

# Overcoming difficult times: the behavioural resilience of a marine predator when facing environmental stochasticity

Vitor H. Paiva<sup>1,3,\*</sup>, Pedro Geraldes<sup>2</sup>, Ivan Ramirez<sup>2</sup>, Antje C. Werner<sup>1</sup>,  
Stefan Garthe<sup>3</sup>, Jaime A. Ramos<sup>1</sup>

<sup>1</sup>IMAR-CMA Marine and Environment Research Centre, Department of Life Sciences, University of Coimbra,  
Coimbra 3004-517, Portugal

<sup>2</sup>SPEA-Sociedade Portuguesa para o Estudo das Aves, Rua João Crisóstomo, 18–4° Dto, Lisboa 1000-179, Portugal

<sup>3</sup>Research and Technology Centre (FTZ), University of Kiel, Hafentörn 1, Büsum 25761, Germany

**ABSTRACT:** Annual changes in the behaviour and distribution of top predators at sea may be linked to environmental variability. Here we report, for the first time to our knowledge, the inter-annual (2007–2011) foraging ecology during the pre-laying period of female Cory's shearwaters *Calonectris diomedea* from Berlenga (Portugal), based on biotelemetry data. Our aim was to examine the degree of flexibility in the at-sea distribution, behaviour and habitat selection of foraging birds, and relate this with marine environmental stochasticity. Productivity proxies in the closer foraging areas decreased noticeably between 2007 and 2011 (i.e. an increase of sea surface temperature and a decrease of primary productivity). Female Cory's shearwaters perceived the oceanic changes, and shifted their distribution to an area that could have the food resources required for egg formation. In 2011, in order to exploit the productive Grand Banks and Newfoundland Shelf domains, female Cory's shearwaters embarked on one of the largest foraging excursions of the pre-laying period when compared to other seabird species (nearly 4000 km). The option to forage on such a distant area in 2011 decreased the females' body condition and reduced their hatching success, which may be interpreted as an adaptation to local productivity during this energetically highly demanding period to favour their own survival. Long-term monitoring of the foraging behaviour of top predators such as Cory's shearwaters in years to come may serve as a 'sensitive' proxy to help understand the medium- to long-term effects of environmental stochasticity in marine ecological systems.

**KEY WORDS:** Cory's shearwater · *Calonectris diomedea* · Pre-breeding phase · Foraging plasticity · Habitat use · Biotelemetry · Environmental stochasticity

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## INTRODUCTION

Foraging marine predators rely mostly on predictable physical and biological oceanographic features, such as fronts, shelf edges and upwelling areas (Mann & Lazier 2006). These features and oceanographic phenomena congregate prey and enhance food availability, which in turn directly influences the

foraging success of seabirds. Sandvik et al. (2005) reported that local oceanographic parameters, such as sea surface temperature (SST), tended to explain more of the variability in seabird survival than did climatic events (e.g. the North Atlantic Oscillation, NAO) or even prey availability. In fact, seabird breeders seem to be resilient to the immediate effects of climatic events on demographic parameters, which

\*Email: vitorpaiva@ci.uc.pt

may be perceived in population trajectories lagged in time (i.e. when younger birds are supposed to become active breeders). In this respect, tracking the at-sea distribution of marine predators could be a more 'sensitive' proxy of changes in the marine environment. Several studies report a link between oceanic variability and variation in several seabird demographic parameters such as changes in annual survival, breeding distribution and breeding success (e.g. Frederiksen et al. 2004). Yet recently, scientists have started to interpret the influence of environmental stochasticity on the spatial ecology of seabirds, and late contributions have shown the link between the two (e.g. Péron et al. 2010, Péron et al. 2012).

Most studies examining detailed at-sea distribution and foraging behaviour of seabirds during the breeding season have been conducted during the incubation and chick-rearing periods, mostly because it is easier to recover data-loggers as seabirds return often to the nest to incubate the eggs or to feed the chicks. Other periods such as the pre-laying period have been neglected. This is, however, a crucial phase for the overall outcome of the breeding season. Upon arrival at the colony (from their wintering grounds), seabirds require time to assess the condition of their nest site and mate, and defend that site from conspecifics before egg-laying (Warham 1990). Following these activities, pairs often lack sufficient nutrient reserves to form an egg (female) or initiate incubation (male), and thus they depart the colony for 1–2 wk to meet these needs (Warham 1990). Females in particular need predictable foraging areas to form a relatively large egg and lay as soon as possible, and may travel long distances at-sea in search of predictable resources (Phillips et al. 2006, Pinet et al. 2012). Thus, tracking female seabirds at-sea during pre-laying should help monitor potential shifts in foraging distribution due to environmental variability, and contribute to the analysis of their effects on seabird demographic performances.

In petrels such as the Cory's shearwater, it is usually the male that takes the first (long) incubation shift, allowing the female to replenish her energetic body reserves lost during the 'pre-laying exodus' (Warham 1990). We know from previous work during the incubation (June–July) and chick rearing periods (August–September) that Cory's shearwaters from Berlenga forage mostly along the Portuguese continental shelf (Paiva et al. 2010a,d), but also exploit oceanic habitats (seamount regions) on the northwest of mainland Portugal during the incubation period (Paiva et al. 2010c). Before embarking on their tran-

sequatorial spring migration, this population usually utilises an area near in the northwest Atlantic as an extended stopover, and then travels further south to spend the winter over the Brazilian or Benguela Currents (Catry et al. 2011, Dias et al. 2011).

This paper reports, for the first time to our knowledge, the foraging ecology of female Cory's shearwaters during the pre-laying period. We used tracking data-loggers on female Cory's shearwaters breeding on Berlenga Island (Portugal), over 4 breeding seasons (2007, 2008, 2010 and 2011) with contrasted climatic (i.e. NAO) and oceanographic (e.g. SST) conditions. This is also the first time a seabird species has been telemetered during the pre-laying period with such high accuracy devices (i.e. GPS-loggers), allowing a fine-scale exploration of their spatial distribution during this crucial period of their life cycle. Our purpose was to examine the inter-annual degree of flexibility in the at-sea distribution and habitat selection of foraging birds. We also tested how the at-sea distribution of Cory's shearwaters during the pre-laying period responded to proxies of environmental stochasticity, such as anomalies in sea surface temperature (SSTA) and primary productivity (PPA) and the NAO index. Environmental anomalies represented the deviation (difference) between the value of a predictor (e.g. SST) on a specific month and the historical mean SST for that same month. Because some habitat conditions (e.g. primary productivity; PP) may change between years, we expect birds to exhibit year-specific movements and strategies that should result in an improved exploitation of marine resources.

