

Effects of environmental variability on different trophic levels of the North Atlantic food web

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ABSTRACT: The effects of environmental change on the biodiversity, structure and functioning of marine ecosystems is still poorly understood. In fact, very few studies have focused on changes in the at-sea foraging tactics of pelagic seabirds in relation to environmental stochasticity. Aiming at filling this knowledge gap, from 2005 to 2010 we directly measured the influence of climate (as driven by the North Atlantic Oscillation phenomenon) on (1) marine productivity (i.e. chlorophyll *a* concentration), (2) fish prey abundances and (3) the foraging behaviour of a top marine predator, the Cory's shearwater *Calonectris diomedea borealis*. There was a dramatic change in the foraging strategy of the birds during 2010, which seems to be mostly related to a climatic event that occurred during the winter of 2009 to 2010. This event had a negative impact on the productivity of the surroundings of the breeding colony and decreased the abundance of pelagic prey fish, which in turn altered the spatial, feeding and trophic ecology of Cory's shearwater and decreased their reproductive success. However, the negative trend in the abundance of pelagic prey (estimated from acoustic surveys and commercial fisheries landings) may be of concern because it does not seem to be only related to the climatic event of 2010. Long-term monitoring of the interactions between top predators, their prey and lower strata of the food web is crucial for a comprehensive assessment of the impacts that environmental variation may have on coastal ecosystems worldwide.

KEY WORDS: Environmental variability · Foraging behaviour · Trophic ecology · Marine food web · Habitat use models · Fisheries

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INTRODUCTION

There is substantial evidence that climate change is altering the biodiversity, structure and functioning of marine ecosystems (Shackell et al. 2010, Johnston et al. 2012). Climate change is closely related to large-scale atmospheric phenomena, of which the North Atlantic Oscillation (NAO) is one of the best known (reviewed by Stenseth et al. 2003). The NAO refers to a north-south alternation in atmospheric

mass between the subtropical Atlantic and the Arctic and thus involves out-of-phase behaviour between the climatological low-pressure centre near Iceland and the high-pressure centre near the Azores (Hurrell et al. 2003). Within the oceanic environment, negative NAO values are indicative of a noticeable decrease in the sea surface temperature (SST) (due to strong winds that strengthen the upwelling phenomenon), which has been linked to an overall increase in the abundance and availability of a variety of mar-

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ine organisms from lower trophic levels (e.g. plankton, fish prey) to top marine predators (Mann & Lazier 2006).

The winter of 2009 to 2010 represented a record-breaking low value of the NAO index (Osborn 2011). Under these extreme oceanic conditions (i.e. unusually intense upwelling and low SST due to stronger winds), we should expect a lower abundance of plankton (Bakun 2006) and consequently lower abundance and availability of fish prey to top marine predators, such as seabirds. In some upwelling regions, such as the Portuguese coast, an overly intense upwelling may be responsible for a very low recruitment of small pelagics (such as sardine *Sardina* spp.) and low abundance of plankton because, under these conditions, the fish larvae and plankton are driven offshore, which consequently increases mortality of the larvae and creates a spatial mismatch of plankton and juvenile planktonic fishes a few months later (Santos et al. 2007). In addition, the effect of the NAO is regionally dependent, and a reverse effect (i.e. weaker wind fields and higher SST) should have been noticed in the northern Atlantic (Stenseth et al. 2003).

Recent studies have attempted to examine the effects of climate variability on life-history traits of North Atlantic seabirds (e.g. Sandvik & Erikstad 2008), but so far no clear pattern has emerged. Nevertheless, several studies reported a link between changes in ocean climate and fluctuations in seabird demography and population dynamics. Those include variations in breeding success (e.g. Frederiksen et al. 2004), breeding distribution (e.g. Montevecchi & Myers 1997) and annual survival (e.g. Grosbois & Thompson 2005), among others. However, very few studies focused on changes in the at-sea foraging tactics of pelagic seabirds in relation to climatic change, particularly in the Atlantic Ocean (but see Luczak et al. 2011).

Most of the studies documenting the effects of environmental stochasticity on seabirds do so in an indirect manner, often skipping several trophic levels in the process. It is probably mainly the effect of SST on prey availability and abundance that constitutes the direct link between large-scale climate indices and seabird demographic responses (ICES 2008, Sandvik & Erikstad 2008). Despite being used several times as a proxy of productivity, SST remains primarily a climatic index. Studies of climate change impact on seabirds that integrate more trophic levels of the food web (e.g. fish prey abundance and distribution) are still sparse in the literature. In the present study, we used fish prey data collected during annual surveys

within our study area. By joining these data to remote sensing (e.g. SST) and tracking datasets, we built a comprehensive study of the effect of NAO on both seabirds and their fish prey. This enabled us to establish a more 'direct' link between climate variation (i.e. NAO), the abundance of fish prey and the at-sea foraging behaviour of a seabird, Cory's shearwater *Calonectris diomedea borealis*, that forages in the upwelling ecosystem along the Portuguese west coast.

Between 2005 and 2010, we measured the influence of climate (as driven by the NAO) on (1) SST and chlorophyll *a* concentration (i.e. a measure of phytoplankton productivity), (2) fish prey abundances (using the proxy 'species acoustic backscatter') and (3) the foraging behaviour of chick-rearing Cory's shearwaters around Berlenga Island (39.41° N, 9.50° W) on the Portuguese west coast. This is the largest island of an archipelago that also comprises 2 groups of smaller rocky islets, 'Farilhões' and 'Estelas'. Rich foraging grounds surround this area because the bathymetric features, ocean circulation and wind characteristics congregate potential prey at the surface. More broadly, the island is located on the continental shelf platform and is strongly influenced by the Canary Current (12 to 43° N) and continuous upwelling, which naturally enhances productivity in the colony surroundings. If oceanographic conditions change and marine productivity decreases below a certain threshold, we hypothesize that prey fish would (1) change their distribution and abundance, decreasing their availability to seabirds. In response to that, birds would (2) increase their foraging range and effort (e.g. travelling further or diving at a higher rate to obtain food resources), (3) suffer a decrease in their breeding success, (4) alter their diet composition and trophic ecology (evaluated based on their nitrogen and carbon signatures) in response to prey availability and habitats exploited and (5) respond to different oceanographic cues during the spatio-temporal use of specific habitats (i.e. different oceanographic predictors will explain the habitats used by birds).

