sea surface temperature variable (i.e. SST_SUM) had relevant contributions in the models of 2011 (10.5%) and 2014 (14.9%) (Appendix 1, Fig. 9).

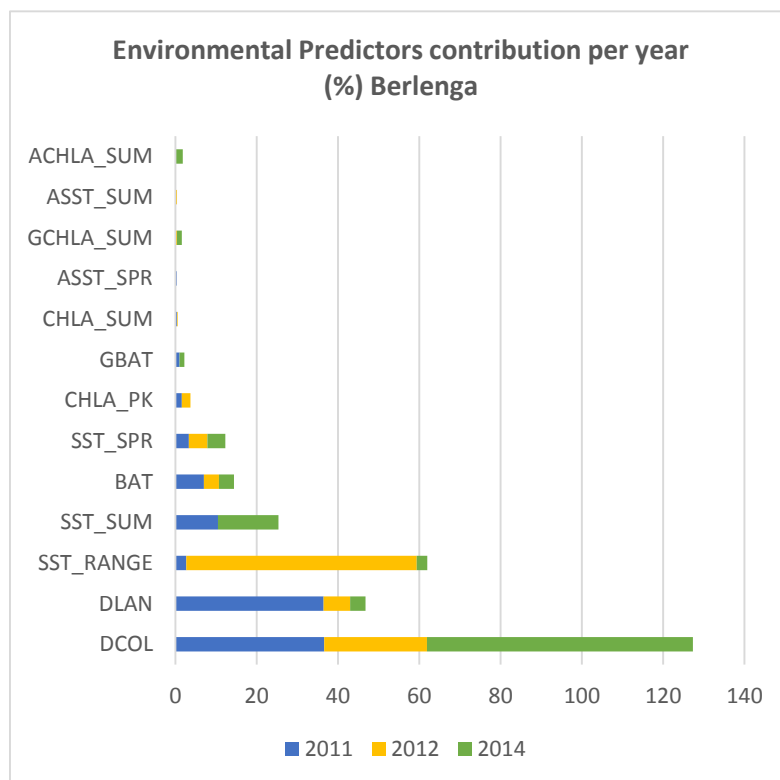


Fig. 9. *Calonectris borealis* illustration of environmental predictors' percentage of contribution to the occurrence of the species in Berlenga. DCOL (distance-to-colony), DLAN (distance-to-land), SST_RANGE (sea surface temperature range), SST_SUM (sea surface temperature summer), BAT (bathymetry), SST_SPR (sea surface temperature spring), CHLA_PK (chlorophyll-*a* peak), GBAT (bathymetry gradient), CHLA_SUM (chlorophyll-*a* summer), ASST_SPR (sea surface temperature spring anomaly), GCHLA_SUM (chlorophyll-*a* summer gradient), ASST_SUM (sea surface temperature summer anomaly), ACHLA_SUM (chlorophyll-*a* summer anomaly)

Results for CIM models indicated that the static variables DLAN and DCOL were consistently the most important predictors in this island. However, in 2011 percentage contribution was more evenly distributed among five parameters that recorded 10% or higher in the SDM (i.e. DCOL, DLAN, GCHLA_SUM, SST_RANGE, SST_SPR,). SST_RANGE was an important factor also in 2014, while SST_SPR was relevant during all three years. In 2014 DCOL and BAT together accounted for nearly 90% of the permutation importance in the model.

