

Comparing the foraging strategies of a seabird predator when recovering from a drastic climatic event

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Abstract Seabirds due to their status as sentinels of the marine environment can indicate qualitative changes at various levels of the food web. Furthermore, 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) index. During the winter of 2009/2010, the second lowest NAO index in history was recorded leading to detrimental conditions that influenced productivity levels in the northeast Atlantic. The response of the Cory's Shearwater *Calonectris borealis*, during the period of ameliorating climatic conditions from this drastic event, was monitored in two islands with contrasting productivity patterns: Berlenga, located on the rich upwelling area of the Portuguese shelf; and Cima Islet (Porto Santo Island), located in a poor oceanic environment in the Madeira Archipelago. We collected a multi-year GPS-tracking data set (2011–2015) from adult breeders during the chick-rearing season to examine their

at-sea foraging distribution. During a year of low productivity, kernel estimations demonstrated that Cima Islet birds expanded their home ranges and core foraging areas all over the northeast Atlantic, whereas Berlenga birds maintained their distribution close to the breeding colony. Once oceanographic conditions ameliorated from 2012 to 2015, birds decreased significantly their foraging effort, and oceanic breeders concentrated their activity closer to the breeding colony. Analysis of habitat use by means of Maximum Entropy Modelling confirmed distance-to-colony as the most important predictor in the distribution of Cory's Shearwater. Environmental variables describing sea surface temperature, bathymetry, and chlorophyll *a* were more influential in Porto Santo, indicating higher sensitivity of the oceanic population to marine productivity proxies. Our study confirms that the Cory's Shearwater possesses enormous 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 the surroundings of their colonies.

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Introduction

Oceanographic features, such as eddies (Rodriguez et al. 2009), upwelling regions (Fréon et al. 2009), or bathymetry (Morato et al. 2008, 2010), have been linked with areas of enhanced biomass and prey aggregation in the vast ocean.

Furthermore, ecological processes within these features are consistently associated with the at-sea distribution and foraging ecology of seabirds (Weimerskirch 2007; Block et al. 2011). Seabirds are central-place foragers during the breeding season and are, therefore, constrained to find those productive patches in close proximity of their breeding colony (Paiva et al. 2010a). Hence, their foraging distribution is closely linked to resource availability. Assisted by the miniaturization of tracking technology, studies in the 21st century have unveiled important information about the spatial ecology and habitat use of seabirds throughout their entire life cycle (Burger and Shaffer 2008). Nevertheless, detailed knowledge of a species foraging range may remain obscured by the nosiness of small data sets or the limitations of tracking a single population. Multi-year and multi-colony GPS tracking are necessary to understand the spatio-temporal distribution of a marine predator (Ramos et al. 2013; Dean et al. 2015).

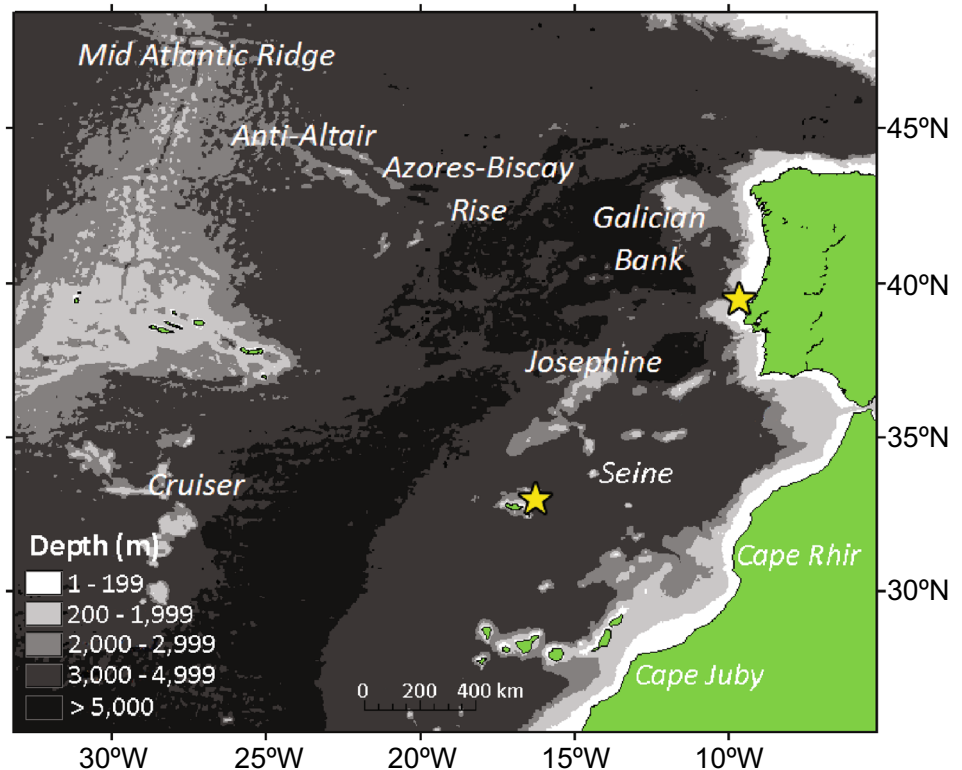
At a large-scale ocean, circulation drives the activity of marine ecosystem worldwide, and changes in its patterns are correlated with fluctuations in atmospheric circulation (Mann and Lazier 2006), depicted in indices, such as the North Atlantic Oscillation (NAO), with strong influences in marine ecological processes (Best et al. 2011). Global warming has provoked an increase in the frequency and intensity of extreme climatic events (Alley et al. 2003). Strong changes are also projected regarding intensity, timing, and spatial structure of coastal upwelling (Wang et al. 2015). Climate change impacts are being recorded in marine ecosystems worldwide, affecting seabirds in a bottom-up manner (Grémillet and Boulinier 2009), and projecting shifts in their foraging range due to changes in prey distribution (Peron et al. 2012; Crawford et al. 2015). Thus, tracking seabirds breeding in environments with contrasting marine productivity and during a period of ameliorating climatic conditions should help us assess changes in its foraging behaviour in relation to environmental variability.