We specifically aimed to answer the following questions: (1) Do pre-laying female Cory's shearwaters rely on consistent localized foraging areas over 4 years of contrasted oceanographic conditions? (2) Do they rely on similar foraging grounds as during the breeding period? (3) Are potential changes in foraging grounds linked to environmental stochasticity? (4) Is there an effect of choice and distance to foraging grounds on breeding performance? During the pre-laying period (April–May), the upwelling strength along the Portuguese shelf is still low (i.e. it is usually stronger during July–September), thus productivity and prey-fish availability should be lower (Santos et al. 2007), and as a consequence we expect that Cory's shearwaters will exploit oceanic seamount areas (Paiva et al. 2010c). The choice to forage over remoter areas (in relation to the breeding colony) may induce a lower body condition on females, which will need to replenish their body reserves at sea after egg laying. If females stay too

long at sea, males will not endure the extreme fasting and thus may abandon the egg (V. H. Paiva pers. obs.). This will result in a poor breeding season and a compromised demographic performance of the species in the future.

## MATERIALS AND METHODS

### Oceanographic processes within the study area

Ocean circulation in the North Atlantic is influenced by a major gyre (Fig. 1B), as a circular current that is confined on one side by the North American and Canadian coasts, and on the other by the Portuguese and African coasts (Mann & Lazier 2006). The Portuguese shelf ecosystem is majorly influenced by the Portuguese Current, descending along the Portuguese coast. This coastal movement, in conjunction with the highly sloped shelf break and wind transport of surface water, promotes the strong upwelling of cold, nutrient-rich waters off both the Portuguese (Sousa et al. 2008) and African (Davenport et al. 2002) coasts. Shelf areas are generally more productive than the open sea, though productivity increases in the surroundings of seamounts and banks of the oceanic area of the North Atlantic. Overall, these oceanographic processes will have a notable effect on the latitudinal variation of the thermal (Fig. 1B) and productivity (Fig. 1C–F) frontal regions (i.e. the subtropical convergence), dividing the north productive and cold waters from the poor and warm waters in the south region (Santos et al. 1995). The upwelling along the Portuguese shelf system enriches the system and the amount of phytoplankton and zooplankton increases, followed by an increase of small pelagic fishes, and consequently the presence of seabirds preying on those fishes. This might not always be the case, however, if spatial mismatches between trophic levels occur (Grémillet et al. 2008).

### Birds' instrumentation and tracking data analysis

The tracking study was performed on Berlenga Island (continental Portugal) each April and May between 2007 and 2011. Only previously ringed individuals were used for telemetry, since their sex and historical demographic information (e.g. past breeding records) was already known. Only female birds were selected for logger deployment and individual tracking. In 2007 and 2008, birds were equipped with

compass-temperature loggers of ~14.5 g (compass-loggers; Earth and OCEAN Technologies), while in 2010 and 2011 GPS tracking devices CatTaq Travel Loggers (GPS-loggers; Perthold Engineering LLC) of ~17 g were employed. Devices represented between 1.6% and 2.6% of the bird's weight, which is below the threshold causing negative effects on seabirds, and is believed to have no deleterious effect on Cory's shearwaters (Paiva et al. 2010b,c,e, Passos et al. 2010). Loggers were attached with TESA tape (Wilson et al. 1997) to the 4 central tail feathers (compass-loggers) or to contour feathers along and in between both scapulars (GPS-loggers). Compass-loggers were set to collect bearings every 5 s, while GPS-loggers recorded positioning data every 5 min. For additional details on the technical characteristics of compass-loggers used and interpretation of bird's behaviour see (Paiva et al. 2010b) or (Quillfeldt et al. 2011). The total handling time when deploying either type of device (i.e. compass- and GPS-loggers) did not exceed 10 min, and birds were returned to their burrows immediately following transmitter attachment.

In order to allow further comparisons between distribution patterns of birds tracked with compass- or GPS-loggers, we resampled the amount of positioning information of the compass-logger datasets to analyse habitat use (1 position each 5 min). By doing so, we approached the amount of data collected by each GPS-log deployment. Positioning information of each foraging excursion was then examined under the 'adehabitat' package (Calenge 2006) generating kernel density estimates with a smoothing parameter of 0.03° and grid cells of 0.1° (similar to the coarsest cell size of remote sensed products). We considered the 50% kernel utilization distribution (KUD) to represent the core area of foraging activity (Foraging Area); the 95% KUD of all track positions was used to construct the total area used by telemetered individuals (Home Range). In addition, we used maximum distance from the colony and total distance covered on each trip as proxies of foraging effort.

### Breeding monitoring and body condition index

Every year, each bird was measured (body weight and wing length) to calculate its 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