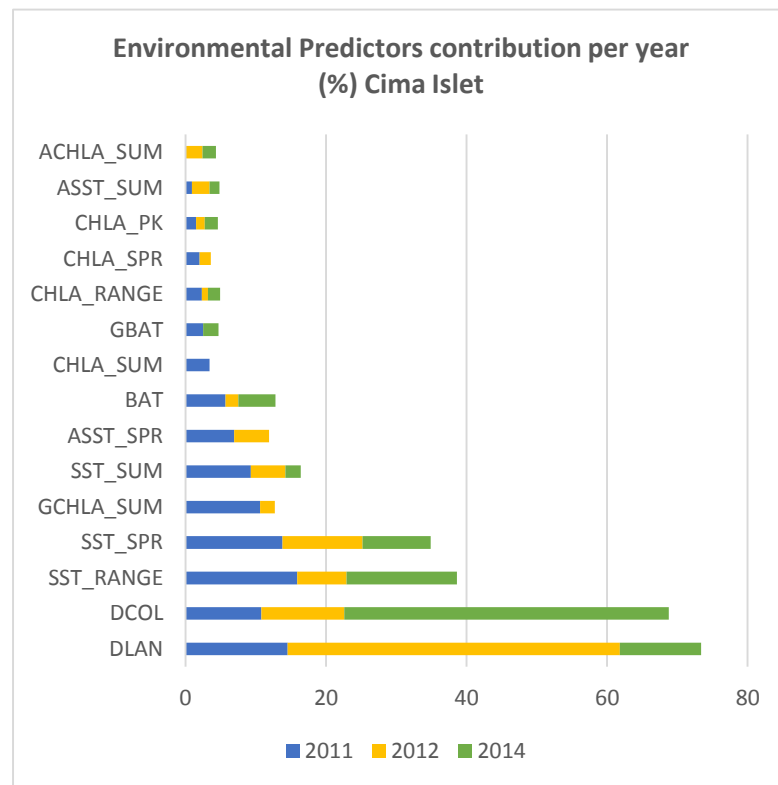


Fig. 10. *Calonectris borealis* illustration of environmental predictors' percentage of contribution to the occurrence of the species in Cima Islet. DLAN (distance-to-land), DCOL (distance-to-colony), SST_RANGE (sea surface temperature range), SST_SPR (sea surface temperature spring), GCHLA_SUM (chlorophyll-*a* summer gradient), SST_SUM (sea surface temperature summer), ASST_SPR (sea surface temperature spring anomaly), BAT (bathymetry), CHLA_SUM (chlorophyll-*a* summer), GBAT (bathymetry gradient), CHLA_RANGE (chlorophyll-*a* range), CHLA_SPR (chlorophyll-*a* spring), CHLA_PK (chlorophyll-*a* peak), ASST_SUM (sea surface temperature summer anomaly), ACHLA_SUM (chlorophyll-*a* summer anomaly)

Chapter 4.

Discussion



This study reveals the flexibility in the foraging behavior of Cory's Shearwaters, which were able to respond to the changing levels of productivity in the proximity of their breeding grounds throughout the study period. As reported in other studies (e.g. Paiva et al. 2013a, 2013b; Haug et al. 2015), our results also detected a link between a negative extended winter NAO index (Hurrell 1995) and the subsequent decrease in productivity (proxied by chlorophyll a concentration and SST) in the Northeast Atlantic for the upcoming breeding season that may have influenced the at-sea foraging behavior of Cory's Shearwater breeding in the continental shelf of Portugal. Our work extends the link between changes in oceanographic characteristics and foraging behavior for seabird top predators further south to the pelagic waters of the Madeira archipelago region. Additionally, studying birds breeding in islands with contrasting productivity patterns in their surroundings enables us to detect similarities and differences in each population strategies. Overall, and according to our first prediction, it appears that the oceanic island of Cima Islet (CIM) was more affected by the low productivity that affected the region in 2011 than the neritic island of Berlenga (BER). Contrastingly to BER birds that consistently foraged over the Portuguese continental shelf each year, CIM birds reacted to the detrimental conditions by dispersing their home ranges (HR) and foraging areas (FA) into more distant regions of the North Atlantic when compared to productive years. On the other hand, and accordingly to our second prediction, BER and CIM birds increased similarly their foraging effort parameters. Nevertheless, because of the more distant FA targeted by CIM birds during 2011 as a result of their foraging tactics, the distances travelled were significantly greater during that year. Finally, and contrary to our third prediction, our study indicates an immediate improvement in the foraging behavior of BER birds, and suggest a more progressive change in CIM birds from 2011 to 2014 as oceanographic conditions ameliorated from the strong negative NAO index of 2011. Due to the influence of another strong negative NAO index recorded in 2013, and a lack of data on the foraging behavior for that year we cannot assess precisely the evolution of the responses.