In the North Atlantic basin, atmospheric conditions have been recorded since 1864 via the North Atlantic Oscillation index (NAO) (Hurrell 1995), providing a good scenario to monitor major climatic fluctuations and its effects in pelagic environments. A recent example of extreme climatic conditions occurred in the northeast Atlantic in the winter of 2009/2010 when the second lowest NAO in history was recorded (-4.64), leading to a dramatic decrease in marine productivity in the Western Iberia Upwelling Ecosystem during 2010 (Paiva et al. 2013a). The foraging ecology of the Cory's Shearwaters *Calonectris borealis* breeding in Berlenga, an island near the Portuguese coast, was examined in response to the reduction of pelagic fish prey. Reproductive success was reduced due to a 58-fold increase in core foraging areas during the chick-rearing season of 2010 compared to years with positive NAO

values (Paiva et al. 2013a). The NAO showed a substantial recovery in 2011 but remained negative (-1.6) (Ceia et al. 2014a, b). Cory's shearwaters were again affected in the pre-laying exodus when they travelled nearly 4000 km to the Grand Banks and Newfoundland shelf in Canada, in search of sufficient resources for egg formation (Paiva et al. 2013a, b). Since 2011, the NAO indicates an improvement in climatic and oceanographic conditions but with high oscillations from 1 year to another.

The aim of this study was to compare the inter-annual changes in the foraging behaviour of a marine apex predator, the Cory's Shearwater, breeding in two islands with contrasting productivity patterns in their surroundings, and during the period of recovery from this drastic climatic event. Berlenga is located over the Portuguese continental shelf, a region of high marine productivity due to the influence of coastal upwelling, and characterized by low sea surface temperature and high concentration of chlorophyll *a* (Sousa et al. 2008; Paiva et al. 2013a). On the other hand, Cima Islet (near Porto Santo Island) is located in the Madeira Archipelago, an oceanic environment expected to have lower productivity compared to Berlenga (Fig. 1). We tracked breeding adults between 2011 and 2015 during the chick-rearing period, a phase when the additional energy demands of the growing chick make parents more sensitive to variability in food resources (Grémillet et al. 2014). In parallel, we measured oceanographic conditions around the breeding colonies using surrogates of climatic conditions (i.e., NAO) and marine productivity (i.e., chlorophyll-*a* concentration and sea surface temperature). A negative winter NAO index is related to an unusually intense coastal upwelling in the Western Iberia Upwelling Ecosystem during the spawning season of small pelagic fish. These conditions drive plankton and fish larvae away from the protection of the continental shelf leading to low recruitment and prey availability for seabirds (Santos et al. 2007; Paiva et al. 2013a; Haug et al. 2015). We expect birds in the neritic area to be buffered to a certain extent against strong environmental variability due to the high marine productivity, while birds in the oceanic area may need to explore distant grounds in search of fish prey. Therefore, we tested the following predictions: (1) Birds from Cima Islet will shift their foraging distribution during years with negative NAO index compared to their distribution during years with positive NAO. On the other hand, birds from Berlenga will remain faithful to their foraging grounds even under the influence of a negative NAO. (2) Less abundance of fish prey means that both colonies are likely to increase their foraging effort during a negative NAO year because of a more exploratory behaviour. However, this increase should be significantly higher in Cima Islet than in Berlenga. The additional foraging effort may induce lower body condition index on adult shearwaters in both colonies, and have

Fig. 1 Seafloor depth (m) in the northeast Atlantic featuring names and locations of some important seamounts of the region. *Yellow stars* represent breeding colonies in our study (Berlenga—BER in the north and Cima Islet, Porto Santo—CI, Madeira in the south)



detrimental effects in their breeding success. (3) Responding to the patchy distribution of fish prey, oceanic birds should rely heavily on dynamic oceanographic variables. Thus, we anticipate marine productivity proxies (i.e., sea surface temperature and chlorophyll *a*) to be more important predicting the distribution of Cory's Shearwaters in Cima Islet than in Berlenga.

Methods

Oceanographic conditions within the study areas

Fieldwork was conducted at Berlenga Island (BER; 39°24'49"N, 9°30'29"W) and Cima Islet, Porto Santo, Madeira (CI; 33°03'19"N, 16°16'54"W). Berlenga Island (78.8 ha) is located ~8 km off the Portuguese coast of Peniche, and together with the islets of Farilhões and Estelas forms the Berlengas Archipelago which features the only breeding populations of pelagic seabirds in continental Portugal (Ramírez et al. 2008). Berlenga is under the influence of the Canary Current Upwelling Ecosystem, a highly productive marine region that covers an area between the south of Senegal (8°N) and the Iberian Peninsula (43°N) (Benazzouz et al. 2014). Berlenga is part of the Western Iberia Upwelling Ecosystem, which constitutes the northern limit of the Canary Current Upwelling System. Cima Islet (32 ha) is a small rocky formation that reaches 111 m

high, and still preserves its native Macaronesian flora and fauna. Cima Islet is located 50 km northeast of Madeira Island, within the Atlantic subtropical gyre. Although it is positioned in an oceanic area, upwelling is particularly dynamic between Madeira and Desertas Islands (Caldeira et al. 2002). Nearby seamounts, such as Ashton, Josephine (Paiva et al. 2010a), Seine, and Ampere (Martin and Christiansen 2009), may also enhance biological productivity (Fig. 1). Oceanographic characteristics that lead to productivity gradients in the northeast Atlantic have been thoroughly described by Paiva et al. 2010b, 2013b.

Study species and loggers deployment

The Cory's Shearwater *Calonectris borealis* is a medium sized procellariiform with a wide distribution, breeding in all remote islands, and islets of the northeast Atlantic except Cape Verde (Onley and Scofield 2007). This species has a high reproductive investment reflected in its 8 month breeding cycle. Eggs hatch in mid-late July and incubation and chick rearing is shared by both parents. By late October/early November, chicks finally fledge (Ramos et al. 2003). From the total population (c. 251,100 pairs) (BirdLife International 2016), 3500 pairs breed in the Madeira archipelago and between 980 and 1070 pairs breed in Berlengas (Lecoq et al. 2011; Ramos et al. 2013). Mini-GPS loggers (see Steiner et al. 2000 for details of the original device) were deployed on breeding adults during

the chick-rearing periods of 2011, 2012, 2014, and 2015 in September in Berlenga and August in Cima Islet (Table 1). About 5 and 10% of individuals were tracked for more than 1 year in Cima Islet and Berlenga, respectively. Loggers were programmed to record one location (± 4 m) every 5 min. Loggers were carefully attached to the birds' back feathers with a small piece of TESA tape. Handling took less than 10 min to minimize stress. Birds were then immediately returned to their nests. Devices weighed below 3% of the bird's body mass (i.e., 1.5–2.2%), the threshold under which several studies have reported no deleterious effects on seabirds (e.g., Phillips et al. 2003), including the study species during short-term deployments (Igual et al. 2005) and in Berlenga, one of our study colonies (Paiva et al. 2010b). However, see Ludynia et al. 2012; Heggøyr et al. 2015 for some of the potential negative impacts. Mean tracking duration for the 2011–2015 period was 9.8 days in Berlenga and 12 days in Cima Islet (see Table 1 for further details on trip characteristics). After logger retrieval, we measured wing length and body mass of birds to compute body condition index (BCI). BCI is considered a measure of structural size (Brown 1996) and was calculated as the residuals of the linear regression of body mass on wing length.