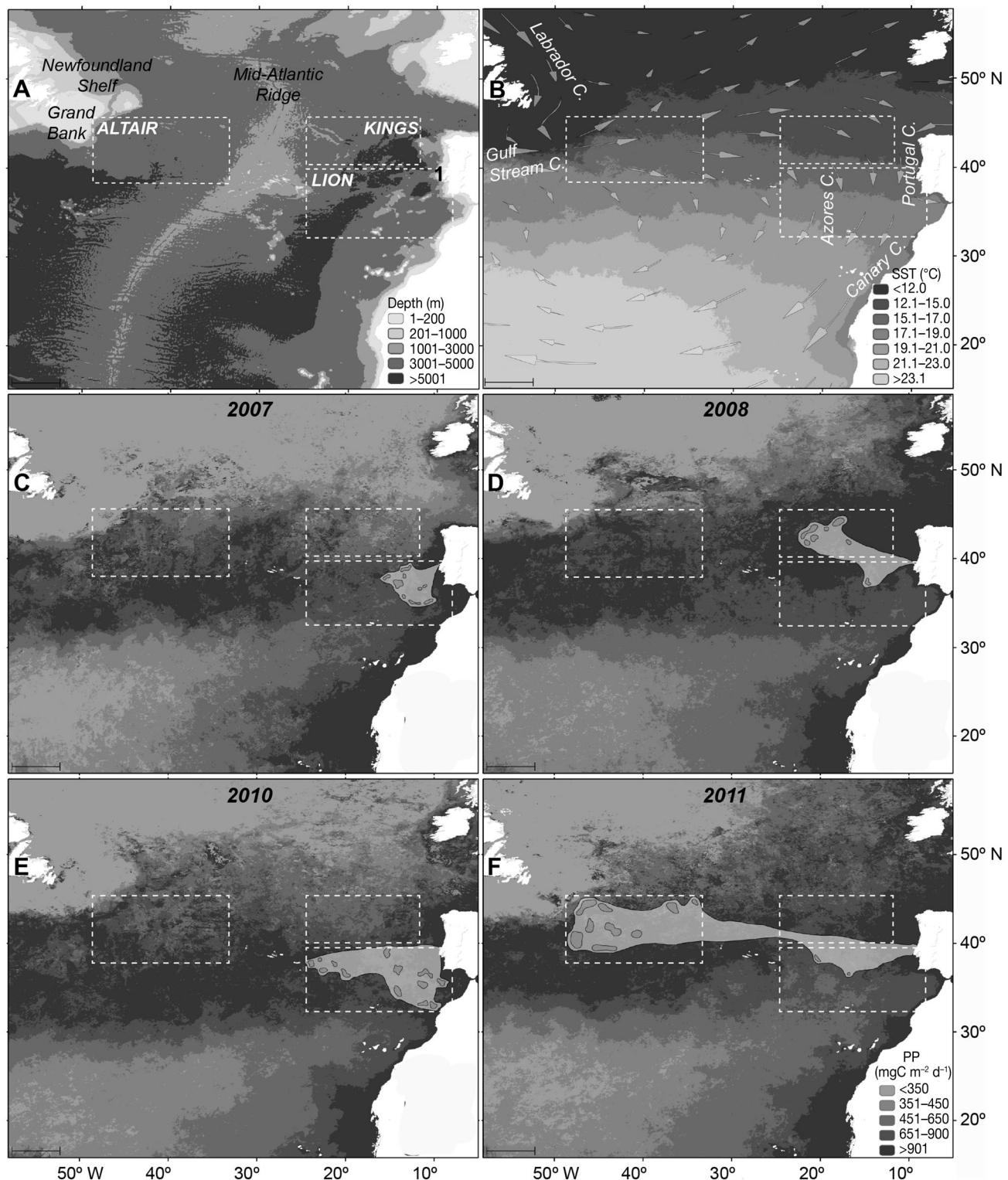


Fig. 1. *Calonectris diomedea*. Main foraging areas (Altair, Kings and Lion) for Cory's shearwater females during the pre-breeding period; 1 indicates the colony location, Berlenga. (A) Seafloor features in the background and (B) major currents (arrows) and mean sea surface temperature (SST, background raster) influencing the North Atlantic during our study. Kernel utilisation distribution (KUD) plots during (C) 2007, (D) 2008, (E) 2010, and (F) 2011. Outer line represents the Home Range (95 % KUD contour) and inner-filled contours represent the Foraging Areas (50 % KUD contour). Mean primary productivity ( $\text{mgC m}^{-2} \text{ day}^{-1}$ ) of March–May of each year represented in the background of maps C–F

mass corrected for size and is considered an indicator of energetic reserves in Procellariiformes (e.g. Chastel et al. 1995). Additionally, laying success (number of eggs laid / number of tracked females) and overall hatching success (number of hatched eggs / number of laid eggs) was obtained for nests of tracked individuals and nearly 90 nests of non-telemetered individuals (to investigate the potential bias of the deployment of devices on the birds' breeding outcome). We expect that immediate effects of environmental variability on the foraging ecology of females will cause changes in laying success, and ulterior effects will cause alterations in hatching success.

### Remote sensing environmental predictors

We selected 3 different variables to characterize marine habitats of the North Atlantic: bathymetry (hereafter termed depth; blendedETOPO1 product), retrieved at a spatial resolution of 0.01°; sea surface temperature (hereafter termed SST; Aqua MODIS NPP), extracted at a scale of 0.04°; and primary productivity (hereafter termed PP; blended AquamODIS and Pathfinder product), obtained at a scale of 0.1°. All variables were obtained using the Xtractomatic routine (<http://coastwatch.pfel.noaa.gov/xtracto/>), allowing automatous data extraction from the BloomWatch website (<http://coastwatch.pfeg.noaa.gov/coastwatch/CWBrowserWW180.jsp>). Dynamic variables (SST, PP) were extracted at a temporal resolution of 1 mo. Each environmental predictor was then aggregated to match a standard spatial grid of 0.1° (i.e. the coarsest scale of the environmental datasets) to allow spatial comparison and combined analysis. To characterize the persistence of the dynamic environmental predictors in our study area, monthly composites were also extracted for the 3 mo prior to bird's telemetry. These 3 layers for each year (i.e. March–May) were then aggregated using the median value of each pixel, as this is a less spurious measure in respect to normality requisites, being less strongly influenced by outliers (Zuur et al. 2007). These aggregated products represent better proxies of the prevalence of dynamic oceanographic features in our study area, representing oceanographic conditions during spring (Louzao et al. 2009). We chose the NAO index computed by Jim Hurrell (Hurrell 1995; [www.cgd.ucar.edu/cas/jhurrell/indices.html](http://www.cgd.ucar.edu/cas/jhurrell/indices.html)) to represent a broad scale climatic state for the North Atlantic area. The March–May PC-based index (Spring NAO) was used, which should give a more

optimal representation of the full NAO spatial pattern within our study area and temporally overlapping the telemetry study. SSTA data for the 3 main oceanic regions exploited by Cory's shearwaters—Altair (38–46°N, 50–34°W), Kings (40–46°N, 25–11°W) and Lion (32–40°N, 25–8°W) (Fig. 1)—were downloaded from [http://ingrid.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.EMC/.CMB/.GLOBAL/.Reyn\\_SmithOIv2/.weekly/.sst/](http://ingrid.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.EMC/.CMB/.GLOBAL/.Reyn_SmithOIv2/.weekly/.sst/) and used to compute monthly and March–May composites (see 'Data analysis'). Both former products (NAO index and SSTA) were obtained for a temporal period larger than tracking (i.e. since 1981), since we wanted to inspect whether oceanic changes at a regional scale (measured by SSTA) had a link with large-scale oceanic phenomenon (driven by NAO). Time-series of PPA were also estimated for the former 3 main oceanic domains. Monthly PPA were derived by subtracting each monthly value of PP from the mean PP value calculated over 2002–2011.