MATERIALS AND METHODS

Individual tracking database

The tracking study was performed at Berlenga Island each September (chick-rearing period) from 2005 to 2010 (Table 1). Cory's shearwaters were equipped with compass-temperature loggers (Compass-Tlog; outer diameter = 16 mm, total length =

Table 1. Inter-annual comparison of foraging and breeding parameters (mean \pm SD) of Cory's shearwaters and oceanographic parameters in the colony surroundings; fledging and breeding success of nests from tracked birds. Environmental predictors are for September of each year, unless otherwise stated. Home range: kernel density contour encompassing 95% of all compass-logger positions; feeding area: kernel density contour encompassing 50% of the diving event positions. SST: sea surface temperature

Year	2005	2006	2007	2010
Foraging parameter				
No. birds [No. tracks]	16 [24]	20 [26]	20 [27]	20 [29]
Trip duration (d) [range]	1.2 \pm 0.9 [1–3]	2.6 \pm 1.4 [1–5]	1.2 \pm 0.6 [1–3]	6.2 \pm 1.9 [1–16]
Total distance covered (km)	67.4 \pm 16.9	85.9 \pm 24.0	101.6 \pm 69.2	3521.8 \pm 798.4
Maximum distance from colony (km)	65.4 \pm 18.7	155.6 \pm 25.1	34.2 \pm 18.3	1345.1 \pm 287.2
Home range (km ²)	3512	5965	7041	418 568
Feeding area (km ²)	89	125	177	7487
Time spent flying trip ⁻¹ d ⁻¹ (h)	7.3 \pm 1.5	7.9 \pm 1.3	6.8 \pm 2.1	11.7 \pm 3.7
No. dives trip ⁻¹ d ⁻¹	15 \pm 5	17 \pm 6	20 \pm 11	25 \pm 10
<i>In situ</i> SST (°C) of diving areas	18.4 \pm 1.1	19.1 \pm 1.4	19.8 \pm 1.8	23.5 \pm 2.1
<i>In situ</i> SST (°C) of resting areas	19.8 \pm 1.6	21.4 \pm 1.6	20.8 \pm 2.5	20.3 \pm 1.7
Breeding parameters				
Chick's body condition index (BCI)	0.18 \pm 0.57	0.24 \pm 0.18	-0.04 \pm 0.60	-0.59 \pm 0.22
$\delta^{13}\text{C}$ signature (‰)	—	-18.8 \pm 0.3	-18.4 \pm 0.2	-19.5 \pm 0.3
$\delta^{15}\text{N}$ signature (‰)	—	12.7 \pm 0.3	13.3 \pm 0.2	14.0 \pm 0.3
Fledging success (%)	79.4	80.5	83.3	63.5
Breeding success (%)	48.3	49.9	51.7	35.5
Environmental predictors within 60 km of the colony				
Mean chlorophyll <i>a</i> (mg m ⁻³)	3.4 \pm 0.8	2.0 \pm 0.5	2.2 \pm 0.9	1.0 \pm 0.6
Mean SST (°C)	18.1 \pm 2.4	19.6 \pm 2.0	18.3 \pm 1.5	18.6 \pm 1.2
Mean winter SST (°C) (December to March)	16.9 \pm 0.5	17.5 \pm 1.2	17.3 \pm 0.7	14.4 \pm 0.4
Environmental predictors within 180 km of the colony				
Mean chlorophyll <i>a</i> (mg m ⁻³)	1.1 \pm 0.3	1.3 \pm 0.7	1.5 \pm 0.8	0.7 \pm 0.2
Mean SST (°C)	21.3 \pm 2.4	20.9 \pm 2.1	20.4 \pm 1.8	19.8 \pm 1.7
Mean winter SST (°C) (December to March)	17.9 \pm 0.4	18.3 \pm 0.8	18.8 \pm 1.1	16.3 \pm 0.5
North Atlantic Oscillation (NAO) index	0.12	-1.09	2.79	-4.64

65 mm and mass 14.5 g; Earth and OCEAN Technologies), which are dead-reckoning data-loggers (Wilson et al. 2007). The devices were attached with TESA tape (Wilson et al. 1997) to the 4 central tail feathers. The loggers' weight represented between 1.3 and 2.1% of the birds' body mass, which is believed to have no deleterious effect in seabird species (Phillips et al. 2003, Igual et al. 2005). A total of 106 foraging trips from 76 birds were gathered during the 4 years of the study: 2005, 2006, 2007 and 2010 (Table 1). Further details about the potential impact of loggers on the natural foraging behaviour of Cory's shearwaters are given by Paiva et al. (2010a,b,d) and Passos et al. (2010). The software MT-Comp v6 (Jensen Software System) was used to reconstruct flight tracks and to interpret behavioural data. This software analyses flight, swimming or other movements using a dead-reckoning technique (Thaxter et al. 2009). The routes taken by Cory's shearwaters were reconstructed using the archived directional information together with their speed (general cruising speed for Cory's shearwater = 10 m s⁻¹; see Paiva et al. 2010c), and the directional information was converted into a vector. Dive events were

identified as sudden changes in the temperature sensor data accompanied with peaks of activity in the compass registry. Doubtful registries of potential dives were always discarded as dives and considered as in-water periods. For additional details on the technical characteristics of the devices used and interpretation of bird's behaviour, see Thaxter et al. (2009), Paiva et al. (2010a) and Quillfeldt et al. (2011).

Biological sampling and stable isotope analysis

The fundamental theory behind the isotopic concept is that the isotopic signature of predators is directly influenced by what they consume (Hobson & Clark 1992a,b). This means that the stable carbon signature ($\delta^{13}\text{C}$, $^{13}\text{C}:^{12}\text{C}$ ratio) of consumers is usually similar to that of their diet, therefore differing among foraging locations, and the stable nitrogen ratio ($\delta^{15}\text{N}$, $^{15}\text{N}:^{14}\text{N}$ ratio) reflects the signature at the base of the food web and the predators' trophic position (Vanderklift & Ponsard 2003). Stable isotopic values obtained from whole blood are believed to retain information on diet and at-sea foraging habitat selection

from a few weeks prior to sample collection (Pearson et al. 2003). Upon logger removal, ~150 µl of blood were collected from the bird's tarsal vein from each tracked bird in 2006, 2007 and 2010 and stored frozen until stable isotope analysis. Isotopic ratios were determined by continuous-flow isotope-ratio mass spectrometry (CF-IRMS). For additional details on stable isotope methods, please consult Paiva et al. (2010d).

Food samples were obtained in 2006 (n = 16), 2007 (n = 18) and 2010 (n = 19) from each telemetered individual after removal of the tracking device. We used the water off-loading technique, which involved pumping of salt water to the bird's stomach, causing regurgitation (Wilson 1984). This technique was used just once for each individual, and birds did not show any ill effects after being forced to regurgitate, spending just a couple of minutes to recompose themselves and, after that, staying at their nest or leaving the colony to the sea. Whenever possible, adults were sampled within the first hour after sunset to increase the probability of obtaining undigested remains of food from their stomachs (Granadeiro et al. 1998). We also evaluated if birds were likely to have undigested prey remains inside their stomach through palpation of the stomach area and based on their weight increment (i.e. difference of weight between deployment and recovery of tracking devices). Birds with empty stomachs (n = 2) were not considered in the analysis. Samples were then frozen until identification and stable isotope analysis. In the laboratory, fresh prey items were washed with water, identified and separated from accumulated items. When needed, identification of fish prey was based on the examination of otoliths and bones (Tuset et al. 2008).

Each year, chicks from tracked birds were measured (body weight and wing length) in order to calculate their body condition index (BCI). This index was obtained from the residuals of the linear regression of body weight on wing length, a measure of structural size (Brown 1996). BCI is therefore a measure of mass corrected for size and is considered an indicator of energetic reserves, and the BCI usually predicts chick survival in Procellariiformes (e.g. Chastel et al. 1995). Additionally, fledging success and overall breeding success was obtained for nests of tracked individuals.