Trip filtering and kernel estimations

GPS data were used to calculate running distance-to-colony from each GPS position to colony location. This information allowed us to divide the data sets into individual foraging trips and calculate trip duration. Foraging positions were selected after applying three filters, i.e.: distance-to-colony > 2 km to avoid the influence of activities of birds manoeuvring or resting nearby, speed > 2 km/h to exclude positions of birds resting or drifting at sea, and finally speed < 15 km/h was applied, since seabirds usually commute to reach an area of interest when their speed decreases for active foraging (Louzao et al. 2009). These speed thresholds were confirmed by our frequency distribution plots of instantaneous speeds for all foraging excursions. The resultant foraging-filtered data sets were used to estimate kernels by utilization distribution (KUD). KUD methods (Worton 1989) enable us to transform location points into polygons that depict probability of occurrence. Total home range was considered as 95% (HR—UD95) and core foraging areas as 50% of foraging positions (FA—UD50). KUDs were calculated with the R package *adehabitatHR* (Calenge 2006). The *least square cross-validation* (LSCV) method was used to determine an optimal smoothing factor (h). Kernel overlaps were performed for each year to compare the consistency of home ranges and foraging areas among individuals. In addition, kernel overlaps were calculated between years and considering all

possible combinations to assess temporal changes in at-sea distribution of the population of each island. The function *kerneloverlap* of the R package *adehabitatHR* was used in these calculations.

Environmental data

Climatic (NAO index) and environmental parameters (chlorophyll-*a* concentration, CHL, and sea surface temperature, SST) were used to assess the influence of oceanographic conditions in the foraging distribution of Cory's Shearwaters. The NAO index refers to a north–south alternation in atmospheric mass between the subtropical Atlantic and the Arctic, and hence, it indicates out-of-phase behaviour between the climatological low-pressure center near Iceland and the high-pressure center near the Azores (Hurrell et al. 2003). Following the previous studies in the region (i.e., Paiva et al. 2013a, b; Haug et al. 2015), we used the extended winter NAO index (December–March) (<https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-indexstation-based>), because this is most pronounced during winter and oscillations leave long-lasting effects on oceanic productivity patterns (Paiva et al. 2013a). Since the chick-rearing season starts in July, the summer NAO index (June–August) was also monitored (from monthly NAO index values). We selected night-time SST because of the lower amplitude of variation than diurnal SST (Paiva et al. 2010a). Several predictors that have previously shown important correlations with distribution and abundance of seabirds, and oceanographic processes were also analyzed (Louzao et al. 2009; Tremblay et al. 2009): (a) bathymetry (BAT) and distance-to-land (DLAN) consider the influence of neritic environments; (b) distance-to-colony (DCOL) account for central-place foraging; (c) anomalies and gradients of SST (ASST and GSST, respectively) and CHL (ACHL and GCHL, respectively) account for small scale variability; (d) CHL peak (CHL_PK) relates to productivity persistence (Haug et al. 2015); and (e) bathymetry gradient (GBAT) indicates the influence of topographic features (e.g., seamounts) by depicting sudden changes in slope. Spatial gradients of SST, CHL, and BAT (GSST, GCHL, and GBAT, respectively) were obtained by estimating the proportional change (PC) within a surrounding 3 × 3 cell grid using a moving window as follows: $PC = [(maximum\ value - minimum\ value) \times 100 / maximum\ value]$ (Louzao et al. 2009). All parameters were calculated with ArcGis 10.0. First, environmental predictors were downloaded as monthly composites, from Aqua MODIS standard mapped image (SMI-HDF format) at ~4 km spatial resolution (<http://oceancolor.gsfc.nasa.gov/cgi/13>). HDF files were subsequently transformed to rasters with the Marine Geospatial Ecology Tools (MGET) toolbox package of ArcGis 10.0. Dynamic variables were

Table 1 Regional (North Atlantic) and local (within 60 km of the breeding colony) environmental predictors, habitat of foraging areas (within 50% KernelUDs), foraging trip characteristics, and body condition index of Cory's Shearwaters *Calonectris borealis* in Berlenga (BER) and Cima Islet (CI; Porto Santo) between 2011 and 2015

Tracking period	2011		2012		2013		2014		2015	
	CI	BER	CI	BER	CI	BER	CI	BER	CI	BER
	4 Aug to 21 Aug	31 Aug to 12 Sept	2 Aug to 25 Aug	4 Sept to 19 Sept			30 July to 14 Aug	3 Sept to 15 Sept	28 July to 10 Aug	2 Sept to 12 Sept
Regional environmental predictors										
Extended winter NAO index	-1.6		3.2		-2.0		3.1		3.6	
NAO index (Jun-Aug)	-1.1 ± 0.4		1.75 ± 0.3		-1.6 ± 0.8		1.4 ± 0.5		1.1 ± 0.1	
Local environmental predictors										
Chlorophyll- <i>a</i> concentration (CHLA; mg m ⁻³)	0.3 ± 0.7	1.7 ± 0.3	1.0 ± 0.2	2.1 ± 0.1	0.5 ± 0.2	1.3 ± 0.5	1.5 ± 0.2	2.3 ± 0.3	1.1 ± 0.4	2.1 ± 0.8
Sea Surface Temperature (SST; °C)	24.5 ± 1.3	20.0 ± 1.5	20.2 ± 1.2	17.2 ± 1.8	23.2 ± 1.2	19.2 ± 1.4	20.3 ± 1.3	16.9 ± 1.5	19.9 ± 1.7	15.9 ± 1.9
Habitat of foraging areas										
Chlorophyll- <i>a</i> concentration (CHLA; mg m ⁻³)	0.5 ± 0.2	1.0 ± 0.3	1.4 ± 0.4	1.9 ± 0.2	-	-	1.7 ± 0.3	2.0 ± 0.5	1.5 ± 0.6	2.1 ± 1.1
Sea Surface Temperature (SST; °C)	22.0 ± 0.9	19.0 ± 0.6	19.2 ± 1.1	17.0 ± 1.2	-	-	18.8 ± 0.6	19.8 ± 0.9	18.5 ± 0.9	17.9 ± 1.2
FA kernel UD area (km ²)	5.9 ± 4.2	3.9 ± 1.7	2.5 ± 1.2	1.8 ± 0.8			2.6 ± 1.1	1.6 ± 0.5	2.9 ± 1.7	0.9 ± 0.4
Foraging trip characteristics										
N tracks [N birds]	38 [11]	42 [11]	24 [6]	76 [9]	-	-	31 [6]	44 [8]	36 [6]	93 [18]
Trip duration (days)	4.5 ± 1.7	2.3 ± 0.6	1.9 ± 0.2	1.1 ± 0.7	-	-	2.1 ± 0.6	1.2 ± 0.4	2.2 ± 1.1	1.0 ± 0.7
Maximum distance from colony (km)	975.4 ± 63.1	625.1 ± 54.0	487.0 ± 47.4	195.4 ± 44.4	-	-	402.2 ± 83.2	129.7 ± 24.0	512.2 ± 110.1	98.8 ± 46.9
Time spent flying trip ⁻¹ day ⁻¹ (h)	8.2 ± 1.5	6.8 ± 1.8	6.5 ± 1.3	5.0 ± 0.6	-	-	6.8 ± 1.9	5.1 ± 0.8	5.9 ± 1.6	4.9 ± 1.9