### Data analysis

Six foraging parameters (trip duration, total distance covered, maximum distance from colony, time spent flying trip<sup>-1</sup> d<sup>-1</sup> and dimension of Home Range and Foraging Area) were compared among years with generalized linear mixed models (GLMM), with foraging strategy parameters as dependent variables and year as a fixed effect. To quantify habitat use, we extracted the values for depth, SST and PP from within the Foraging Areas and Home Range zones of each foraging excursion. Differences in habitat utilization were investigated by comparing (1) 50% KUD vs. 95% KUD within each of the 4 years, and (2) 50% KUD between years for each of the 3 environmental variables. Statistical comparisons for habitat use were also made using GLMMs.

All former GLMMs were fitted by the Laplace approximation and included trip identity nested within the individual as a random term to account for pseudo-replication issues. All dependent variables (i.e. foraging parameters and environmental predictors) were log-transformed in order to meet normality. After that, the data and the error structure approached a normal distribution, and therefore a Gaussian family (link = 'identity') was selected for all models (Zuur et al. 2007). GLMMs were performed using the 'lme4' package (Bates et al. 2008).

Inter-annual changes in the main oceanic domains targeted by birds (i.e. Altair, Kings and Lion; see Fig. 1) were inspected using general linear models

(GLM) with year as a fixed effect, and mean values of (1) PP, and (2) SST as response variables. GLMs were also used to test the effect of year (fixed effect) on both (1) BCI and (2) NAO index. Again, the 4 previous dependent variables were log-transformed to approach a normal distribution. The significance of the relationships between the spring NAO index (since 1991) and spring (March–May) average values of SSTA within (1) Altair, (2) Kings, and (3) Lion oceanic domains were accessed using Spearman's rank correlation tests. Chi-square tests were used to check for inter-annual differences on the proportions of eggs laid and hatched.

All pairwise multiple comparisons were analysed using Bonferroni correction, in order to avoid Type I errors. Variables were visually tested for normality (through Q-Q plots) and homoscedasticity (using Cleveland dotplots) (Zuur et al. 2010) before each statistical test. All analyses were performed using the R software version 2.14 (R Development Core Team 2011) with a significance level of  $p < 0.05$ . Results given are means  $\pm$  SD.

## RESULTS

### Inter-annual variations in spatial distribution of pre-laying females

Spatial distribution of female Cory's shearwaters changed considerably over the 4 years of our study (Fig. 1C–F). During 2007, birds travelled to oceanic domains, exploiting resources on seamount areas southwest of continental Portugal (Fig. 1A,C; Lion region), known for their attractiveness to marine top

predators. In 2008, females also targeted seamount regions to the northwest of Portugal (Fig. 1A,D; Kings region). During 2010, birds exploited the seamount areas between continental Portugal and the Azores archipelago (Fig. 1A,E), foraging mostly closer to the Azores and the African coasts. In 2011, birds dramatically shifted their distribution, crossing the North Atlantic to forage closer to the Newfoundland Shelf and the Grand Banks, and also over the productive seamount areas of the Altair region (Fig. 1A,F).

### Inter-annual oceanographic and climatic changes in the main foraging grounds

Oceanographic parameters within the main areas targeted by birds (Fig. 1A) varied considerably between years (Table 1). Within the Altair region, PP increased significantly between 2007 and 2011, while SST decreased significantly during the same period (Table 1). Within the Kings area a significantly higher value of PP occurred during 2008 compared to previous and subsequent years, while SST did not change significantly over the years (Table 1). Inside the Lion region, PP was significantly higher during 2010 compared to former and later years and SST was significantly lower during 2007 and 2010 in relation to 2008 and 2011 (Table 1). The spring (between March and May) NAO index was significantly lower in 2010 and 2011 when compared to 2007 and 2008 (Table 1).

The annual winter NAO index (December–March) was significantly correlated with average spring SSTA values (March–May) within the Altair region (Spearman's  $r_s = 0.81$ ,  $p < 0.001$ ,  $N = 29$ ), but not with

**Table 1.** Inter-annual comparison of mean  $\pm$  SD oceanographic characteristics at the main foraging regions of Cory's shearwaters *Calonectris diomedea*. Oceanographic regimes are averages of median values for March–May (spring season) of each year. PP: primary productivity ( $\text{mgC cm}^{-2} \text{ d}^{-1}$ ); SST: sea surface temperature ( $^{\circ}\text{C}$ ); NAO: North Atlantic Oscillation. General linear models (GLMs) were used to compare mean oceanographic values and NAO index between years. Superscript lettering indicates multiple comparison results (2009 values are merely descriptive and were not included in the statistical analysis)