Prey abundance estimates and fishery landings

The at-sea survey for estimation of prey abundance by means of acoustic sampling followed a regular sampling design with an average inter-transect dis-

tance of 8 nautical miles (n miles) around Berlenga Island (~30 km north and south of the island) covering the continental Portuguese shelf between the 20 m isobath (east) and the shelf break (west; 200 m isobath). Data were collected during April of each year, from 2005 to 2010. The timing of the acoustic surveys (each April) and tracking study (each September) did not overlap directly. However, the abundance of pelagic fish caught in April should be a good proxy of the amount of prey-fish in our study area later that year (Zwolinski et al. 2009).

Acoustic surveys were carried out by the Portuguese Fisheries Research Institute (INRB/IPIMAR). Acoustic samples were taken every n mile along parallel transects, 8 n miles apart (ICES 1998), by means of a calibrated (Foote et al. 1987) 38 kHz Simrad EK500 echosounder with a split beam transducer (equivalent beam angle: $10\log\psi = -20.2$ dB; pulse duration = 1 ms). Acoustic data were acquired and stored on a personal computer and post-processed using the software MOVIES+ (Weill et al. 1993). Biological samples for echo classification and biological characterization of pelagic fish community were taken mainly by a midwater trawl with the aid of a Netsounder (Scanmar trawl-eye and depth sensor) towed at speeds of 3.5 to 4.5 knots. Trawl stations were opportunistic, whenever the echo traces were relevant in terms of acoustic backscatter and potential species composition. The pelagic fish acoustic backscatter density (nautical area scattering coefficient [NASC]) was partitioned into species, taking into account the proportion of the species in the fishing trawls and the specific acoustic target strength of the involved species. The species acoustic backscatter was used as a proxy of the prey abundances (further details in Zwolinski et al. 2009).

Information on fishery landings (2000 to 2010) was provided by DGPA (the governmental authority for the management of fisheries). Data were filtered to encompass only species of interest to Cory's shearwaters (i.e. species that are potentially important prey for Cory's shearwaters). Those included sardine *Sardina* spp., mackerel *Scomber* sp., Atlantic horse mackerel *Trachurus trachurus*, blue jack mackerel *T. picturatus* (hereafter collectively called small pelagic fishes) and different species of squid. Three different temporal and spatial scales were used to inspect for trends in the landings of these 4 groups of prey: (1) fish landed in the port of Peniche during September of each year from 2005 to 2010, (2) fish landed annually in the port of Peniche from 2000 to 2010 (for a temporal and spatial overlap of fish landings with our tracking data) and (3) fish landed annu-

ally within a 180 km radius of Berlenga Island (see Fig. 1A for a broader annual picture of what was caught within the usual maximum foraging range of Cory's shearwaters).

Oceanographic predictors

To characterize the oceanographic conditions in the surroundings of Berlenga Island and habitats

used at sea by foraging birds, we selected 7 different environmental predictors: seafloor depth (DEP), chlorophyll a concentration (CHL), SST, gradients of the previous predictors (DEPG, CHLG and SSTG, respectively) and distance to colony (DCOL). DCOL was used as a measure of the breeding colony influence on the central-place foraging behaviour. All remote sensing products were downloaded from <http://coastwatch.pfeg.noaa.gov/coastwatch/CWBrowserWW180.jsp>. DEP (ETOPO 1 product) was extracted

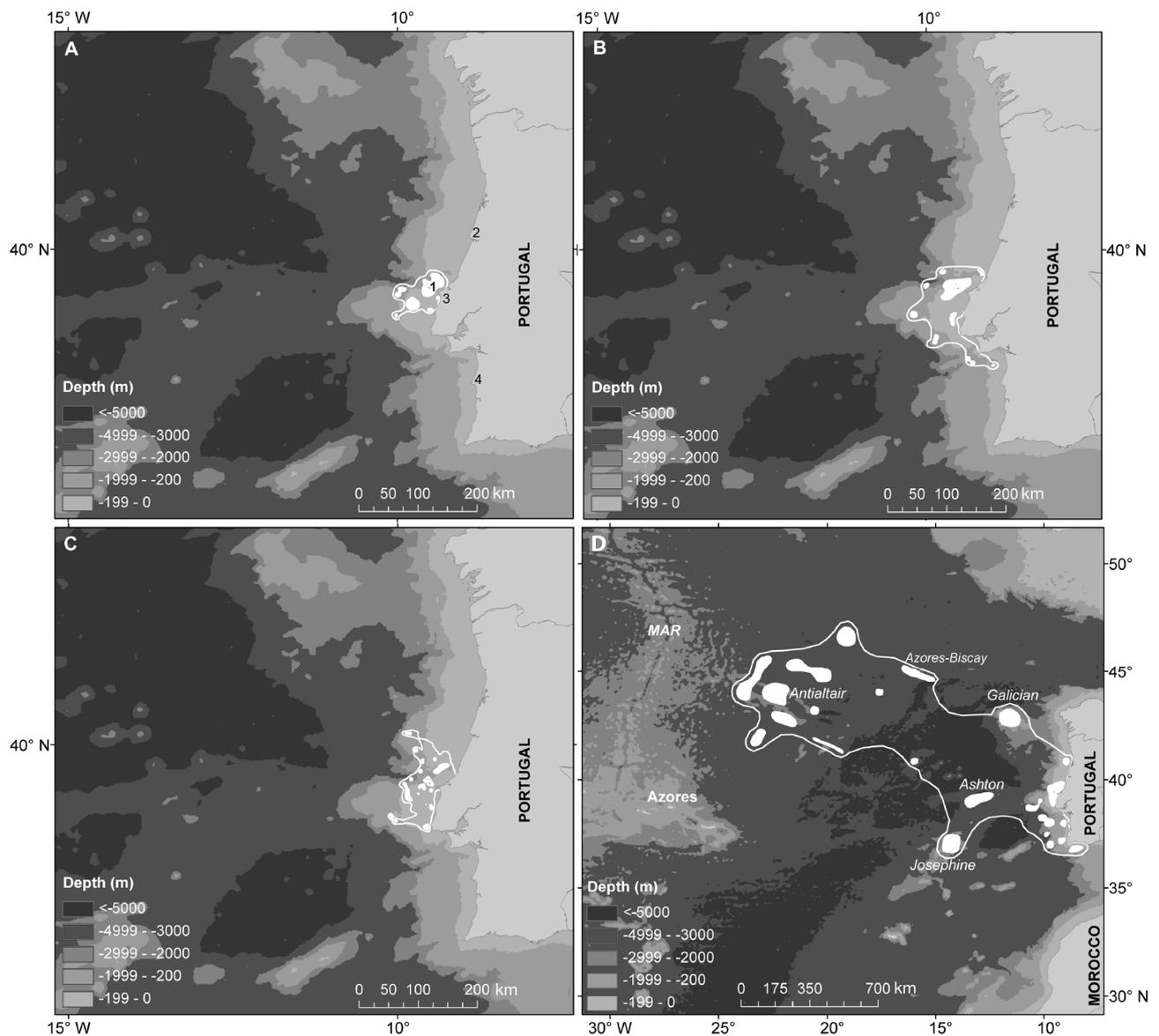


Fig. 1. Foraging distributions of Cory's shearwaters as estimated by fixed kernel density analysis. Outer line: home range (95% fixed kernel density contour of complete tracks); filled circles: feeding area (50% fixed kernel density contour of dive events). Birds were tracked during the chick-rearing periods of (A) 2005, (B) 2006, (C) 2007 and (D) 2010. Bathymetry is represented in the background of the figures. MAR: Mid Atlantic Ridge; 1: breeding colony (Berlengas); 2: Figueira da Foz; 3: Peniche; 4: Setúbal