Table 1 (continued)

Tracking period	2011		2012		2013		2014		2015	
	CI	BER	CI	BER	CI	BER	CI	BER	CI	BER
	4 Aug to 21 Aug	31 Aug to 12 Sept	2 Aug to 25 Aug	4 Sept to 19 Sept	–	–	30 July to 14 Aug	3 Sept to 15 Sept	28 July to 10 Aug	2 Sept to 12 Sept
% of time spent in foraging areas	48.9±9.6	38.1±5.8	33.1±5.7	20.1±2.5	–	–	32.3±8.4	19.4±3.6	30.2±10.1	18.6±7.7
Fitness parameter										
Adult's body condition index (BCI)	-1.1±0.5	-0.9±0.3	0.6±0.2	0.8±0.3	–	–	0.5±0.2	1.0±0.4	0.8±0.3	1.3±0.6

The extended winter (December–March) North Atlantic Oscillation (wNAO) index was downloaded from: <https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-indexstation-based>

aggregated in periods of 3 month composites using the median value of each pixel, because they account for better proxies of the persistency of oceanographic features (Louzao et al. 2009). Composites corresponded to two seasons: spring (SPR: March–May) and summer (SUM: June–August). CHL_PK was computed from multiple layers of CHL (March–August) during the last 13 years (2002–2015). Cells with a CHL concentration >1 mg m⁻³ were assigned a value of 1 and lower values assigned 0 (Louzao et al. 2009, 2012; Suryan et al. 2012; Afán et al. 2014). BAT 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>).

Species distribution modelling (SDM)

Environmental variables were used to perform habitat niche models based on Maximum Entropy with the software MaxEnt 3.3.3k. MaxEnt was chosen, because it is able to model species distribution from presence-only data and maintain a predictive performance at the same level of the highest rated methods (Elith et al. 2006). Initially, tracking data were rescaled into a spatial grid with cell size 0.0417° (4 km) 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 for Berlenga and Cima Islet for each year were run for internal validation, including all predictors and five replicates of random bootstrap subsamples. In addition, to avoid collinearity, we performed all pairwise Spearman correlation matrices with the R software. Strongly correlated pairs of variables were assessed at $|r_s| \geq 0.70$ (see Table S1). When two variables were strongly correlated, percentages of contribution from the preliminary models were evaluated to discard the least important variable. Finally, MaxEnt models were run only with the selected variables and the following settings: logistic output format, duplicates removed, 30% random test percentage, and 50 replicates of random bootstrap subsamples. Results are summarized as the mean of the 50 models. Outputs considered were: a jackknife test result chart, response curves, percentage of contribution, and a graphic of the receiver operating characteristic (ROC) curve which appraise the predictive performance of the model with the Area Under the receiver operating characteristic Curve (AUC). AUC values range from 0 to 1, with 0.5 indicating that model performance equals 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).

Data analysis

Generalized linear mixed models (GLMM) were used to test the effect of (1) year (2011, 2012, 2014, and 2015), (2) Island (Cima Islet and Berlenga Island), (3) the interaction between year and Island (i.e., independent fixed effects) on (1) the monthly NAO index, (2) chlorophyll-*a* concentration (CHLA), and (3) sea surface temperature (SST) in the colony surroundings (60 km around the breeding colony, i.e., the typical foraging range of Cory's Shearwaters breeding in Berlenga); (4) the CHLA, (5) SST, and (6) area of the 50% kernel UD; (7) the trip duration, (8) maximum distance from colony, (9) time spent flying trip⁻¹ day⁻¹, (10) percentage of time spent in foraging areas, and (11) the adults' body condition (i.e., dependent variables). GLMMs were fitted by the Laplace approximation, and trip identity was nested within the individual as a random term to avoid pseudo-replication problems. Q-Q plots and Cleveland dot-plots were used to check normality and homoscedasticity (Zuur et al. 2010) in all variables before each statistical test. When needed, variables were log-transformed. After that, the data and error structure approached a normal distribution; therefore, we selected a Gaussian family (link = identity) for all models (Zuur et al. 2007). GLMMs were performed with the *lme4* package (Bates et al. 2015). All pairwise *pos-hoc* multiple comparisons were analyzed with Bonferroni correction to account for Type I errors. The R software 3.1.3 was used in all statistical analyses. Results are expressed in means ± SD with a significance level of $p < 0.05$.

Results

Inter-annual environmental stochasticity in the North Atlantic

The extended winter NAO index indicated high oscillations in climatic conditions in the North Atlantic throughout the entire study period. Strong negative indices were recorded in 2011 (-1.6) and 2013 (-2.0), contrasting with strong positive values in 2012 (3.2), 2014 (3.1), and 2015 (3.6). Even though the NAO in 2014 was lower than in 2012, there was a higher amplitude of variation in the transition from 2013 to 2014 than from 2011 to 2012, suggesting a greater recovery in marine productivity. The summer NAO index showed an identical pattern, with negative years significantly different than positive ones. The lowest NAO indices of the study period were registered in 2013, but no tracking data were collected that year (Tables 1, 2).