4.1. The foraging plasticity of oceanic and neritic populations of a seabird top predator

Cory's Shearwaters in BER maintained most of their HR and all of their FA over the continental shelf and close to the breeding colony during the entire study period, whereas birds from CIM clearly expanded their HR and FA during 2011 to several regions that were not targeted during productive years. The foraging ecology of a marine predator highly depend on the abundance and distribution of prey (Bell 1991), and their dispersion is associated to large scale ocean productivity (Hyrenbach et al. 2002). Thus, the differences in responses may be given by the contrasting productivity in the proximity of each island. For instance, in tropical areas where prey is more unpredictably distributed and the productivity of the marine environment is low (Mann & Lazier 2006) seabirds generally adopt flexible foraging strategies (Weimerskirch et al. 2005b), while in temperate and polar waters species show higher fidelity to their foraging grounds (Weimerskirch 2007). The decrease in productivity along CIM birds usual grounds in an already poor environment, probably caused birds to spread their home ranges and foraging areas to other regions.

Retaining their fidelity to a certain degree, CIM birds may have targeted familiar regions during other periods of the breeding season. No previous work has tracked the at-the foraging behavior of Cory's Shearwaters in CIM, but tracking studies on the population of the same species breeding on the Desertas island (in the same Madeira Archipelago) identified several FAs in the region between the Anti-Altair seamount and the Galician bank (Paiva et al. 2010b). Therefore, CIM birds are likely to be familiar with these productive oceanic regions. Furthermore, prey disturbance is reported to cause seabird predators to travel to more distant areas to obtain food due to the effect of intra-specific competition (Lewis et al. 2001). In this sense, BER hosts a small population of only a few hundred individuals compared with thousands breeding in Madeira (<http://www.birdlife.org/>).

BER birds in our study followed the same pattern reported in most tracking studies over the last decade during the chick-rearing season (Paiva et al. 2010b, 2010c; Alonso et al. 2012). However, Paiva et al. (2013a) provided the only report of the chick-rearing season for BER in response to environmental stochasticity in 2010. During that year, birds drastically shifted their distribution to target distant seamounts regions off the continental

Portugal neritic system (i.e. Josephine, Ashton, Galician, Azores-Biscay, and even Anti-Altair). As a result, the extent of their HR and FA increased radically. In contrast, our results showed that BER birds remained in the continental shelf even under the detrimental conditions of 2011. The comparison of the two NAO values (2010; -4.64 and 2011; -1.6) suggests a large difference in oceanographic conditions (Osborn 2011). Therefore, there may be a threshold in the surroundings of BER when the structure and functioning of marine ecosystems is severely affected (Walther et al. 2002) to force birds to leave their habitually productive grounds in search of higher prey availability.

Conversely, CIM birds persistently targeted three zones every year: the colony surroundings, the seamounts nearest to Madeira, and the north Moroccan coast. Nevertheless, in 2011 birds were especially explorative when their HRs covered most of the northeast Atlantic, and their FAs reached further grounds (i.e. the continental shelves at the southern end of Western Sahara and near Berlengas, the Anti-Altair seamount, and even beyond the Mid-Atlantic ridge). All these areas correspond to very productive neritic environments (Aristegui et al. 2009b) or seamounts that have been associated with high diversity of pelagic species (Morato et al. 2010) and significant levels of endemism (Cartes et al. 2013). While most of the northeast Atlantic underwent a trend of decreased productivity during 2010-2011 (Paiva et al. 2013a, 2013b; Haug et al. 2015), the opposite pattern was recorded in the northwest Atlantic (Paiva et al. 2013b) in the Altair region, which is in the vicinity of the most distant FA recorded for CIM in 2011. Thus, some individuals may have actually found a more productive region (~2,000 km away) but the central-place foraging constrain during the chick-rearing season conditioned birds to mostly remain closer to their breeding colony.