| Year   | Altair                      |                           | Kings                       |                | Lion                        |                           | NAO index          |
|--------|-----------------------------|---------------------------|-----------------------------|----------------|-----------------------------|---------------------------|--------------------|
|        | PP                          | SST                       | PP                          | SST            | PP                          | SST                       |                    |
| 2007   | $698.3 \pm 32.7^{\text{a}}$ | $20.6 \pm 0.6^{\text{a}}$ | $425.2 \pm 32.8^{\text{a}}$ | $22.2 \pm 0.8$ | $475.5 \pm 58.7^{\text{a}}$ | $21.2 \pm 1.1^{\text{a}}$ | $1.20^{\text{a}}$  |
| 2008   | $722.6 \pm 25.2^{\text{a}}$ | $20.8 \pm 0.9^{\text{a}}$ | $494.1 \pm 11.2^{\text{b}}$ | $21.4 \pm 0.9$ | $415.3 \pm 42.6^{\text{a}}$ | $23.7 \pm 0.6^{\text{b}}$ | $1.10^{\text{a}}$  |
| 2009   | $703.4 \pm 20.1$            | $21.0 \pm 0.5$            | $422.3 \pm 19.2$            | $21.6 \pm 1.1$ | $419.6 \pm 33.9$            | $22.7 \pm 0.9$            | $0.07$             |
| 2010   | $814.3 \pm 24.8^{\text{b}}$ | $19.1 \pm 0.7^{\text{b}}$ | $415.2 \pm 62.3^{\text{a}}$ | $21.2 \pm 1.1$ | $574.7 \pm 51.2^{\text{b}}$ | $21.0 \pm 1.3^{\text{a}}$ | $-2.57^{\text{b}}$ |
| 2011   | $945.1 \pm 27.9^{\text{b}}$ | $18.4 \pm 0.9^{\text{b}}$ | $398.3 \pm 53.6^{\text{a}}$ | $22.5 \pm 0.7$ | $310.2 \pm 23.1^{\text{c}}$ | $24.2 \pm 0.9^{\text{b}}$ | $-0.65^{\text{a}}$ |
| GLM, F | 12.11                       | 24.54                     | 28.98                       | 1.94           | 20.44                       | 33.22                     | 5.11               |
| df     | 3, 3624                     | 3, 3624                   | 3, 3201                     | 3, 3201        | 3, 3898                     | 3, 3898                   | 3, 8               |
| p      | <b>&lt;0.001</b>            | <b>&lt;0.001</b>          | <b>&lt;0.001</b>            | 0.12           | <b>&lt;0.001</b>            | <b>&lt;0.001</b>          | <b>0.03</b>        |

SSTA values inside the Kings and the Lion regions ( $r_s = 0.21$ ,  $p = 0.29$ , and  $r_s = 0.14$ ,  $p = 0.47$ , respectively,  $N = 29$ ) (Fig. 2A). SST and PP patterns were similar between all 3 main foraging regions from January 2007 until June 2009 (Fig. 3B,C). From July 2009 onwards, SST of Kings and Lion was generally high, whereas it decreased within Altair. During the same period, monthly cycles of PP within Kings and Lion had a slight decrease, while it increased within Altair (with peaks of PP each March).

### Inter-annual changes in foraging parameters and links with oceanography

There was a general and yearly increase in all the foraging parameters (i.e. proxies of foraging effort) between 2007 and 2011 (Table 2). In 2011 and when compared to 2007, birds foraged on average 11 extra days, travelled distances of about 6800 km more, for-

aged on areas about 3200 km farther from their breeding colony and spent an additional 4.5 h (on average) flying each day (Table 2). From 2007 to 2011, there was a steady and significant increase in the Home Range (by 5.1 times) and Foraging Area (by 2.2 times) of female Cory's shearwaters (Table 2).

Environmental characteristics within the Foraging Areas (50% KUD) differed significantly from those of Home Range (95% KUD) each year (Fig. 2). Individuals foraged in shallower habitats (Table 3), colder water regimes and over more productive grounds than those of their Home Range (Table 3).

In 2011, birds exploited habitats about 1400 m deeper than in 2010, and around 2500 m deeper than in 2007–2008, revealing an increasing preference for oceanic regimes. Water temperature was about 3°C colder in 2011 than in 2007–2008 and 5°C colder than in 2010 (Table 3). Productivity was about 400 mgC  $m^{-2} d^{-1}$  higher than in 2010 and 600 mgC  $m^{-2} d^{-1}$  than in 2007–2008 (Fig. 2, Table 3).