at a spatial resolution of 0.01° . CHL and SST (Aqua-MODIS imagery at 0.04°) were retrieved as 8 d composites, matching the periods in which birds were tracked. In addition to the previous predictors, we also looked into the variation of winter SST between years in the colony surroundings. By doing so, the temporal scale of mean winter SST (i.e. the averaged composite of December to March) fit the scale at which the winter NAO index was measured, and should therefore be representative of a contemporaneous effect of climatic phenomenon on the ocean temperatures.

Since the NAO is most pronounced during winter, and fluctuations during this season leave long-lasting imprints on sea surface conditions over the oceans, the extended winter (December to March) NAO index from Hurrell (1995) (http://gcmd.nasa.gov/records/GCMD_NCAR_NAO.html) was selected for our study. Indeed, many biological studies have found this index to be the most suited for studying both contemporaneous and subsequent ecological effects (e.g. Ottersen & Stenseth 2001).

All environmental predictors included in the habitat models (i.e. DEP, DEPG, CHL, CHLG, SST, SSTG and DCOL) were interpolated to the same spatial grid of 0.1° (i.e. the coarsest scale of the environmental datasets) to allow spatial comparison and combined modelling. ArcGIS v9.2 was used to compute gradients for the remote-sensing variables and extract mean values of the environmental variables. Gradients in DEP, CHL and SST were determined by estimating rates of change per 0.1° grid square and using a moving-window function (0.3° wide; function = $[(\text{max. value} - \text{min. value}) \times 100] / \text{max. value}$) in Spatial Analyst. Thus, an SST 'gradient' (SSTG, for instance) was then assigned to each 0.1° grid square by computing the maximum rate of change in SST between it and the following 0.1° grid squares. Fronts, as zones of strong SST variations, appear more clearly when using SSTG than using SST values alone. Gradient in depth was used as a proxy of slope.

Modelling foraging behaviour, breeding performance and oceanographic parameters

Generalized linear mixed models (GLMM) were used with foraging strategy parameters as response variables to assess inter-year differences. Because some habitat conditions (e.g. chlorophyll *a* concentration) may change between years, we expect birds to exhibit year-specific movements and strategies

that should result in an improved exploitation of marine resources. Thus, our response variables to test the previous hypothesis comprised (1) trip duration, (2) home range, (3) feeding area, (4) total distance covered, (5) maximum distance from colony, (6) number of dives $\text{trip}^{-1} \text{d}^{-1}$, (7) time spent flying $\text{trip}^{-1} \text{d}^{-1}$ and the SST of (8) diving and (9) resting areas. All GLMM included trip identity nested within the individual as a random term to account for pseudo-replications. A quasi-Poisson error distribution with a logarithm link function for the count data was used in all models.

Interannual changes in the environment surrounding the breeding colony (60 and 180 km radius) were inspected using general linear models (GLM) with year as a fixed effect and mean values of (1) CHLA, (2) SST and (3) DEP as response variables. GLM were also used to test the effect of year (fixed effect) on both the BCI of chicks and the NAO index. Differences in the NAO index were tested using monthly NAO values (http://gcmd.nasa.gov/records/GCMD_NCAR_NAO.html) from December to March of each year ($N = 24$ values).

Modelling prey abundance, diet composition and trophic ecology

Chi-squared tests were used to investigate differences in the numerical frequency of the main prey items in the diet of the Cory's shearwaters among years. Because the sampling effort was not even among the years, differences in the trophic segregation (i.e. carbon and nitrogen isotopic signatures) among years were tested using GLMM. Bird identity nested within island was included in all models as a random term. The GLMM used a quasi-Poisson error distribution with a logarithmic link function for the count data.

Modelling habitat use

To inspect inter-annual differences among the habitats used by the birds, annual habitat models were built relating the spatial location of feeding events (dependent variable) with the different environmental predictors (independent variables). Bird tracks were transformed from points to raster into a grid of 0.1° (to match environmental predictors). Each cell was coded as 1 (occurrence of at least 1 feeding event) or 0 (no feeding event; travelling portions of the track), creating a dichotomous response variable (feeding or not feeding). For modelling

procedures, a random number of 0-cells was selected, corresponding to the number of 1-cells within each foraging trip. These random cells were selected within the overall 95% kernel utilization distribution (UD) of each study year. Kernel UD were generated with a smoothing factor (h) of 0.3 and a cell size of 0.1° (similar cell size as the satellite imagery data) using the R *adehabitat* package (Calenge 2006). All environmental predictors were standardized to have a mean of 0 and an SD of 1 due to differing ranges of variables. Thus, the coefficients of different habitat-use models could be directly compared and interpreted, roughly determining the importance of each variable (Zuur et al. 2007). Environmental variables were firstly checked for collinearity by computing all pairwise Spearman rank correlation coefficients (r_s) (Zuur et al. 2007). One of each pair of highly correlated variables (i.e. $r_s > 0.7$) was excluded from the model. The variable to exclude from each pair was selected based on the highest Akaike's information criteria (AIC; Anderson et al. 1998) (meaning the variable explaining the least deviance) upon the univariate run of the model.

GLMM were then built using the *lme4* package for R v2.14 (R Development Core Team 2011) to relate feeding events to oceanographic variables, accounting for the non-independence of the feeding points belonging to the same foraging excursion. Feeding behaviour (0 or 1) was then included as a response term fitted with a binomial error distribution (logit link). Habitat non-correlated variables (CHL, SST, DEP, their gradients and DCOL) were included as fixed effects and retained only if they improved model fit. Trip identity nested within the individual was included as a random effect in all models, to account for the hierarchical structure of the data (Bolker et al. 2009). The maximum likelihood method was selected because it allows comparison between models with different fixed-effects structures (Crawley 2007). The AIC value and an ANOVA function were used to compare and rank models with different fixed-effect structures (Crawley 2007) and identify the most parsimonious one. Δ AIC (i.e. the difference between the estimated AIC of the final model and the estimated AIC of the previous model) and the Akaike weight (w_i) were also used as a measure of model fit and relative likelihood of candidate models (Anderson et al. 1998). The area under the receiver operating characteristic curve was used as a measure of global fit of the final model.

All possible combinations of main effects were considered. During the model selection process, we constructed quantile-quantile (Q-Q) and partial residual

plots to check the model fit and the distribution and spatial autocorrelation of the residuals. All model residuals were examined for potential inflated influence on the model output, though no significant evidence was found, and therefore we did not consider any spatial autocorrelation structure in GLMMs. Final models were interpreted according to the model coefficient's sign and value of the selected environmental variables (Anderson et al. 1998).