In spite of the irregular patterns depicted in 2011, the analysis of kernel overlaps strongly suggests that both oceanic (CIM) as much as neritic (BER) populations showed high fidelity to its foraging grounds during chick-rearing. HR recorded a mean overlap among years of 73% and 69%, while FA overlap was 80% and 64% respectively for BER and CIM. The differences especially concerning FA overlap should relate again to the productivity levels in the surroundings of each island. The fact that CIM birds registered a high overlap in the comparison of 2011 (when HR and FA are visible more sparse) with the other two years implies that the highest proportion of their foraging activity was concentrated in the regions that were commonly targeted each year. This inference is

further strengthened considering that the extension of FA did not vary significantly among years.

Individuals from both BER and CIM drastically increased their foraging effort parameters in 2011 in response to the oceanographic changes, but each island did so adapting to their differing foraging tactics. On one hand, BER birds are reported to use a strategy of almost exclusively short trips during chick-rearing, increasing their foraging effort to cope with the demands of the growing chick (Paiva et al. 2010b), a pattern that was confirmed throughout our study period. Since the length of foraging trips is highly dependent on food availability (Uttley et al. 1994), the additional foraging effort of 2011 may be explained by a more stochastic and explorative behavior in an environment with reduced productivity. Furthermore, Sardines *Sardina pilchardus* and Garfish *Belone belone* are generally the most consumed prey of Cory's Shearwaters in BER (Paiva et al. 2010e), but the overly intense winter upwelling over the Portuguese coast that is inferred from a negative NAO index may have driven sardines and other small pelagic fish larvae offshore inducing a high mortality (Santos et al. 2007). Therefore, BER birds may have been originally attempting to target prey that was not present on the usual productive spots because of a spatial mismatch (Grémillet et al. 2008). This probably caused birds to practically doubled mean trip duration, percentage of time spent in FAs, and tripled maximum distances from the colony (i.e. to ~ 625 km) compared to 2012 and 2014.

On the other hand, shearwaters in CIM depicted a typical pattern of dual foraging strategy, i.e. alternating short and long foraging excursions, and similar to that of other oceanic populations of the species (Granadeiro et al. 1998; Magalhães et al. 2008; Paiva et al. 2010c). Analyzing the kernel graphical outputs we can infer that CIM birds concentrated their foraging efforts in three main locations: in short trips around Madeira, and in long trips to the nearby seamounts and the north Moroccan coast, a pattern similar to the species in Selvagens and the Canary Archipelagos which rely on the resources off the upwelling system of the African shelf (Navarro et al. 2009; Alonso et al. 2012; Ramos et al. 2013). Nonetheless, CIM birds additionally exploited the nearby seamounts due to the greater distance of Madeira to the African coast. Hence, birds probably spent higher foraging effort during short trips because of the lower productivity of 2011 to successfully feed their chicks and venture in much longer trips in search of productive grounds to recover their extra-depleted energy reserves (Chaurand & Weimerskirch 1994). This may explain CIM birds' increase in foraging effort, with maximum distance from the colony

indicated as the highest significant parameter on both islands and during all study years. CIM birds reached in average distances ~1,000 km away from their colony (more than twice compared to 2012 and 2014), suggesting that they were more affected than BER birds in low productivity years. Such outcome is not surprising as most studies have reported proxies of foraging effort always comparatively higher in oceanic than in neritic populations (Paiva et al. 2010b; Alonso et al. 2012).

