BIODIVERSITY RESEARCH

Meta-population feeding grounds of Cory's shearwater in the subtropical Atlantic Ocean: implications for the definition of Marine Protected Areas based on tracking studies

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ABSTRACT

Aim Apical pelagic species forage in predictable habitats, and their movements should signal biologically and ecologically significant areas of the marine ecosystem. Several countries are now engaged in identifying these areas based on animal tracking, but this is often limited to a few individuals from one breeding population, which may result in biased portrayals of the key marine habitats. To help identify such foraging areas, we compiled tracking data of a marine top predator from the main breeding colonies in the Central Macaronesia.

Location North-east Atlantic Ocean.

Methods Over seven years, we tracked the foraging movements of Cory's shearwaters (*Calonectris borealis*) from several populations during the chick-rearing period using global positioning system and platform terminal transmitter devices.

Results We obtained foraging trips from 174 shearwaters breeding on six important colonies representative of the range occupied in the Macaronesian Archipelagos of Madeira, Salvages and Canaries. Our results show that birds orient and move rapidly towards the closest neritic waters over the African continental shelf. Birds from different colonies show substantial spatial segregation in their foraging grounds but consistently overlap in some specific foraging areas along the Canary Current characterized by high productivity. By weighting the use of foraging grounds according to the size of each study population, we inferred the overall exploitation of such areas.

Main conclusions Our meta-population approach provides a more comprehensive picture of space use from both perspectives: the studied species and the Canary Current system. Foraging grounds consistently used by several populations may not be adequately identified by tracking a single population, and therefore, multiple population tracking studies are needed to properly delineate key conservation areas and inform conservation planning in the marine ecosystem. Finally, we highlight the long-term stability and sustainability of identified foraging areas and propose that countries with geographical jurisdictions over the Canary Current area should work towards multilateral agreements to set management plans for this key marine ecosystem.

Keywords
Biologging, *Calonectris borealis*, Canary Current, meta-population feeding grounds, seabird at-sea distribution, tracking top predators.

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Diversity and Distributions

INTRODUCTION

Human-induced changes at sea, such as massive fishery activities, global change and increasing concentrations of hazardous contaminants, are altering the structure and stability of the entire marine food web (Halpern *et al.*, 2008). The increasing awareness of the impacts of these pressures on the whole marine environment has led to the development of conservation measures on a wider scale, and the establishment of marine protected areas (MPAs) is one of the most promising management tools within this context, contributing to the protection and long-term sustainability of important key marine ecosystems (Lascelles *et al.*, 2012).

Many MPAs have been specifically defined around locally restricted breeding sites of endangered or vulnerable marine top predators, but much less attention has been given to remote foraging waters. For instance, many seabirds are currently well protected in their breeding colonies, but they have received considerably less attention at pelagic sites where they forage (but see Arcos *et al.*, 2012). In fact, quality, location and extent of feeding areas during the breeding season are among the most important factors in determining physiological status, breeding success and survival of top predators, which ultimately condition their population dynamics (Davis *et al.*, 2005). At the same time, because these foraging places are often associated with dynamic oceanographical features, a deep understanding of these wildlife-habitat associations is critical for evaluating the feasibility and design of MPAs (e.g. Hooker *et al.*, 1999).

Recent advances in biologging studies have revealed the existence of locally restricted areas with specific oceanographical features where marine vertebrates predictably occur in high abundance (Block *et al.*, 2011). This is of conservation relevance because it suggests that marine fauna hotspots not only occur around the breeding grounds but also in remote areas apparently unconnected to the breeding sites. Nonetheless, most of these investigations are based on tracking animals from a single population. However, different populations may forage in distinct areas or may overlap extensively, and therefore, identifying whether foraging grounds are shared by several populations becomes essential to assess the importance of specific areas. Moreover, determining the degree of overlap among populations in such foraging areas is essential to assess the extent to which different populations are exposed to specific threats.