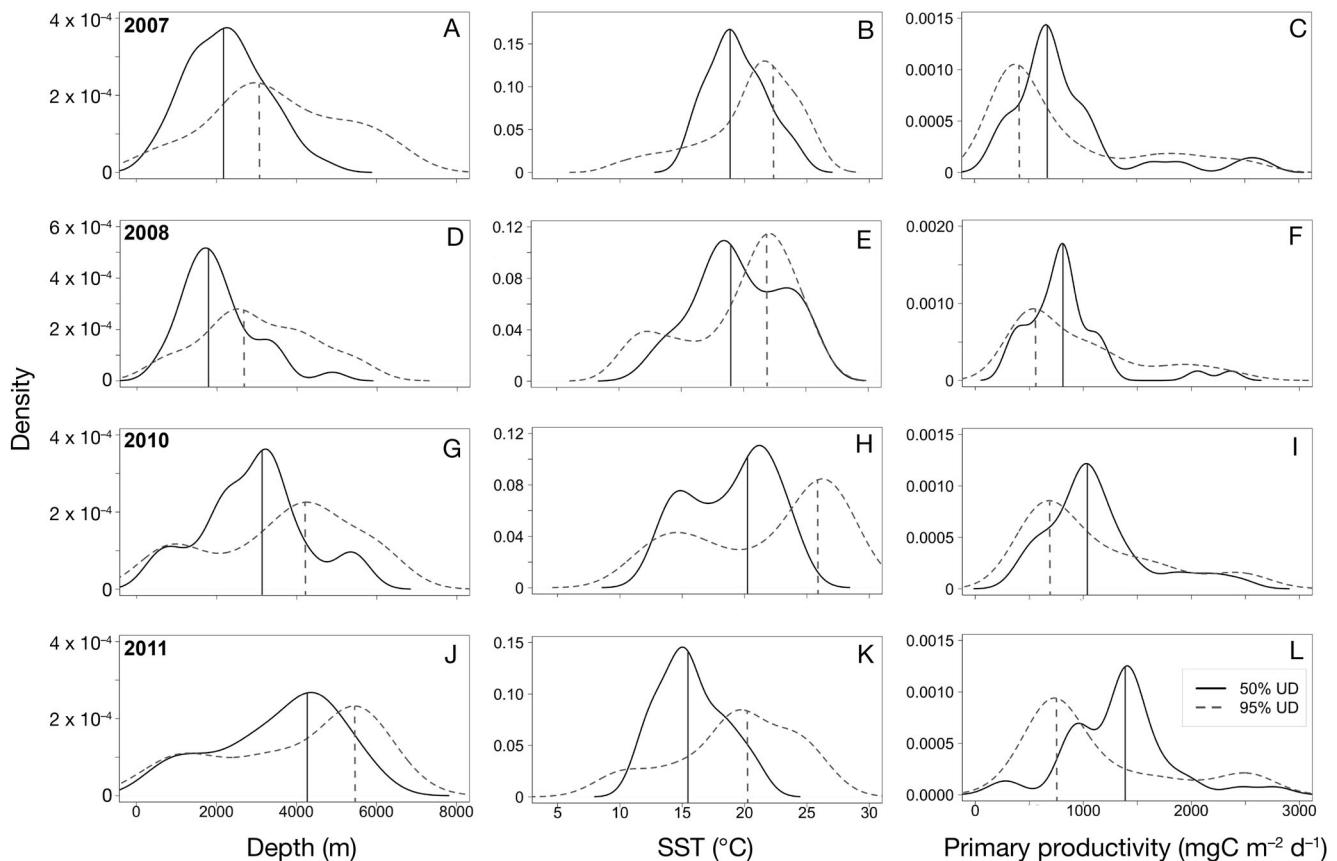


Fig. 2. Frequency distribution of 3 oceanographic parameters (depth, sea surface temperature [SST] and primary productivity) within female Cory's shearwater *Calonectris diomedea* ranges (delimited by kernel utilisation distribution [KUD] contours) during (A–C) 2007, (D–F) 2008, (G–I) 2010 and (J–L) 2011. Dashed grey line: Home Range (95 % KUD); solid black line: Foraging Area (50 % KUD). Projections of values on the x-axis correspond to medians of the oceanographic parameters

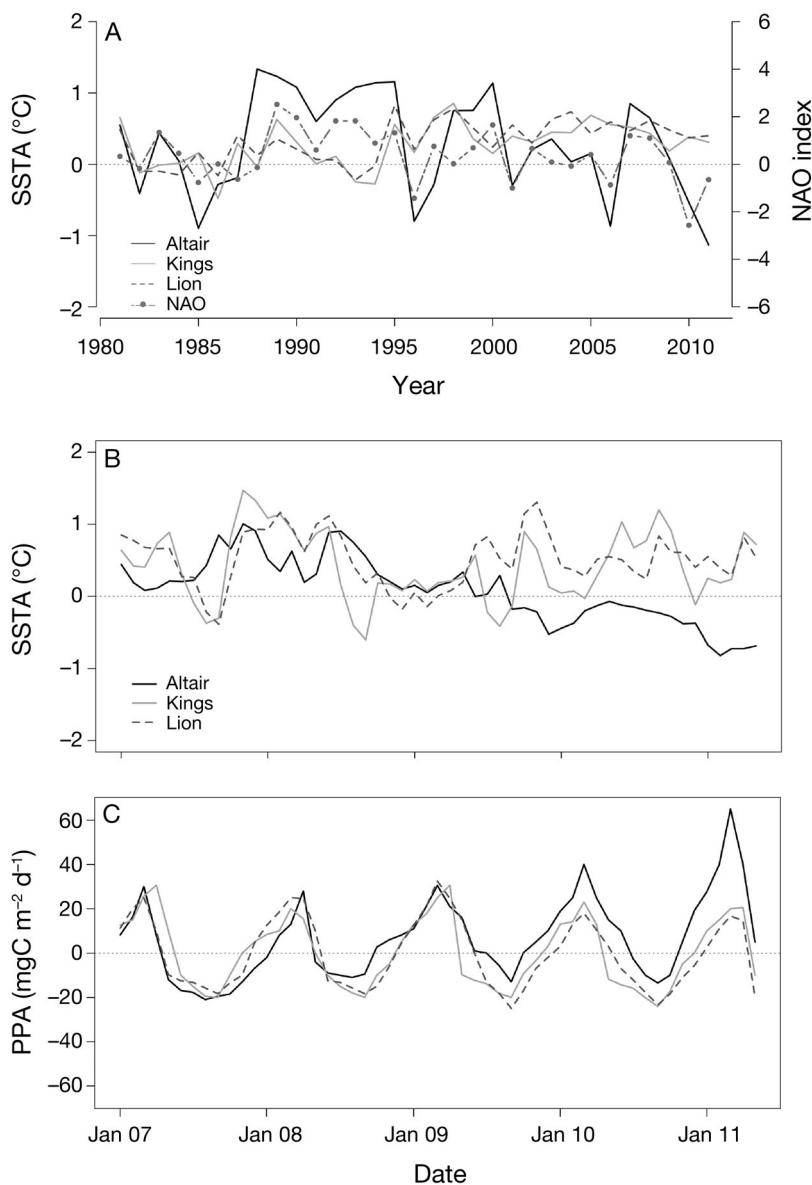


Fig. 3. (A) Historical variation in the annual mean sea surface temperature anomaly (SSTA) within the 3 main areas exploited by female Cory's shearwaters *Calonectris diomedea*—Altair (38–46°N, 50–34°W), Kings (40–46°N, 25–11°W) and Lion (32–40°N, 25–8°W)—and the North Atlantic Oscillation (NAO) index, between 1981 and 2011. (B,C) Monthly anomalies of (B) SST and (C) primary productivity (PPA) between January 2007 and May 2011 of the same 3 main foraging areas in the North Atlantic

#### Effects of shifting distribution on body condition and breeding success

BCI of female Cory's shearwaters was significantly lower in 2011 compared to previous years (Table 2). There were no inter-annual differences in laying success, but there were significant differences for hatching success, which also decreased significantly

in 2011 (Table 2). During each of the study years, laying and hatching success of telemetered individuals was similar to that of 20 non-telemetered birds randomly selected from the breeding population ( $t < 1.25$ ,  $p > 0.11$ ).

#### DISCUSSION

Our study demonstrates the foraging flexibility of female Cory's shearwaters, which seem to have responded to a negative productivity trend that occurred in the foraging areas closer to their breeding colony by targeting more productive domains within the North Atlantic region. Indeed, this behaviour could be related to the observed decrease in PP between 2007 and 2011 that occurred within the main foraging grounds (located closer to the breeding colony), accompanied by a decrease of SST and an increase of PP within the main foraging region of 2011 (the Altair region—an oceanic domain located close to the Grand Banks and Newfoundland Shelf). These oceanic changes on a regional scale seem to have a link with large-scale oceanic phenomenon, driven by NAO. Thus, female Cory's shearwaters were able to adjust to the effects of environmental variability by perceiving the oceanic changes, and shifting their distribution to an area that could have the food resources to better meet their unique nutritional needs. To exploit the productive Altair area, female Cory's shearwaters embarked in one of the largest known foraging excursions of the pre-laying period (nearly 4000 km

of total distance covered). Compared with other Procellariiform species (Phillips et al. 2006, Pinet et al. 2012), distances travelled by pre-laying females Cory's shearwater in 2011 were among the largest, even doubling the distance travelled by white-chinned petrels *Procellaria aequinoctialis* (~2000 km) when foraging over the productive Patagonian shelf region (Phillips et al. 2006).