The high foraging effort invested during the chick-rearing season corroborates the tendency of Cory's Shearwaters to deviate from their previously known foraging patterns under stochastic conditions. Earlier that year, a good proportion of females had completed a pre-laying excursion to the Northwest Atlantic with over 8,100 km of total distance covered (Paiva et al. 2013b), adding up to an extremely demanding breeding year which was similarly exhausting in 2010 (Paiva et al. 2013a). Even though we do not possess records for other breeding periods from CIM birds during 2010-2011, considering that their parameters were comparatively more affected than BER birds during our study, it is likely that they depicted similar energy expenditure than BER birds during those two breeding seasons. Cory's Shearwater has been recognized as an exceptionally plastic species in its foraging behavior throughout different times of the year: i.e. breeding (Paiva et al. 2010c), migratory (Dias et al. 2011) and wintering seasons (Dias et al. 2012). However, the consequences of such plasticity should also be severe. Food availability plays an important role in breeding success and adult survival (Davis et al. 2005), and body condition index is the main factor regulating chick-provisioning in seabirds such as petrels and albatrosses (Tveraa et al. 1998; Weimerskirch et al. 2000). Our study recorded significantly lower body condition index in CIM and BER birds for 2011, a similar outcome provoked birds in the pre-laying and chick-rearing periods to affect hatching, fledging, and ultimately reproductive success in BER birds (Paiva et al. 2013a, 2013b).

Subsequently, the NAO indices and various environmental parameters indicate an exceptional recovery in primary productivity over the northeast Atlantic in 2012 and 2014. In order to assess the reactions of BER and CIM birds to the ameliorating conditions of the surrounding environment, the temporal evolution of kernel overlaps among individuals in each island provides important insights. Seabird predators are expected to have higher fidelity with increasing latitude, as well as with increasing productivity. Therefore, it should be anticipated for both islands to have higher distribution overlaps as productivity improves. At the same time, BER birds should record higher percentages of

overlap than CIM birds each year. Our results suggest that BER birds seemed to react immediately to the positive NAO index of 2012, while CIM birds depict a progressive increase until 2014. Both islands appeared to record similarly high values of distribution overlaps, which given the sparse and dynamic nature of marine hotspots, and the link between experience and seabirds' foraging efficiency (Péron & Grémillet 2013; Gutowsky et al. 2014) reveal the outstanding capacity of Cory's Shearwaters to find prey in oceanic and neritic environments.

However, a few aspects should be considered before accepting such inference. Firstly, BER birds showed a high decrease in FA overlap in 2014, a year of hypothetically very high productivity. This segregation may be partly explained by the explorative behavior described for inexperienced breeders in BER (Haug et al. 2015), but inexperienced seabirds can be as efficient as experience birds when productivity is elevated (Weimerskirch et al. 2005a; Haug et al. 2015). Furthermore, this factor should affect CIM and BER birds equally. It is more likely that breeding in a productive environment with low intraspecific competition offers BER birds a higher number of large and profitable areas to explore. Secondly, environmental conditions were not continuously ameliorating from 2011 to 2014, as, 2013 had an even lower NAO index than 2011. But unfortunately there is no tracking data to investigate the foraging patterns of birds during that year. Finally, the very high NAO indices of 2012 and 2014 imply that they were years with abnormally high productivity over the northeast Atlantic, therefore HR and FA especially for CIM may not represent that of years with standard productivity. Ultimately, it is necessary to track oceanic and neritic populations continuously during longer temporal scales to clarify their patterns of change during years of environmental stochasticity and ameliorating conditions.

4.2. Effects of a changing marine environment in the feeding behavior of Cory's Shearwater

Our study has adopted the NAO as a surrogate of marine productivity. Recently, more details about the relationship among large scale atmospheric phenomena (driven by the NAO) and its effects on different levels of the food web have been disclosed (Osborn 2011; Paiva et al. 2013a). Negative values in the NAO (2011 and 2013) coincided with significant increases in SST and reductions in CHLA in the proximities of BER and CIM,