RESULTS

Changes in oceanographic conditions

Oceanographic conditions in the surroundings of the breeding colony varied considerably among years. Within 60 km of the colony (i.e. the typical foraging range of Cory's shearwater breeding in Berlenga during 2005 to 2007), CHL and winter SST (December to March) were significantly lower in 2010 than in the period from 2005 to 2007. However, no inter-annual difference was noticed for September SST (Tables 1 & 2). In addition, within a 180 km radius from Berlengas (i.e. maximum foraging range in 2005 to 2007), winter SST and CHL were significantly lower in 2010 than in 2005 to 2007. However, no differences in September SST occurred among years. Likewise, the NOA index was also significantly lower in 2010 than in 2005 to 2007 (Tables 1 & 2, Fig. 2). Interestingly, in 2010, the NAO index was the lowest (-4.64) since 1648 (NAO index in 1969 = -4.89 ; http://gcmd.nasa.gov/records/GCMD_NCAR_NAO.html). Both fledging success and breeding success were significantly correlated with the NAO index (Spearman correlation: $r_s = 0.72$, $p < 0.01$; $r_s = 0.68$, $p < 0.01$, respectively).

Trends for fishery landings

From 2005 to 2010, total landings of sardine in the nearby (~ 12 km, Fig. 1A) port of Peniche during September decreased by 41.5%, 701.7 t lower in 2010a than in 2005. Compared to 2005, the fishing fleet landed 90.9% less weight in mackerel in 2010 (a reduction of 367.9 t), while the quantities of horse mackerel and cephalopods landed were reduced only by 16.0 and 25.3%, respectively (Fig. 3B). Between 2005 and 2010, the abundance of sardine and small pelagic fishes in general (in April) decreased drastically around Berlenga. Sardines decreased by $\sim 38.9\% \text{ yr}^{-1}$ from $345 \text{ m}^2 \text{ n mile}^{-2}$ (NASC, a proxy for

fish abundance) to zero individuals estimated in 2010. As a whole, the variation in the abundance of small pelagic fishes did not show any clear tendency, though it decreased from 384.3 to 220.0 m² n mile⁻² in 5 yr (Fig. 3C).

Table 2. Results of the generalized linear mixed models (GLMM) investigating the year effect on diverse foraging and breeding parameters of Cory's shearwaters and oceanographic parameters at the colony surroundings. Differences in the isotopic signatures were tested using general linear models, while yearly differences in the NAO index were tested using a chi-squared test. Environmental predictors are for September of each year, unless otherwise stated. Home range: kernel density contour encompassing 95% of all compass-logger positions; feeding area: kernel density contour encompassing 50% of the diving event positions

Year	F	df	p
Foraging parameters			
Trip duration (d)	15.07	3,102	<0.001
Total distance covered (km)	6.17	3,102	<0.001
Maximum distance from colony (km)	9.97	3,102	<0.001
Home range (km ²)	10.85	3,102	<0.001
Feeding area (km ²)	11.07	3,102	<0.001
Time spent flying trip ⁻¹ d ⁻¹ (h)	4.02	3,102	<0.01
No. dives trip ⁻¹ d ⁻¹	2.10	3,102	0.10
<i>In situ</i> SST (°C) of diving areas	9.68	3,102	<0.001
<i>In situ</i> SST (°C) of resting areas	1.55	3,102	0.23
Breeding parameters			
Chick's body condition index (BCI)	5.08	3, 72	<0.01
δ ¹³ C signature (‰)	2.10	3,72	0.11
δ ¹⁵ N signature (‰)	4.11	3,72	<0.01
Environmental predictors within 60 km of the colony			
Mean chlorophyll <i>a</i> (mg m ⁻³)	8.75	3, 7	<0.01
Mean SST (°C)	3.35	3, 7	0.09
Mean winter SST (°C) (December to March)	18.78	3, 7	0.001
Environmental predictors within 180 km of the colony			
Mean chlorophyll <i>a</i> (mg m ⁻³)	5.73	3, 14	<0.01
Mean SST (°C)	1.72	3, 14	0.23
Mean winter SST (°C) (December to March)	5.60	3, 14	<0.01
North Atlantic Oscillation (NAO) index	16.31	3	<0.001

From a broader perspective, annual landings of sardines in the port of Peniche decreased by 59.8% (a decrease of 7908 t) in 10 yr (2000 to 2010). During the same period, landings of horse mackerel and cephalopods increased by 61.7 and 54.6%, respectively. The amount of mackerel landed in 2010 was just slightly higher (2.3%) than in 2000 (Fig. 4A). The sum of annual landings for all the main fishery ports between Figueira da Foz and Setúbal (maximum home range of birds in 2007; Fig. 1A,C) revealed a decrease of 65.8% in the amount of sardine from 2000 to 2010. Again, weaker reductions were noticed in the amounts of horse mackerel (41.8%), cephalopods (25.3%) and mackerel (16.8%) (Fig. 4B).

Inter-annual variation in foraging behaviour and diet of Cory's shearwater

The spatial distribution of birds was remarkably different in 2010 than from 2005 to 2007 (Fig. 1). Overall, in each at-sea excursion in 2010, birds foraged on average 4.5 d more, covering distances ~3000 km longer. Also, they foraged ~1200 km farther from their colony than in the period from 2005 to 2007. Between 2005–2007 and 2010, the birds increased their home range area 84-fold and their feeding area 58-fold (Tables 1 & 2).

Table 3. Feeding habitat use models (GLMM) of Cory's shearwaters during the chick-rearing period of 2005 to 2010. Presented are coefficients ($\beta \pm SE$) of the variables included in 1 top-ranked model for each year. All variables main effects were tested, and significant cases are presented in **bold**. AIC: Akaike's information criteria; w_i : Akaike weights; (-) independent variable not included in the model due to collinearity with other covariate(s); AUC: area under the receiver operating characteristics (ROC) curve

Environmental variable	2005	2006	2007	2010
Constant	-1.458 ± 0.052	0.372 ± 0.062	-0.062 ± 0.081	0.759 ± 0.034
Chlorophyll <i>a</i> (CHL)	-	0.137 ± 0.096	-	0.051 ± 0.005
CHL gradient (CHLG)	0.023 ± 0.095	-	0.062 ± 0.0231	0.276 ± 0.140
Sea surface temperature (SST)	-0.132 ± 0.076	-0.383 ± 0.033	-0.596 ± 0.042	0.027 ± 0.054
SST gradient (SSTG)	-0.046 ± 0.125	0.062 ± 0.023	-	0.529 ± 0.089
Sea depth (DEP)	-	-0.224 ± 0.163	-	-
Sea basin slope (DEPG)	0.329 ± 0.032	-	-0.092 ± 0.049	0.124 ± 0.096
Distance to colony (DCOL)	-0.560 ± 0.027	-0.153 ± 0.046	-0.635 ± 0.108	0.171 ± 0.032
AIC	365.69	125.43	354.58	234.68
ΔAIC	0.47	1.37	0.65	0.28
w_i	0.77	0.47	0.64	0.82
AUC (%)	89.72	78.25	95.53	92.67