Table 2. *Calonectris diomedea*. Inter-annual comparison of mean ( $\pm$  SD) foraging and breeding parameters of Cory's shearwaters. Reported laying and hatching success are from nests of tracked birds. All foraging parameters (i.e. from trip duration until Foraging Areal) were compared using generalized linear mixed models (GLMM); trip identity nested within the individual as a random term. Mean body index condition (BCI) compared using a general linear model (GLM) and laying and hatching successes compared using Chi-square ( $\chi^2$ ) tests. Home Range: kernel utilization distribution (KUD) contour encompasses 95% of all geolocations; Foraging Area: KUD contour encompasses 50% of all geolocations. Superscript lettering indicates multiple comparison results (2009 values are merely descriptive and were not included in the statistical analysis)

| Year       | N birds<br>[N tracks] | Trip<br>duration<br>[range] (d)    | Total distance<br>covered (km)   | Maximum<br>distance from<br>colony (km) | Time spent<br>flying trip <sup>-1</sup><br>d <sup>-1</sup> (h) | Home<br>Range<br>(km <sup>2</sup> ) | Foraging<br>Area<br>(km <sup>2</sup> ) | BCI                           | Laying<br>success<br>(%) | Hatching<br>success<br>(%) |
|------------|-----------------------|------------------------------------|----------------------------------|---|--|-------------------------------------|--|-------------------------------|--------------------------|----------------------------|
| 2007       | 7 [12]                | 7.2 $\pm$ 3.9 [4–17] <sup>a</sup>  | 1323.3 $\pm$ 135.6 <sup>a</sup>  | 712.3 $\pm$ 102.1 <sup>a</sup>          | 5.3 $\pm$ 1.1 <sup>a</sup>                                     | 192 125 $\pm$ 2354 <sup>a</sup>     | 4084 $\pm$ 243 <sup>a</sup>            | 0.23 $\pm$ 0.04 <sup>a</sup>  | 81.5                     | 74.5                       |
| 2008       | 8 [10]                | 10.6 $\pm$ 4.4 [5–16] <sup>a</sup> | 3047.5 $\pm$ 678.2 <sup>b</sup>  | 1297.2 $\pm$ 391.2 <sup>b</sup>         | 5.5 $\pm$ 1.4 <sup>a</sup>                                     | 301 142 $\pm$ 3621 <sup>b</sup>     | 4748 $\pm$ 342 <sup>a</sup>            | 0.12 $\pm$ 0.02 <sup>a</sup>  | 79.1                     | 73.4                       |
| 2009       | –                     | –                                  | –                                | –                                       | –  | –                                   | –                                      | –                             | 82.1                     | 74.9                       |
| 2010       | 10 [14]               | 12.1 $\pm$ 2.6 [6–21] <sup>a</sup> | 3104.2 $\pm$ 1052.4 <sup>b</sup> | 1947.3 $\pm$ 501.3 <sup>b</sup>         | 6.0 $\pm$ 1.5 <sup>a</sup>                                     | 462 313 $\pm$ 5728 <sup>c</sup>     | 6524 $\pm$ 462 <sup>b</sup>            | -0.14 $\pm$ 0.08 <sup>a</sup> | 80.2                     | 75.2                       |
| 2011       | 10 [12]               | 17.2 $\pm$ 1.9 [6–20] <sup>b</sup> | 8132.6 $\pm$ 2116.3 <sup>c</sup> | 3945.3 $\pm$ 1245.7 <sup>c</sup>        | 9.8 $\pm$ 1.0 <sup>b</sup>                                     | 987 524 $\pm$ 8512 <sup>d</sup>     | 9024 $\pm$ 962 <sup>c</sup>            | -1.02 $\pm$ 0.07 <sup>b</sup> | 77.9                     | 61.0                       |
| Statistics |                       |                                    |                                  |   |  |                                     |  |                               |                          |                            |
| df         | 4, 36                 | 6, 69                              | 5, 01                            | 4, 88                                   | 10, 18   | 12, 51                              | 4, 18                                  | 1, 03                         | 14.09                    |                            |
| p          | 3, 44                 | 3, 44                              | <0.001                           | 3, 44                                   | <0.001   | 3, 44                               | 3, 32                                  | 3                             | 3                        | <0.001                     |

Table 3. Generalized linear mixed model (GLMM) results comparing mean depth, sea surface temperature (SST) and primary productivity (PP) within core habitats (Foraging Areas—50% KUD) between years. Also shown, GLMM results of yearly comparisons (2007, 2008, 2010, 2011) of environmental characteristics within Foraging Areas with those of bird's Home Range (95% KUD) within each year. All GLMMs included trip identity nested within the individual as a random term

| Variable                                  | F     | df    | p      |
|---|-------|-------|--------|
| Depth (m)                                 | 18.84 | 3, 44 | <0.001 |
| 2007                                      | 6.31  | 1, 46 | <0.01  |
| 2008                                      | 3.97  | 1, 46 | <0.01  |
| 2010                                      | 9.23  | 1, 46 | <0.001 |
| 2011                                      | 10.56 | 1, 46 | <0.001 |
| SST (°C)                                  | 13.72 | 3, 44 | <0.001 |
| 2007                                      | 8.02  | 1, 46 | <0.001 |
| 2008                                      | 5.13  | 1, 46 | <0.01  |
| 2010                                      | 14.35 | 1, 46 | <0.001 |
| 2011                                      | 21.42 | 1, 46 | <0.001 |
| PP (mgC m <sup>-2</sup> d <sup>-1</sup> ) | 6.11  | 3, 44 | <0.01  |
| 2007                                      | 4.13  | 1, 46 | <0.01  |
| 2008                                      | 3.69  | 1, 46 | <0.01  |
| 2010                                      | 15.75 | 1, 46 | <0.001 |
| 2011                                      | 25.98 | 1, 46 | <0.001 |

### The importance of studying the spatial ecology of pre-laying female seabirds

Former telemetric studies conducted during the breeding period have shown that Cory's shearwaters possess a remarkable foraging plasticity (Paiva et al. 2010b), being able to respond to a vast array of environmental cues. Those include underwater elevations (e.g. seamounts or shelf upwellings; Navarro & González-Solís 2009, Paiva et al. 2010c), frontal zones (Paiva et al. 2010a), or coping with oceanic phenomena that occur at different spatio-temporal scales (Paiva et al. 2010a). In accordance with this, female Cory's shearwaters (independently of the year or main foraging area) always targeted colder waters and productive regimes to meet their unique foraging needs during this period.