As an example, many large predators of conservation concern occur in the highly productive coastal upwelling off the north-west African coast, the so-called Canary Current, throughout the year: cetaceans, seals, sea turtles and many seabird species (Oro & Martínez-Vilalta, 1994; Forcada *et al.*, 1999; Wynn & Knefelkamp, 2004; Camphuysen & Van der Meer, 2005; Stenhouse *et al.*, 2012). Although most of these species are endangered or protected, there are few monitoring data available for the region compared to other upwelling systems (e.g. the California Current; Block *et al.*, 2011).

Here, we looked at the at-sea distribution of a medium-sized apex predator, the Cory's shearwater (*Calonectris borealis*), while breeding on different islands of Madeira, Salvages and Canaries. It is possibly the most abundant seabird during the summer in the large marine ecosystem of the Canary Current, and the above populations are known to forage in the northern part of this major upwelling area during the chick-rearing period. Although the biology and foraging distribution of these seabird populations have been relatively well studied during the breeding season, they have often been evaluated independently, at intra-population level (Navarro & González-Solís, 2009; Paiva *et al.*, 2010a; Alonso *et al.*, 2012), ultimately hampering a comprehensive perspective on the spatio-temporal patterns of the entire population. Thus, with the ultimate aim of bringing to light the biological importance of the poorly known Canary Current ecosystem (e.g. Cury *et al.*, 2011), we aimed to (1) identify precise foraging areas of the main Cory's shearwater populations breeding in the Central Macaronesia, (2) evaluate the relative importance of these foraging areas by quantifying the number of breeding birds, which forage on them, (3) assess the spatial overlap among six of these populations as well as the interannual variability in their at-sea distributions and, finally, (4) characterize the environmental conditions of the foraging areas used by shearwaters at a meta-population scale.

METHODS

Species ecology and study area

Cory's shearwater is a medium-sized procellariiform that undertakes long transoceanic migrations from its Atlantic breeding grounds (from the Azores to the Canaries, including Madeira, Salvages and Berlengas Islands) to its wintering areas in the North, central and South Atlantic (González-Solís *et al.*, 2007; Dias *et al.*, 2011). This species breeds annually in remote islets and islands, and it has a high reproductive investment: adults arrive at the colony in early March, females lay a single egg in late May, chicks hatch in mid-late July and fledge in late October/early November (Thibault *et al.*, 1997). During the long chick-rearing period (over 90 days), the chick is left alone in its burrow while both male and female forage at sea, alternating chick provisioning duties every 1–10 nights.