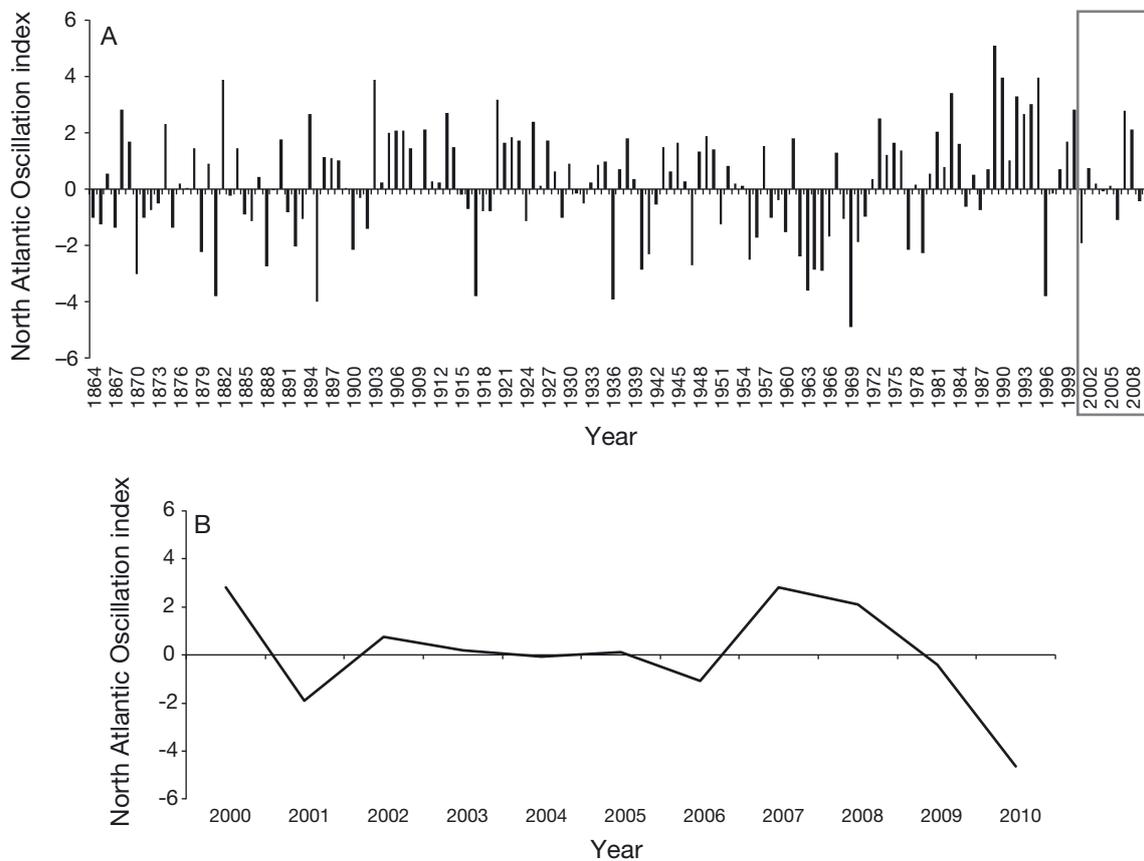


Fig. 2. North Atlantic Oscillation index as computed by Hurrell et al. (2003), based on the difference of normalized sea level pressure between Lisbon, Portugal, or Ponta Delgada, Azores, and Stykkisholmur/Reykjavik, Iceland, (A) since 1864 and (B) amplified for 2000 to 2010 (http://gcmd.nasa.gov/records/GCMD_NCAR_NAO.html)

The at-sea foraging behaviour was also noticeably different in 2010 when compared to the 2005 to 2007 period. In 2010, the birds were airborne for longer during each trip and dived for prey in warmer waters than in 2005 to 2007. Yet, no differences were found in the birds' diving frequency and water regimes (i.e. *in situ* SST) used to rest between 2010 and 2005–2007 (Tables 1 & 2). Chicks' body condition decreased significantly between 2005–2007 (average BCI = 0.12 ± 0.19) and 2010 (BCI = -0.59 ± 0.22). Consequently, both the fledging and breeding success were significantly lower in 2010 than in 2005–2007 (82.3 and 51.9%, respectively). Fledging and breeding success were also higher in 2008 (78.2 and 49.3%, respectively) and 2009 (74.0 and 43.1%, respectively) than in 2010 (Table 1).

During 2005 to 2007, chick-rearing Cory's shearwaters responded to similar environmental cues while feeding (Table 3). During these years, birds

dived for prey closer to the colony and within colder waters (negative coefficients for both DCOL and SST). Moreover, during 2006, the birds selected more productive areas (CHL) and shallower regions (DEP) to feed. However, this pattern changed in 2010, when the birds' feeding activity was more likely to occur in frontal regions (CHLG and SSTG), in steeper areas (DEPG) and within regions farther from the breeding colony (DCOL) (Table 3).

Diet varied considerably among the 3 study years. The proportion of sardine (38.7% in 2007), garfish (19.8%) and horse mackerel (14.8%) were similar between 2006 and 2007 ($\chi^2_1 = 2.82$, $p > 0.13$ for the 3 species). From 2007 to 2010, there was a shift in the birds diet, with a significant decrease in sardine (-27.0% ; $\chi^2_1 = 6.34$, $p = 0.01$) and a significant increase in garfish ($+23.2\%$; $\chi^2_1 = 6.98$, $p = 0.01$). Atlantic saury *Scorpaenopsis scorpaenoides* (13.9%) and Atlantic horse mackerel (9.8%) were also abundant in 2010 (Fig. 3A).