Oceanographic changes were detected in composites of spring sea surface temperature (SST_SPR) in the north-east Atlantic basin during 2011–2015. A warming trend

was visible over the Portuguese and African shelves in 2011 presumably due to the atmospheric conditions of the negative NAO index. These regions were recurrent foraging areas of birds in Berlenga and Cima Islet. Mean SST_SPR south of Lisbon and a narrow band over the north African shelf appeared under isotherms 2–4 °C higher compared to years of positive NAO values. Waters north and east of the Canary Islands were also 2 °C warmer, while south of Azores SST_SPR recorded values 2 °C cooler in 2011 (Fig. 2). Inter-annual changes were also detected in summer sea surface temperature (SST_SUM) within 60 km of Berlenga and Cima Islet. Both islands recorded significantly higher SST_SUM in 2011 and 2013 compared to 2012, 2014, and 2015. Concerning summer chlorophyll *a* (CHL_SUM), Berlenga and Cima Islet registered lower mean values of in 2011 and 2013, but the differences were not significant. Comparing islands, productivity proxies (SST and CHL) were significantly higher in Berlenga than in Cima Islet (Tables 1, 2).

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

Cory's Shearwaters presented more exploratory patterns of foraging during the chick-rearing season of 2011 under the influence of a negative NAO phase. On one hand, birds from Cima Islet targeted very distant foraging grounds, spreading their home ranges (HR) and foraging areas (FA) all over the Northeast Atlantic and even beyond (Fig. 3a). Once oceanographic conditions improved in 2012, 2014, and 2015, HR were reduced and FA were mostly concentrated in the surroundings of Madeira, the nearby seamounts, and the African shelf (Fig. 3b–d). These three regions were also targeted in 2011, and were thus the most exploited FA during the study period in Cima Islet. On the other hand, birds from Berlenga maintained their FA over the Portuguese shelf during all the study period. Occasionally, some individual extended their HRs, mainly in 2011 (Fig. 3a–d).

Cory's Shearwaters showed a significant increase in their foraging effort parameters during 2011: (a) trip duration was more than 1 day longer in Berlenga, and more than 2 days longer in Cima Islet when compared with positive NAO years ($F_{7,376} = 2.47$, $p = 0.02$); (b) birds from Berlenga and Cima Islet reached maximum distances from colony approximately 400–500 km longer ($F_{7,376} = 2.78$, $p = 0.01$); and (c) and spent almost 20% more time in foraging areas in 2011 than in the other study years ($F_{7,376} = 2.43$, $p = 0.02$). Consequently, FA were at least twice as large in 2011 in both islands. The amount of extra energy expenditure of this chick-rearing season significantly

Table 2 Generalized linear mixed effect models (GLMMs) testing the effect of the interaction between year (2011, 2012, 2014, and 2015) and Island (Cima Islet, CI vs Berlenga, BER) on regional and local environmental predictors in the colony surroundings (60 km around the breeding colony)

Variables	Year			Island			Year × Island		
	GLMM	<i>P</i>	Effect	GLMM	<i>P</i>	Effect	GLMM	<i>P</i>	Effect
Regional environmental predictors									
Extended winter NAO index (December–March)	–	–	–	–	–	–	–	–	–
NAO index (Jun–Aug)	$F_{4,10} = 25.6$	<i><0.001</i>	11,13 < 12,14,15	–	–	–	–	–	–
Local environmental predictors									
Chlorophyll <i>a</i> concentration (CHLA) (mg m ⁻³)	$F_{9,148} = 1.50$	0.16	–	$F_{9,148} = 2.62$	0.01	CI < BER	–	–	–
Sea Surface Temperature (SST; °C)	$F_{9,148} = 2.59$	0.01	11,13 > 12,14,15	$F_{9,148} = 2.30$	0.02	CI > BER	–	–	–
Habitat of foraging areas									
Chlorophyll <i>a</i> concentration (CHLA) (mg m ⁻³)	$F_{7,376} = 2.72$	<i><0.01</i>	11 < all others	$F_{7,376} = 2.37$	0.03	CI < BER	$F_{7,376} = 2.05$	0.05	CI 11 < all others
Sea Surface Temperature (SST; °C)	$F_{7,376} = 2.25$	0.03	11 > all others	$F_{7,376} = 2.91$	<i><0.01</i>	CI > BER	$F_{7,376} = 2.19$	0.04	CI 11 > all others
FA kernel UD area (km ²)	$F_{7,376} = 2.31$	0.03	11 > all others	$F_{7,376} = 3.01$	0.01	CI > BER	$F_{7,376} = 2.09$	0.05	CI and BER 11 > all
Foraging trip characteristics									
N tracks [N birds]	–	–	–	–	–	–	–	–	–
Trip duration (days)	$F_{7,376} = 2.47$	0.02	11 > all others	$F_{7,376} = 1.61$	0.13	–	$F_{7,376} = 1.48$	0.18	–
Maximum distance from colony (km)	$F_{7,376} = 2.78$	0.01	11 > all others	$F_{7,376} = 14.69$	<i><0.001</i>	CI > BER	$F_{7,376} = 2.47$	0.02	CI 11 > all others
Time spent flying trip ⁻¹ day ⁻¹ (h)	$F_{7,376} = 1.11$	0.16	–	$F_{7,376} = 1.46$	0.18	–	$F_{7,376} = 1.43$	0.19	–
% of time spent in foraging areas	$F_{7,376} = 2.43$	0.02	11 > all others	$F_{7,376} = 2.88$	0.01	CI > BER	$F_{7,376} = 1.39$	0.21	–
Fitness parameter									
Adult's body condition index (BCI)	$F_{7,376} = 2.81$	<i><0.01</i>	11 < all others	$F_{7,376} = 1.67$	0.12	–	$F_{7,376} = 2.04$	0.05	CI 11 < all

Foraging habitat (within 50% KernelUDs), trip characteristics, and fitness parameters shown in Table 1 and Fig. 3. The individual was used as a random effect to avoid pseudo-replication issues. Significant differences ($P < 0.05$) marked in italics. Effect was evaluated with post-hoc multiple comparisons with Bonferroni correction. Years are represented by the last two digits (e.g., 11=2011). The extended winter (December–March) North Atlantic Oscillation (wNAO) index downloaded from: <https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-indexstation-based>