The present study was conducted at six breeding colonies of Cory's shearwater spread throughout Macaronesia (Fig. 1), where a relevant number of birds are known to breed (Table 1). During the breeding period, these populations largely forage in the very productive upwelling off the African coast, namely the Canary Current (Navarro & González-Solís, 2009; Paiva *et al.*, 2010a; Alonso *et al.*, 2012). However, other Atlantic populations of the species, such as Azorean birds and those breeding in Berlengas Islands, do not exploit this upwelling system while rearing their chicks (Paiva *et al.*, 2010a). The Canary Current upwelling consti-
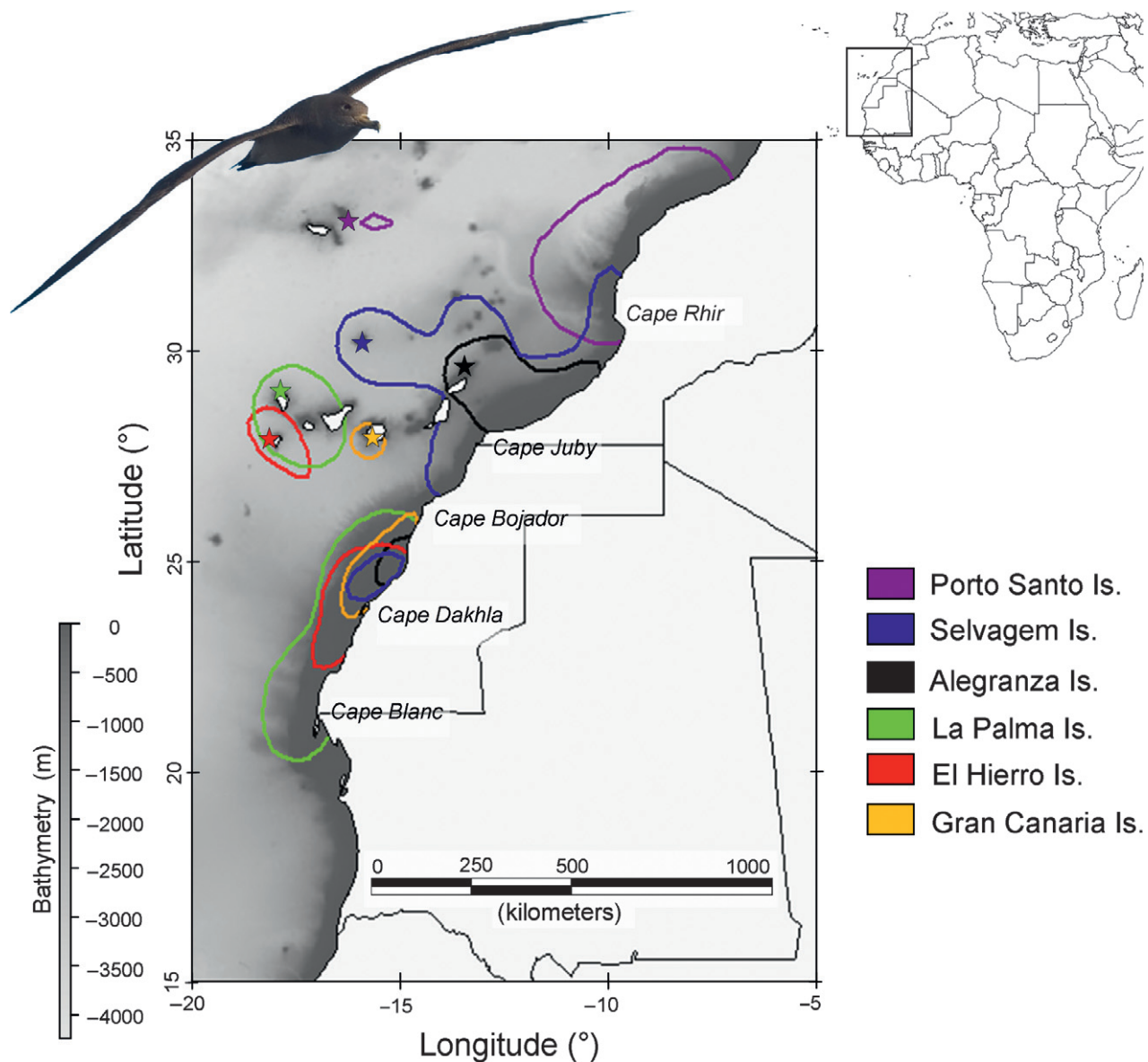
Figure 1 Cory's shearwater kernel density distributions (50% contours) of breeding populations from Porto Santo (magenta), Selvagem (blue), Alegranza (black), La Palma (light green), El Hierro (red) and Gran Canaria (orange) during the chick-rearing period (July, August and September). Bathymetry of the studied area is depicted in greyscale.

tutes one of the major productive ecosystems of the world (Barton *et al.*, 1998), hosting high marine productivity as well as an important fishery. North-east trade winds along the north-west African coast transport surface waters offshore, which subsequently implies a net onshore flow of cold and nutrient-rich waters from the depths (Davenport *et al.*, 2002). This upwelling feature extends from 10°N up to 43°N as a 50–70-km band alongshore (i.e. over the continental shelf; Mittelstaedt, 1991), and it results in a very favourable environment for the proliferation of zooplankton, small pelagic fish and cephalopods, which tend to be highly abundant in this relatively restricted area of the north-east Atlantic (Arístegui *et al.*, 2009).