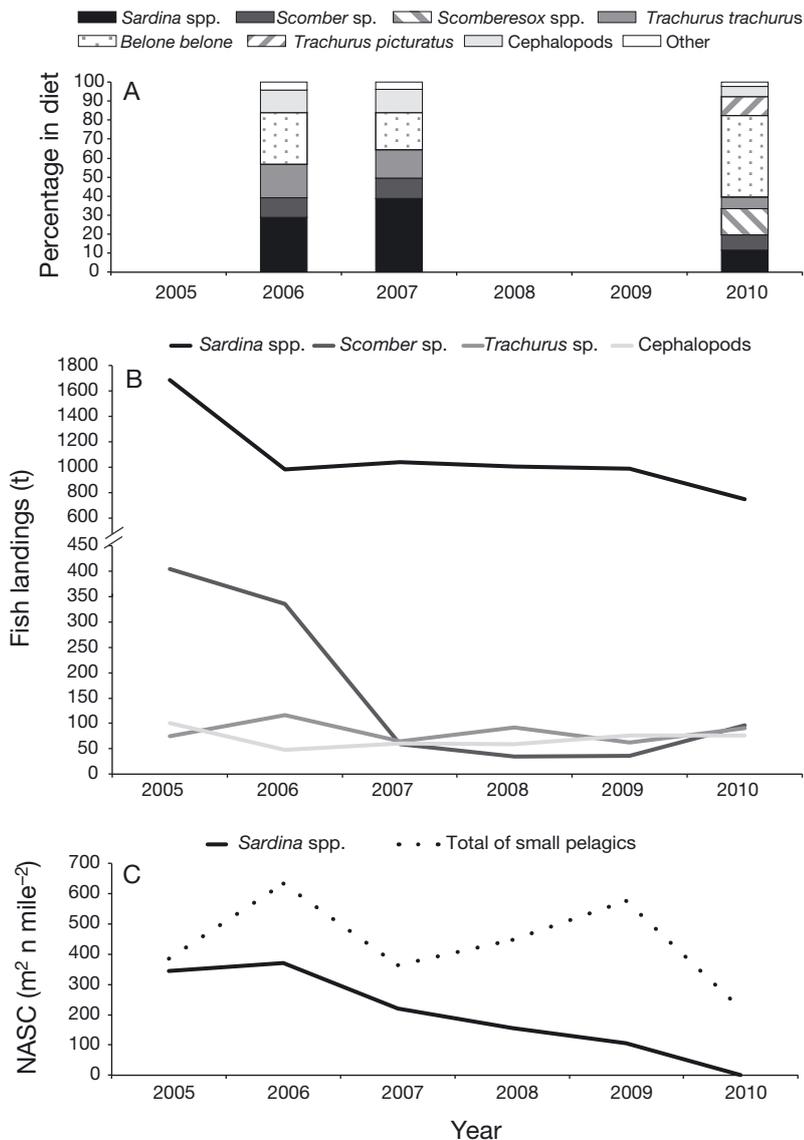


Fig. 3. Visual comparison between (A) numerical frequency (%) of the main prey items composing the stomach content of birds, (B) fish landings in the port of Peniche (fisheries port closest to Berlengas; ~12 km) and (C) at-sea nautical mile acoustic scattering coefficient (nautical area scattering coefficient, NASC, a proxy for fish abundance) of sardines and small pelagic fish within the usual bird's foraging range (roughly in a radius of 60 km around Berlengas colony), each April in 2005 to 2007. Only a negligible amount of garfish *Belone belone* (<0.20 t) was landed at the fishery ports

GLM explained 33.6 and 48.3% of the original deviance in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures, respectively. There were no inter-annual differences in the whole blood carbon signature of the birds. However, the nitrogen signature was significantly higher in 2010 than in 2006 to 2007. Thus, Cory's shearwaters foraged at increasing trophic levels between 2006 and 2010.

DISCUSSION

Effect of environmental variability on the foraging behaviour of an apex predator

In the present study, the foraging behaviour and foraging range of Cory's shearwater changed remarkably from 2005–2007 to 2010. This was connected to a significant decrease in the food availability in the colony surroundings, caused by a change in oceanographic conditions (noticeably lower NAO index and SST during winter 2010) in the months before the birds were tagged. In all likelihood, an upwelling stronger than usual in the Western Iberia Upwelling Ecosystem (WIUE) during winter, the spawning period for most pelagic fish, drove fish larvae from shelf to oceanic areas, where they usually do not survive (Santos et al. 2007). These changes in oceanography shaped the lower marine productivity later that year (i.e. low prey fish abundances in April 2010 and low CHL in September 2010). Conspicuous differences existed in all foraging parameters; birds exploited more remote areas and dived for food in warmer, less productive waters in 2010 than in 2005–2007. The longer foraging trips birds performed during the chick-rearing period of 2010 when compared to 2005 to 2007 resulted in a lower body condition index, lower fledging success and decreased overall reproductive success in that year. The birds probably reduced chick provisioning due to the scarcity of food in the colony surroundings. Consequently, after being 'forced' to exploit remote areas, parents stayed away from their nests for

longer periods. Overall, our results seem to show that the climate (measured by the NAO index and SST) impacted the foraging distribution and effort of chick-rearing Cory's shearwaters during 2010. Also, climate variability seems to have prejudiced the birds' breeding success, which decreased continuously and yearly from 2005 until 2010. However, we cannot exclude the possibility that 2010, being an ex-

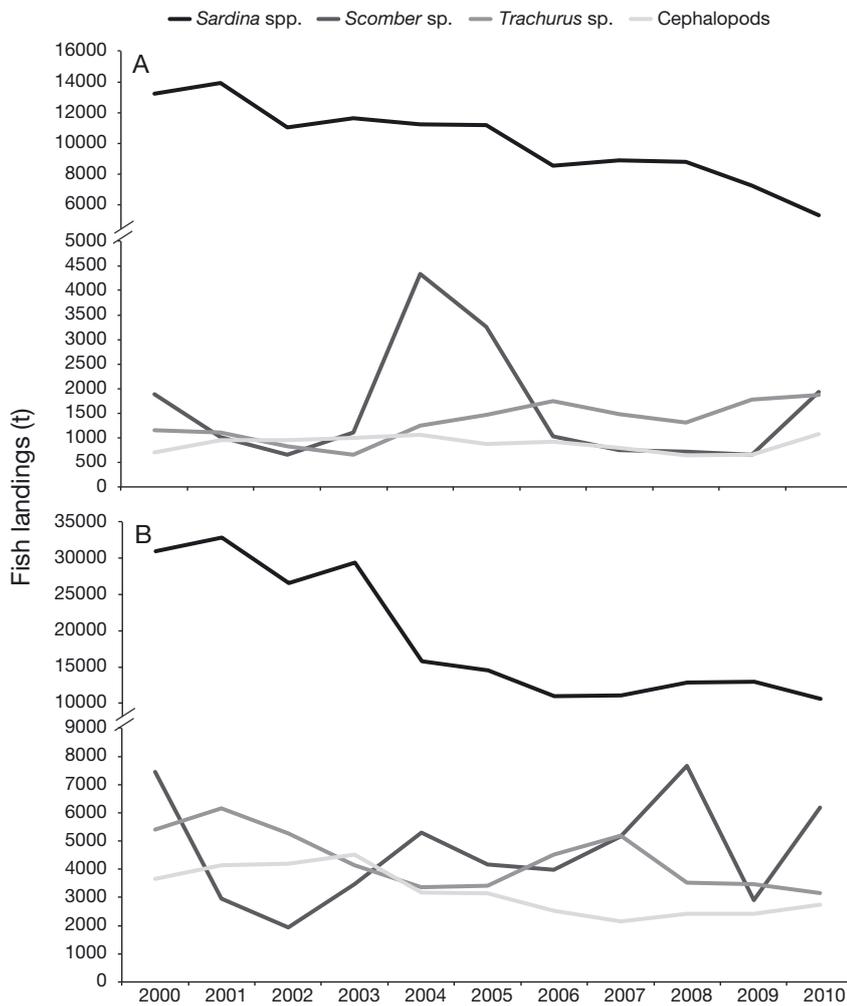


Fig. 4. Yearly fish landings (A) at the port of Peniche and (B) at Portuguese ports in a 180 km radius from Berlengas (i.e. maximum foraging range of Cory's shearwaters in most of the study years)

traordinary year, could have represented an 'outlier' in the general climate pattern. Inter-annual changes in the foraging behaviour, distribution and diet composition of apex predators due to changes in climate and availability of prey have been identified in other studies (Garthe et al. 2011) and are the reason for using marine predators as guardians of the marine environment (Boyd & Camphuysen 2006).