but the reverse effects occurred when a positive NAO was recorded (2012 and 2014). Thus, we expect productivity to be higher around Berlengas in years of a positive NAO index, as indicated by previous studies (e.g. Ceia et al. 2014; Haug et al. 2015). Changes in different levels of the food web (e.g. plankton, benthos, and fish stocks) have been correlated in the past two decades with changes in atmospheric circulation at an ocean basin scale indicated by the NAO, or the El Niño Southern Oscillation Index (ENSO) in the Pacific Ocean (Mann & Lazier 2006). The NAO is an indicator of climatic conditions in the North Atlantic Region, while the ENSO influences climate variability worldwide. Similarly to the NAO, ENSO driven changes are reportedly affecting the reproductive success of seabird predators in tropical (Surman & Nicholson 2009; Ancona et al. 2011) and temperate regions of the world (Smithers et al. 2003). Therefore, global indices are a useful approach to assess changes in marine ecosystems. The main advantage is that they offer ecologists the opportunity to make predictions on the biological effects of climatic conditions (Stenseth et al. 2003; Peron et al. 2012).

The results demonstrate graphically and statistically the strong fluctuations in oceanographic conditions that affected the northeast Atlantic during the study period. Such oscillations most likely induced the changes in foraging tactics showed by BER and CIM birds in 2011. Specifically, the warmer trend identified in SST around both islands, and the Portuguese and African shelves relates to the influence of the NAO in the upwelling regime of the Canary Current (Mann & Lazier 2006; Osborn 2011). These regions were recognized as the most important foraging grounds in this study. Olfactory navigation is recognized as the mechanism that enables procellariiforms to discern environmental cues at various spatial scales (Nevitt 2008), thus Cory's Shearwaters were able to perceive these changes.

The increase in SST and decrease in primary productivity also triggered pre-laying females in BER to shift their foraging distributions in 2011 (Paiva et al. 2013b). Initially, the statistical results suggested that only CIM birds seemed to favor FA with lower SST and higher CHLA, which may be explained by the differences in SST and CHLA between study islands. During the study period, SST was on average 3-4°C lower, and CHLA was 0.8-2.4 mg m⁻³ higher around BER than around CIM. However, the influence of SST was subsequently evidenced in the SDM that displayed relevant contributions of environmental variables such as SST_SUM, SST_SPR and SST_RANGE throughout the entire study period in CIM, but also in BER. SST has been identified as the only

environmental predictor correlated with higher species diversity of several major marine taxa (from zooplankton to marine mammals) at an ocean basin scale (Tittensor et al. 2010). Concerning seabirds, SST and GCHLA were the most important parameters explaining the foraging distribution during chick-rearing of White-chinned Petrels *Procellaria aequinoctialis* in the Southern Indian Ocean (Péron et al. 2010). Consistent with our findings, the alteration of SST has reported severe consequences in the reproductive success of pelagic seabirds in other regions of the world (Smithers et al. 2003).

Certainly, the static variables DCOL and DLAN were the most important factors in predicting the foraging occurrence of Cory's Shearwaters in BER and CIM in the SDM, revealing the influence of the central place foraging constrain during the chick-rearing season, and the preference to feed in shallow waters. During 2011, the warming pattern around CIM forced shearwaters to shift their distribution, thus five parameters (i.e. SST_RANGE, SST_SPR, SST_SUM and GCHLA) displayed similar percentages. We can infer that birds were not dispersing randomly but actually intended to target seamounts, upwelling zones and shelf breaks of which all these predictors are proxies. Furthermore, analyzing the response curves we can easily observe the tendency of CIM birds to forage closer to the breeding colony as oceanographic conditions improved from 2011 to 2014 (Fig. 11).