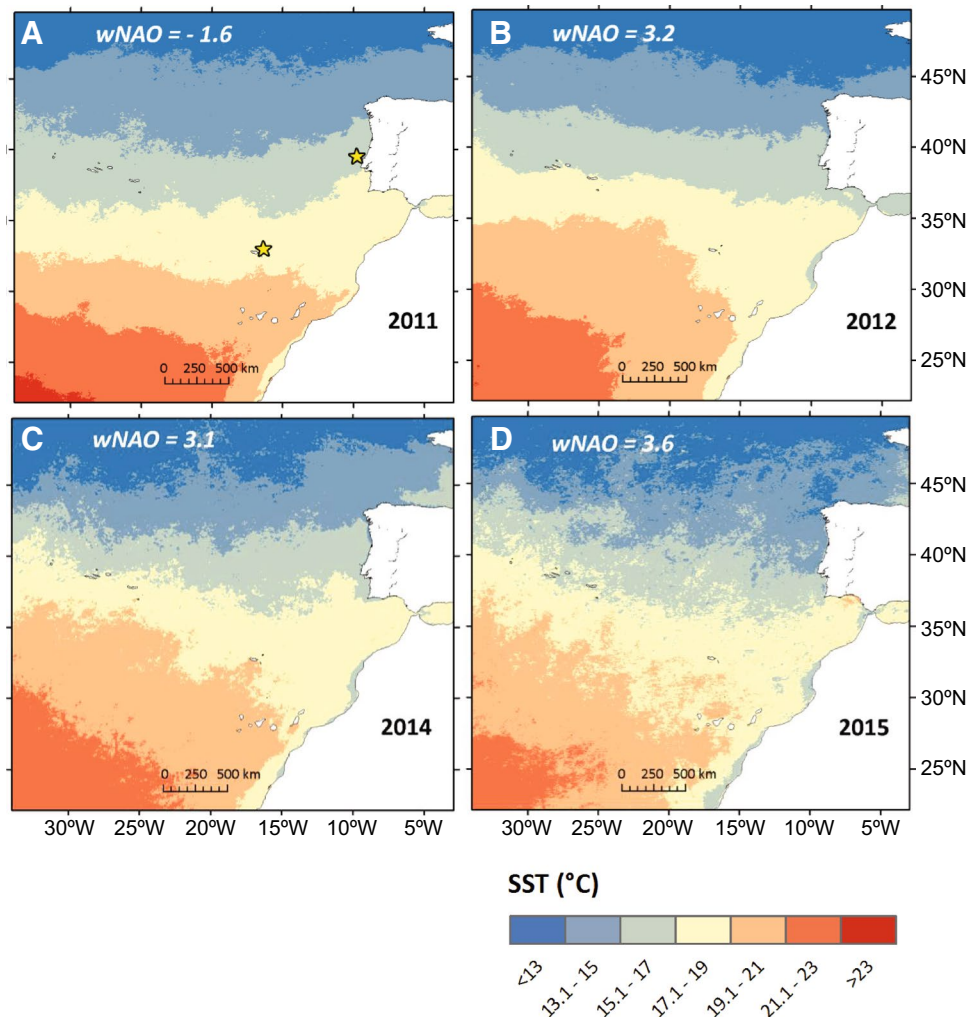
decreased body condition index (BCI) of breeding adults (Tables 1, 2).

Comparing islands, and in accordance with the previous studies involving oceanic and neritic populations, the extent of FA was significantly higher in Cima Islet than in Berlenga. Birds from Cima Islet targeted FA with significantly lower CHLA and higher SST than birds from Berlenga. Two foraging effort parameters were significantly higher for Cima than for Berlenga birds (maximum distance from colony and time spent in foraging areas), but differences in trip duration were not significant. Considering the combined effects year*island, our results indicated

that birds from Cima Islet were more affected by detrimental conditions of 2011. Birds from Cima attained the furthest maximum distances from colony, targeted FA with the lowest productivity proxies (low CHLA and high SST), and recorded the lowest BCI of the entire study period that year (Tables 1, 2).

When analysing the evolution of the foraging distribution over time (i.e., kernel overlaps between pairs of years: 2011–2012, 2011–2014, 2012–2014, etc), our results confirm that birds from Berlenga relied consistently on the same locations year after year (mean overlaps: HR = 77%, FA = 80%), including high overlaps when comparing

Fig. 2 Three-month mean composites corresponding to spring sea surface temperature (SST_SPR: March–May) in the surroundings of Berlenga (BER—1), and Porto Santo (CI—2) between 2011 and 2015 (a–d). From <http://oceancolor.gsfc.nasa.gov/cgi/l3>. Also shown in the figure the extended winter (December–March) North Atlantic Oscillation (wNAO) index (<https://climate-dataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-indexstation-based>)



the foraging distribution of 2011 with the distribution of positive NAO years: $HR \geq 70\%$ and $FA \geq 77\%$. Unexpectedly, birds from Cima Islet also maintained a consistent distribution over time, though the mean overlaps were lower than in BER ($HR = 69\%$ and $FA = 67\%$). The lowest mean overlaps were recorded between 2011 and 2012 ($HR = 64\%$ and $FA = 61\%$). Kernel overlaps among birds showed high segregation in both colonies in 2011, recording the lowest FA overlaps: 29% for BER and 18% for CI, compared to the mean overlaps of the study period: 40% for BER and 41% for CI. HR overlaps were also the lowest in 2011 (BER = 54%, CI = 30%) compared to the mean (BER = 62%, CI = 47%).

Habitat use in response to inter-annual environmental variability

Species Distribution Models for Cory's Shearwater in Cima Islet and Berlenga showed excellent predictive

performances (all AUC values > 0.80). Certain similarities were found in the habitat use throughout the study period. Distance-to-colony (DCOL) was the only parameter displaying each year a high percentage of contribution in both islands (Table 3). During 2011 birds from Berlenga and Cima Islet exploited areas furthest from the colony, as indicated by the response curves of DCOL (Fig. S1). This same variable also reduced the most gain when omitted from the models. Sea surface temperature (SST) represented by various parameters ranked second in importance but in different manners in each island. Every year, at least one SST variable had an important contribution to the model for Cima Islet but not necessarily for Berlenga. Either distance-to-land (DLAN) or bathymetry (BAT) was always major contributors in models for Cima Islet but not in Berlenga. Summer chlorophyll *a* (CHL_SUM) was only an important contributor for Berlenga. During 2011, six parameters recorded contributions of 10% or higher for Berlenga (Table 3).