Sardines in the Portuguese coastal upwelling food web

The strong and continuous decrease of sardine around Berlengas each April of 2005 to 2010 remains unexplained. The same negative pattern was observed in the size of sardine landings in Peniche (dur-

ing September of each year). Likewise, off the South African coast, a distributional shift in the anchovy (*Engraulidae*) population was attributed to a sudden change in environmental conditions (Roy et al. 2007). Such rapid change rather than a prolonged and gradual effect in the distributional patterns of small pelagic fishes may be caused by their dependence on plankton-based food webs. The biological characteristics of small pelagic fish, such as sardines, make them highly sensitive to environmental fluctuations (Jones 2001). The sardine population inhabiting the Portuguese shelf feeds mostly on zoo-, phyto- and ichthyoplankton (Garrido et al. 2007), which themselves are highly sensitive to changes in oceanographic conditions (Bakun 2006). The extremely low SST in the winter of 2010 (the lowest winter NAO index value in history) could have affected the survival, distribution and availability of plankton to sardines and other strata of the food web. Similarly, Lirman et al. (2011) reported an unprecedented mortality of corals in Florida due to the severe cold-water event in the winter of 2010. Despite the negative tendency in the abundance of sardine from 2005 to 2010 (according to both environmental measurements and records of fish landings), sardines remained abundant in

the birds' diet in 2006 and 2007 and diminished significantly only in 2010 after the extreme negative NAO index. Moreover, the strong upwelling in the 2010 winter (imprinted on the very low SST value) could be responsible for a low recruitment of several pelagic fish species inhabiting the Portuguese coast (e.g. sardine and horse mackerel). Indeed, these fish species spawn during winter, and a strong upwelling at the WIUE is known to be responsible for the offshore transport of larvae, which increases their mortality (Santos et al. 2001, Santos et al. 2007). Nevertheless, after inspecting the tendency of sardine landings from 2000 to 2010 on a broader spatio-temporal scale, we cannot exclude the possibility that environmental change, overfishing or a combination of both may be responsible for the decrease in abundance/availability of sardines on the Portuguese

shelf both for fisheries and apex predators (Jackson et al. 2001). Similarly, in the Benguela upwelling ecosystem, the combined pressure of rapid climate change and increasing fishing activity changed the ecosystem functioning, led to a spatial and temporal mismatch of Cape gannets *Morus capensis* and their prey (Grémillet et al. 2008) and is placing this top predator at risk of extinction (Pichegru et al. 2009). The link between environmental stressors, such as climate variability, and marine predators' behaviour is more complex than the analysis we show here, and is obviously far from being a direct and linear relation. Adding human-related stressors, such as overfishing, to the former relationship obviously increases its complexity. Indubitably, this issue deserves continued monitoring and further investigation in the near future. Furthermore, we only had access to commercial fisheries landings data to interpret the 'fishing pressure' on this coastal ecosystem, but future studies should consider more accurate measures of the amount of prey fish that the fishery fleet harvested from the ecosystem, such as data on catches per unit effort.

Modelling habitat use in a changing environment

To understand which environmental cues prompted the foraging interest of birds (Weimerskirch 2007), annual habitat models were constructed that linked the feeding behaviour of Cory's shearwaters with scale-dependent processes (Lima & Zollner 1996). Between years, the SST was the variable that kept its importance in triggering the occurrence of bird feeding events. However, from 2005 to 2007, feeding behaviour was more likely to occur with decreasing SST, while during 2010, this relationship was inverted, and the birds were more likely to be found feeding in warmer waters. Because warm water regimes are assumed to encompass lower productivity levels, birds could be exploiting these areas due to scarcity of food availability in their colony surroundings. Moreover, gradients in the dynamic oceanographic variables in 2010 (i.e. fronts in SST and CHL) were the most important triggers of feeding behaviour (i.e. variables with higher coefficient values). It appeared that the birds were targeting concentrations of marine prey patches (between 10 and 100 km from their colony) (Weimerskirch 2007). At this scale, enhancement of ocean productivity and concentrations of prey and predators is supposed to be maintained by hydrographical (e.g. fronts) and physical (e.g. seamount slopes) features (Hyrenbach

et al. 2007). The birds increased their foraging range in 2010 and exploited known seamount areas (e.g. the Antialtair seamount) and fronts of SST and CHL of the North Atlantic (see Fig. 1D, Table 2).

Not surprisingly, in 2005 to 2007, it was more likely to sight a bird feeding in the colony surroundings than farther from Berlengas (i.e. there was a negative sign for DCOL coefficient). However, this situation switched during 2010, when the likelihood of sighting feeding birds grew with increasing distance from the breeding colony. This may be interpreted as a result of a considerable decrease in the availability of preferred prey near the colony that forced the birds to exploit remoter oceanic areas, with higher energetic foraging costs (Garthe et al. 2011). Across years, the environmental predictor bathymetry (both DEP and DEPG) kept its importance in explaining the higher probability of feeding events in shallower (DEP) and steeper (DEPG) grounds. In 2005 to 2007, the shearwaters foraged mainly in relatively shallow waters over the continental shelf, where the variables DEP and DEPG may also be interpreted as a proxy of other small-scale oceanographic processes, such as shelf-break fronts (Mann & Lazier 2006). Moreover, the diet of Cory's shearwaters is mostly composed of small epi- and meso-pelagic fishes (Granadeiro et al. 1998, Xavier et al. 2011), which are more abundant in shallow habitats than in deep oceanic regions. Examples of this include the sardines, abundant on the shelf upwelling areas (Zwolinski et al. 2009) and in the birds' diet in 2006 and 2007. In contrast, the blue jack mackerel, more typical of seamount areas, was present in the birds' diet during 2010. The selection of different feeding habitats in 2010 also resulted in a significantly different isotopic signature for the birds' whole blood when compared to 2006 and 2007. In 2010, the birds clearly foraged more in oceanic areas, which most probably caused the lower carbon isotopic signature of their blood (France 1995). Additionally, in 2010, the birds had a higher nitrogen isotopic signature, which might be indicative of the use of fishery discards and/or prey from higher trophic levels as an extra source of food.

CONCLUSIONS

The dramatic change in the distribution and foraging behaviour of Cory's shearwaters during 2010 (in relation to previous years) seems to be mostly related to a climatic event that occurred during the 2009 to 2010 winter. This climatic phenomenon significantly

affected the productivity in the surroundings of Berlengas and decreasing the abundance of pelagic prey fish, which in turn altered the foraging and feeding ecology of Cory's shearwaters and decreased their reproductive success. However, the negative trend in the abundance of pelagic prey may be of concern because it seems that it was influenced not only by the climate event of 2010, but also by intensive commercial fishing activities. We expect this to be confirmed in the near future through collaborative studies currently in place in which a more sensitive fishing index, such as catch per unit effort, is being computed. Thus, long-term monitoring of the interactions between top predators, their prey and lower strata of the food web is crucial for a comprehensive assessment of the impacts that climate change may have on coastal ecosystems worldwide.

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