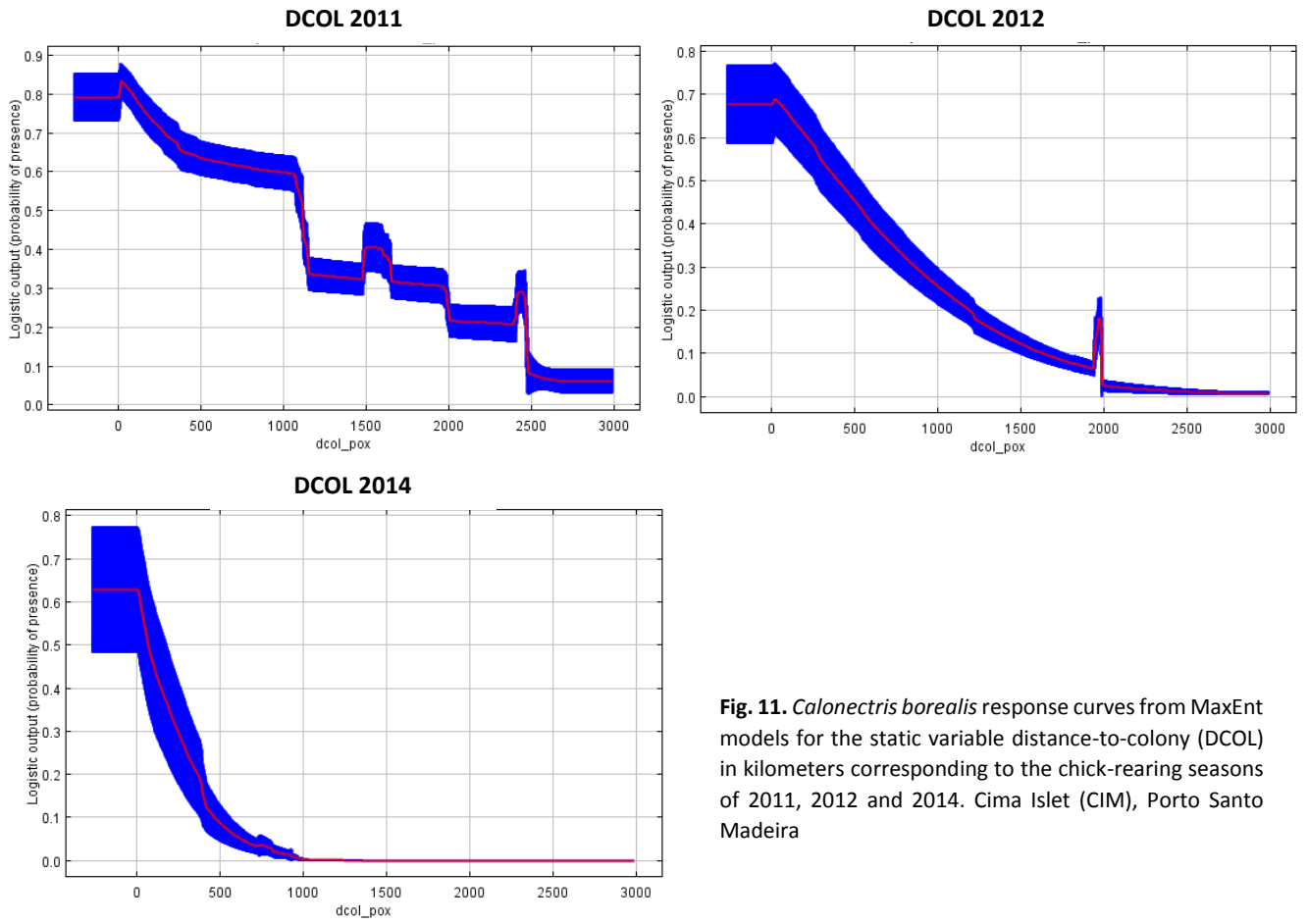


Fig. 11. *Calonectris borealis* response curves from MaxEnt models for the static variable distance-to-colony (DCOL) in kilometers corresponding to the chick-rearing seasons of 2011, 2012 and 2014. Cima Islet (CIM), Porto Santo Madeira

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Appendix.