Fig. 3 Cory’s Shearwater *Calonectris borealis* kernel utilization distribution (KUD) plots for Berlenga—BER (blue; 1) and Cima Islet—CI (red; 2) during chick-rearing phases of 2011 to 2015 (a–d). Stars indicate the breeding colonies. Outer lines represent Home Ranges (UD 95), and filled polygons represent core Foraging Areas (UD 50). All maps plotted over bathymetry (m). Also shown in the figure the extended winter (December–March) North Atlantic Oscillation (wNAO) index (<https://climate-dataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-indexstation-based>)

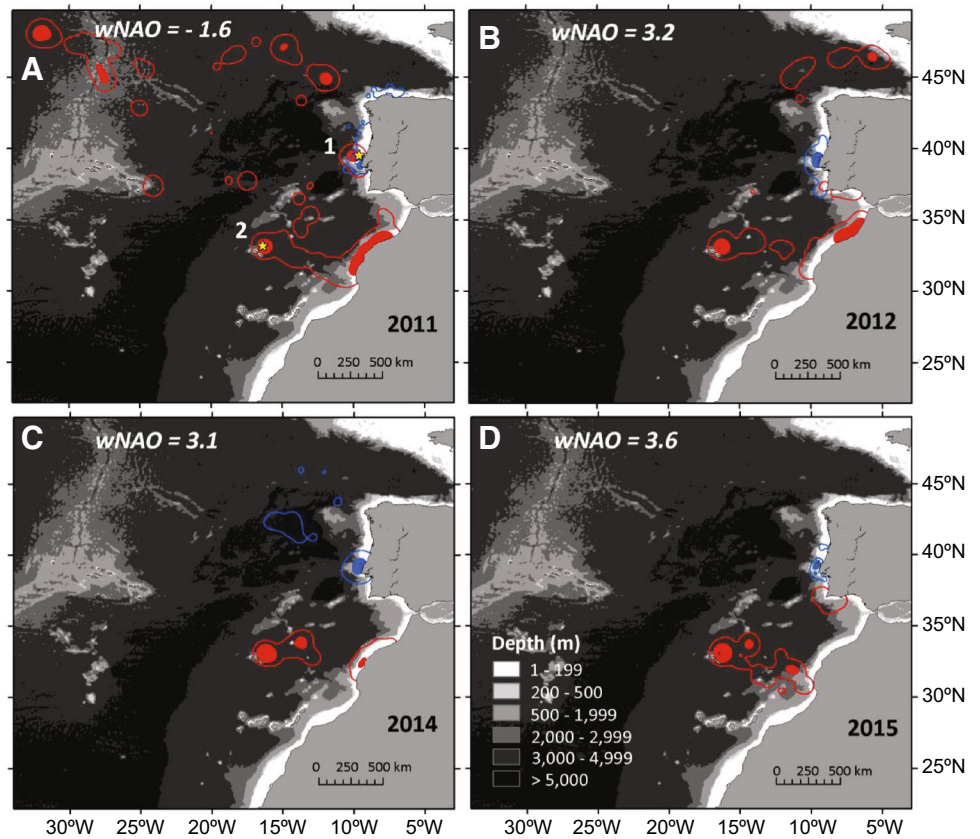


Table 3 Estimates of relative contributions of the environmental variables to the MaxEnt models for Cory’s Shearwater *Calonectris borealis* in Berlenga (BER) and Cima Islet (CI; Porto Santo)

	2011		2012		2014		2015	
	BER	CI	BER	CI	BER	CI	BER	CI
Test AUC	0.87	0.81	0.98	0.87	0.97	0.89	0.99	0.88
DCOL	39.1	23.5	36.0	12.2	69.4	47.3	53.8	46.6
DLAN	42.3	–	6.5	49.3	–	12.2	15.5	–
BAT	–	16.4	–	–	5.8	–	20.0	15.1
GBAT	–	–	39.3	–	–	–	–	–
SST_SUM	11.6	–	–	10.2	16.1	18.0	–	9.3
SST_SPR	–	17.6	–	–	–	11.4	–	–
ASST_SPR	–	15.8	–	5.0	–	–	–	–
GSST_SUM	–	16.5	–	–	–	–	–	10.0
CHLA_SUM	–	8.5	–	12.6	–	–	–	13.2

Values shown are averages over 50 replicate runs. Only values above 5% are shown. Values not shown correspond to variables not used in the models due to high collinearity ($|r_s| > 0.7$) in pairwise correlations (see Table S1)

Discussion

Our study confirms the flexibility in the at-sea foraging tactics 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 (2011–2015). As reported in other studies (Paiva et al. 2013a, b; Haug et al. 2015), we identified a correlation

between a negative extended winter NAO index and a subsequent decrease in productivity proxies (SST and CHLA) in BER for the upcoming breeding season. This may have influenced the foraging distribution of Cory’s Shearwaters. Furthermore, our work extends the link between changes in oceanographic conditions in the northeast Atlantic and the foraging behaviour of seabird predators further south to the pelagic waters of the Madeira archipelago. By studying

birds breeding in islands with contrasting marine productivity, we could detect similarities and differences in each population strategies. Overall, and according to our first prediction, birds breeding the oceanic island of Cima Islet were more affected by the low productivity of 2011 than the neritic island of Berlenga. Contrastingly to birds from Berlenga that consistently foraged over the Portuguese continental shelf each year, birds from Cima Islet reacted to the detrimental conditions by dispersing their home ranges (HR) and foraging areas (FA) to very distant regions of the North Atlantic when compared to productive years. Birds from Berlenga and Cima Islet similarly increased their foraging effort parameters to cope with the lower marine productivity of 2011. Nevertheless, and according to our second prediction, the increase in foraging effort was significantly higher for Cima Islet, where birds recorded greater maximum distances travelled, lower productivity proxies in their FA, and lower body condition index (BCI). Species Distribution Models showed that distance-to-colony (DCOL) was the most important predictor in the foraging distribution of Cory's Shearwaters in the northeast Atlantic. Agreeing with our third prediction, sea surface temperature (SST) and chlorophyll *a* (CHL) were more important parameters for Cima Islet than for Berlenga. Moreover, due to the lower productivity in their surroundings, only birds from Cima Islet favoured FA with higher CHL and lower SST, evidencing the importance of productivity proxies for oceanic breeders.

The foraging plasticity of oceanic and neritic populations of a marine apex predator

This study confirmed the foraging pattern for Berlenga reported in tracking studies over the last decade during chick-rearing (Paiva et al. 2010a, b; Alonso et al. 2012). Concerning Cima Islet, we identified the colony surroundings, the Seine seamount, and the African shelf (north of Cape Rhir) as the more persistent core foraging areas for birds from this colony, and to a lesser degree the Seine seamount. While birds from Berlenga maintained their distribution over the Portuguese shelf in 2011, buffered by the productivity of the Upwelling Ecosystem, birds from Cima Islet expanded their distribution in response to the decreased marine productivity. The foraging ecology of a marine predator is highly dependent on the abundance and distribution of prey (Morato et al. 2008), thus the patchy distribution of resources around Madeira and the decrease in fish prey should have influenced oceanic birds in increasing their range. We located HR all around the northeast Atlantic. FA included far-off regions, such as Berlenga, the Mid-Atlantic Ridge, and close to Altair. These areas correspond to rich neritic environments (Aristegui et al. 2009), temperate regions with abundant fish stocks (Bellier et al.