Female Cory's shearwaters adapted to changes in environmental conditions by switching their usual foraging area during the pre-laying period for a much remoter region. Overall, all foraging parameters (i.e. proxies of foraging effort) increased annually between 2007 and 2011, with birds exploiting remoter areas, travelling longer and covering greater distances, which also lead to a tremendous increase of their home ranges and foraging areas. When relieved of their breeding duties, the same

birds were able to change their wintering ground from one year to another (Dias et al. 2011), which may be seen as a capacity of the species to adapt to changes in the environment during different phases of their life cycle. Nonetheless, during pre-laying (a nutritionally and physically demanding phase for females because of egg production), environmental stochasticity may have a stronger impact on them—limiting their capacity to display their foraging flexibility without noticeable effects on their body condition or breeding performance. In this respect, it seems that the price for exploiting such remoter areas in 2011 was a lower body condition (upon arrival at the colony) and a decrease in hatching success. Productivity in the colony surroundings (i.e. within the Portuguese continental shelf area) remained poor during chick-rearing of 2011 (September), ‘forcing’ breeders to frequently exploit seamounts within the Lion area where PP was slightly higher (V. H. Paiva pers. obs.). This is an unusual behaviour by this population during chick-rearing (an observation based on yearly tracking data since 2005), when birds forage mostly over the Portuguese shelf to feed their chicks (Paiva et al. 2010c).

### **Environmental stochasticity changed the productivity regimes of the North Atlantic region**

Both the Kings and Lion areas were influenced by an increase in SST over our study period (2007–2011), as evidenced by the consistently higher values of SSTA. This warming probably affected the distribution and availability of the prey of Cory’s shearwaters, which shifted their distribution in search of more productive areas. Similarly, Pinaud et al. (2005) reported a shift in the foraging distribution of yellow-nosed albatrosses *Thalassarche chlororhynchos* in the Southern Indian Ocean, in search of more productive grounds as a response to an increase in SST in the closer, formerly preferred foraging habitats. In the same ocean basin, Péron et al. (2012) predicted southward shift of nearly 38 km decade<sup>-1</sup> in the distribution of king penguins *Aptenodytes patagonicus* as a response to increasingly warmer water temperatures, derived from climate change scenarios over the next 100 yr.

The main foraging regions used by Cory’s shearwaters between 2007–2010 (Kings and Lion areas) are known to be used by different populations of Cory’s shearwaters breeding in the Atlantic islands, and other seabird species inhabiting the North Atlantic region. Both areas are also known to be highly

utilised by populations breeding in the Azores (Magalhães et al. 2008), Madeira and Berlenga (Paiva et al. 2010c), mostly during the incubation period. In addition, Macaronesian shearwaters breeding in the Santa Maria, Azores and Selvagens, visit and depend upon these areas throughout the year (Neves et al. 2012, I. Fagundes unpubl. data). From 2007 to 2011, productivity within these regions decreased progressively, with increasingly warmer waters. Though progressive, this decrease on the productivity indexes was much more evident and prevalent during 2010 and 2011 (when compared to 2007 and 2008). In fact, in 2010, the North Atlantic region experienced one of the lowest NAO in the last 30 yr (Osborn 2011), and although the NAO value in 2011 was higher, it remained negative. A very low NAO represents a winter with very cold waters (low SST) and ocean winds stronger than usual (within our study area; Stenseth et al. 2003). Usually, the combination of the former oceanic conditions would boost the upwelling in shelf break areas of neritic and seamount areas, thus increasing the availability of nutrients for plankton, which in turn would be more available for planktivorous fish (Santos et al. 2007). However, if the upwelling is too strong and occurs during the spawning events of most small pelagic fish species (Santos 2001), the eggs would be dispersed out of shallower (and protective) grounds, with resultant lower recruitment of fish-prey for Cory’s shearwaters. According to the ‘ocean triad hypothesis’ (Bakun 1996), nutrient enrichment, concentration of larval food and retention of larvae, are the main factors required for successful recruitment of small pelagics over neritic ecosystems worldwide (Santos et al. 2007). The disruption of this triad must have impacted the prey availability for birds, to a point where it was no longer efficient to forage within these regions; forcing birds to exploit remoter areas where prey availability may be more persistent (i.e. less affected by climatic events).

### **CONCLUSION**

Our study indicates that inter-annual foraging decisions of female Cory’s shearwaters were influenced by environmental stochasticity linked with NAO. When productivity proxies in the closer foraging areas decreased, females exhibited a phenomenal behavioural flexibility by crossing almost the entire width of the North Atlantic basin (from Portugal almost to Canada) to forage on a comparatively much more productive oceanic region. This area is

recently becoming known for holding large numbers of a considerable array of seabird species during different parts of the year, which enhances its importance as a seabird diversity hotspot (e.g. González-Solís et al. 2011, Hedd et al. 2012, Ramírez et al. 2013). The option to forage in such a distant area in 2011 decreased the females' body condition and reduced their hatching success (mostly because eggs were abandoned during incubation). Nevertheless, the link between foraging choices due to environmental change and the breeding output is not easy to establish with just 1 yr of contrasting low breeding success. Future studies should continue monitoring birds during this period, in order to unravel the true durable impact of environmental pressure on the demographic parameters of Cory's shearwater. Results from this long-term monitoring may help us understand the medium- to long-term effects of environmental stochasticity in the North Atlantic Ocean.

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