Appendix 1. MaxEnt model results for *Calonectris borealis* from Berlenga in 2011, 2012 and 2014. Estimates of model fit and relative contributions of the environmental variables, normalized to percentages. Values are means of 50 replicate runs. Most relevant parameters ($\geq 10\%$) are shown in bold. DCOL (distance-to-colony), DLAN (distance-to-land), SST_RANGE (sea surface temperature range), SST_SUM (sea surface temperature summer), BAT (bathymetry), SST_SPR (sea surface temperature spring), CHLA_PK (chlorophyll-*a* peak), GBAT (bathymetry gradient), CHLA_SUM (chlorophyll-*a* summer), ASST_SPR (sea surface temperature spring anomaly), GCHLA_SUM (chlorophyll-*a* summer gradient), ASST_SUM (sea surface temperature summer anomaly), ACHLA_SUM (chlorophyll-*a* summer anomaly).

BERLENGAS						
	2011		2012		2014	
AUC test	0.974		0.981		0.97	
Variable	Contribution	Permutation	Contribution	Permutation	Contribution	Permutation
DCOL	36.6	42.9	25.3	30.4	65.4	70.3
DLAN	36.5	34.3	6.5	8.3	3.8	6.2
SST_RANGE	2.7	1.1	56.7	27.8	2.6	1.4
SST_SUM	10.5	8.6	-	-	14.9	11.6
BAT	7	2.1	3.7	2.1	3.7	1.8
SST_SPR	3.3	5.3	4.6	17	4.4	1.8
CHLA_PK	1.6	1.6	2.1	8	-	-
GBAT	1	1.5	-	-	1.2	0.9
CHLA_SUM	0.4	1	0.2	2.2	-	-
ASST_SPR	0.3	1.7	-	-	-	-
GCHLA_SUM	-	-	0.4	2.1	1.2	0.8
ASST_SUM	-	-	0.4	2.2	-	-
ACHLA_SUM	-	-	-	-	1.8	1.3

Appendix 2. MaxEnt model results for *Calonectris borealis* from Cima Islet in 2011, 2012 and 2014. Estimates of model fit and relative contributions of the environmental variables, normalized to percentages. Values are means of 50 replicate runs. Most relevant parameters ($\geq 10\%$) are shown in bold. DLAN (distance-to-land), DCOL (distance-to-colony), SST_RANGE (sea surface temperature range), SST_SPR (sea surface temperature spring), GCHLA_SUM (chlorophyll-*a* summer gradient), SST_SUM (sea surface temperature summer), ASST_SPR (sea surface temperature spring anomaly), BAT (bathymetry), CHLA_SUM (chlorophyll-*a* summer), GBAT (bathymetry gradient), CHLA_RANGE (chlorophyll-*a* range), CHLA_SPR (chlorophyll-*a* spring), CHLA_PK (chlorophyll-*a* peak), ASST_SUM (sea surface temperature summer anomaly), ACHLA_SUM (chlorophyll-*a* summer anomaly).

CIMA ISLET						
	2011		2012		2014	
AUC test	0.922		0.981		0.985	
Variable	Contribution	Permutation	Contribution	Permutation	Contribution	Permutation
DLAN	14.5	5.1	47.3	47.3	11.6	2
DCOL	10.8	22	11.8	18.7	46.2	71.4
SST_RANGE	15.9	12.7	7	7.6	15.7	2.8
SST_SPR	13.8	15.6	11.4	7.4	9.7	0.8
GCHLA_SUM	10.6	2.6	2.1	0.4	-	-
SST_SUM	9.3	17.6	4.9	4.8	2.2	0.6
ASST_SPR	6.9	3.7	5	1	-	-
BAT	5.7	6.5	1.8	2.9	5.3	18.1
CHLA_SUM	3.4	3.9	-	-	-	-
GBAT	2.5	0.9	-	-	2.2	0.2
CHLA_RANGE	2.3	3.1	0.9	2.8	1.7	0.6
CHLA_SPR	2	1.8	1.6	1.7	-	-
CHLA_PK	1.5	2.9	1.2	0.9	1.9	2.2
ASST_SUM	0.9	1.5	2.5	4.2	1.4	0.7
ACHLA_SUM	-	-	2.4	0.3	1.9	0.6