2007), or in the case of Altair in the northwest Atlantic, it appears to be more productive during a negative NAO phase (Paiva et al. 2013a, b). Despite the noticeable expansion of HR and FA in 2011, as a population Cima Islet showed high fidelity to its foraging grounds with an overlap of at least 61% compared to productive years. Furthermore, birds targeted regions that were possibly familiar during other breeding periods, such as the section between the Anti-Altair seamount and the Galician bank, which is an important foraging area for Cory's Shearwaters in nearby Desertas (Madeira) during incubation (Paiva et al. 2010a).

Birds from Berlenga and Cima Islet drastically increased their foraging effort in 2011, but birds of each island did so adapting to their differing tactics. On one hand, BER birds adopt a unimodal strategy of short trips, and increase their foraging parameters compared to other phases of their breeding cycle to cope with the chick's demands (Paiva et al. 2010a, this work). Length of foraging trips depends on food availability (Uttley et al. 1994), and hence, the additional effort should be explained by a more stochastic behaviour due to the reduced productivity of 2011. Furthermore, low availability of sardines *Sardina pilchardus* and Garfish *Belone belone*, reported as the most consumed prey of Cory's Shearwaters in BER (Paiva et al. 2010d), may have caused birds to switch their diet. On the other hand, we recorded in Cima Islet the typical dual foraging strategy similar to that registered for other oceanic colonies. Birds combined an average of four short trips around Madeira archipelago with one long excursion to the African shelf, or more rarely to the Seine seamount. In 2011, individuals seemingly spent higher effort in their short trips to feed their chicks and venture to very distant grounds (mean maximum distances from colony ~1000 km) in an attempt to recover their extra-depleted energy reserves (Chaurand and Weimerskirch 1994).

Colony-specific foraging biology may differ heavily as a result of intraspecific competition. Even though population sizes do not vary substantially between Berlenga and Madeira, birds from Cima Islet are constrained by the close presence of over 43,000 pairs from Selvagens and Lanzarote foraging north of Cape Juby and with which Cima Islet birds reported a 22% overlap (Ramos et al. 2013). Small colonies of seabirds can target colony-specific foraging areas (Ainley et al. 2016) or even sub-colony-specific (Ceia et al. 2014a, b), where they avoid larger colonies due to resource depletion. Therefore, it relates once again to food availability. Another aspect to consider is that tracking data between both islands were approximately 1 month apart. Our study benefited from a long-term database collected in Berlenga every September since 2005, but data collection for Cima Islet occurred in August, which could confound our results as all chicks in Berlenga were in the linear

growth phase already. Birds from Cima Islet may have experienced a higher impact on food resources near the colony due to the presence of non-breeders, juveniles, and fail breeders. Nevertheless, such individuals are not constrained by central-place foraging and can be more dispersed (Phillips et al. 2005) specially during periods of food scarcity, thus the influence of this factor should be minimal.

The Cory's Shearwater is recognized as an exceptionally plastic species in its foraging behaviour during the breeding (Paiva et al. 2010c), migratory (Dias and Granaideiro 2011), and wintering seasons (Dias et al. 2012). Yet, the consequences can be severe, food availability is crucial in breeding success and adult survival (Davis et al. 2005), and body condition index is the main factor regulating chick-provisioning in petrels and albatrosses (Tveraa et al. 1998; Weimerskirch et al. 2000). Our study recorded significantly lower body condition index in both populations in 2011 with a more pronounced impact for Cima Islet birds. A similar outcome has provoked birds in Berlenga to reduce their hatching, fledging, and ultimately reproductive success (Paiva et al. 2013a, b).

The foraging distribution of Cory's Shearwater and its relation with environmental parameters

Our study detected a correlation between a negative NAO phase and a decrease in marine productivity proxies (increase in sea surface temperature and decrease in chlorophyll *a*) around the most important foraging areas of Cory's Shearwaters in Berlenga and Cima Islet. This provides further evidence of the NAO as an ideal surrogate of environmental conditions and marine productivity in the northeast Atlantic. Seabirds rely heavily on environmental cues for the processes involved in first passage time (Paiva et al. 2010c). Our models provide evidence that parameters, such as sea surface temperature (SST), chlorophyll *a* (CHL), and bathymetry (BAT), are more important cues in oceanic populations of a widespread seabird species. Furthermore, these variables appear even more influential in low productive environments and during periods of environmental stochasticity as it happened for Cima Islet in 2011. Several studies have already highlighted the importance of SST, CHLA, and BAT predicting the habitat use of procellariiforms (e.g., Péron et al. 2010; Paiva et al. 2010c), but other variables may also need consideration. According to our results, information should be revealed by continuously tracking marine predators during periods of decreased productivity.

Conclusion

Our inter-annual, multi-colony tracking study provides strong evidence that the foraging choices of a seabird predator were highly dependent on marine productivity around the breeding colony. Productivity patterns at the same time appeared closely linked to environmental variability. During the 5-year span of this study, we recorded two strong negative NAO values (2011 and 2013), and three even stronger positive NAO values (2012, 2014, and 2015), which indicate a continuous influence of climate stochasticity in the marine environment. Though we do not possess data of 2013, our results are supported and in agreement with the findings of Paiva et al. 2013a; Paiva et al. 2013b. We showed that only Cory's Shearwaters in the poorer oceanic environment of CI expanded dramatically their HR and FA to explore almost every region of the northeast Atlantic in response to the negative NAO phase of 2011 and the decrease of productivity proxies in the colony surroundings. Nevertheless, the richer neritic population of BER also increased its foraging effort parameters, which resulted in both populations reducing their BCI and most likely their breeding success for that year. Oceanic breeding birds specially, exhibited enormous plasticity, relying heavily on environmental cues to target areas continuously associated with high pelagic diversity and fish prey even when constrained by conditions of climate stochasticity. The current and future threats posed by climate change require a continuous monitoring of seabird to assess the impacts of environmental change in marine productivity. On one hand, species breeding in neritic environments should provide valuable information about the level of resilience of the productive Eastern Boundary Upwelling Ecosystems. On the other hand, species breeding in oceanic environments may reveal subtle changes in the complex marine food web within certain oceanographic features, which is important for conservation. In the future, we need to take this work one step further and include as many intermediate trophic levels as possible to appraise more accurately the impacts that environmental change will have in the oceans.

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Compliance with ethical standards

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they have no conflict of interests. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Specifically, the experimental approach was conducted with permission from the Portuguese Government—‘Instituto de Conservação da Natureza e Florestas (ICNF)’—with Permit No. 89/2011/CAPT. All methods used in this study comply with the Portuguese laws No. 140/99, No. 49/2005, No. 316/89, and No. 180/2008.

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