Cory's shearwater tracking data

We collected at-sea distribution data of adult breeding birds tracked during chick-rearing periods (July, August and September) during seven consecutive years (Table 2). Data come from Argos satellite-linked platform terminal transmitters (PTT) powered either by a battery or a solar panel (Bird Borne from North Star Science and Technology, King George, Virginia, USA) and global positioning system loggers (GPS: Earth&OCEAN Technologies, Kiel, Germany, and CatNip Technologies, Sheung Wan, Hong Kong). Such devices were attached to the back or the tail feathers of birds with Tesa® tape (Wilson *et al.*, 1997) and weighed 30 g for

Table 1 Geographical characteristics and minimum estimated breeding pairs of the main Cory's shearwater populations in Madeira, Salvages and Canaries. The six sampled populations included in the study are depicted in bold.

Breeding population	Sampled colony	Latitude (°)	Longitude (°)	Min distance to the African coast (km)	Estimated population (breeding pairs)	Reference
Madeira Archipelago*	**Porto Santo**	33.05	−16.28	633	**3500**	Oliveira & Menezes (2004)
Salvages Is.	**Selvagem Grande**	30.14	−15.87	376	**29,840**	Granadeiro *et al.* (2006)
Lanzarote Is.†	**Alegranza Islet**	29.39	−13.50	170	**13,375**	Rodríguez *et al.* (2003)
Fuerteventura Is.‡		28.75	−13.82	125	4000	Lorenzo (2007)
La Palma Is.	**In the main island**	28.75	−17.69	426	**3000**	Lorenzo (2007)
Tenerife Is.		28.47	−16.92	349	3000	B. Rodríguez's unpublished data
La Gomera Is.		28.17	−17.10	340	3000	B. Rodríguez's unpublished data
El Hierro Is.	**In the main island**	28.17	−18.14	425	**2000**	B. Rodríguez's unpublished data
Gran Canaria Is.	**In the main island**	27.84	−15.79	223	**2000**	Lorenzo (2007)

*Including Madeira, Porto Santo and Desertas Is.
†Including five islets: Alegranza, Montana Clara, La Graciosa, Roque del Este and Roque del Oeste.
‡Including Lobos Islet.

battery-powered PTTs, 20 g for solar PTTs, and between 15 and 30 g for GPSs (depending on the size of the attached battery), which corresponded to 1.9–3.7% of bird body mass (<4% of adult mass; Passos *et al.*, 2010). PTTs were programmed with 60-s repetition rates and duty cycles of continuous transmission, providing variable intervals between transmissions (179 min on average, ranging from 1 to 1080 min), while GPSs recorded the position of birds every 5 or 15 min.

To homogenize our dataset, we first removed repeated locations at the colony leaving only the last position as the starting point of each trip. Secondly, we filtered PTT locations (Class 3 through Class B) using a speed-distance-angle filter ('SDAfilter' function with maximum threshold speed at 80 km h^{-1} and default settings for distance and turning angles, from the ARGOSFILTER package; Freitas *et al.*, 2010) in the statistical program R (R Development Core Team, 2012). Thirdly, we interpolated filtered PTT data to hourly locations in a continuous-time movement modelling using functions provided by the CRAWL package ('crwMLE' and 'crwPredict'; Johnson, 2012), but restricting interpolations between those PTT locations separated by <6 h. Finally, we subsampled GPS locations at 1-hour intervals to make PTTs and GPSs positions comparable.

Comparative analyses of trip parameters and foraging range of colonies

Using interpolated location data, we estimated three parameters for every complete foraging trip: total distance travelled (in km), duration (in hours) and maximum foraging range (maximum distance from the respective colony; in km). Additionally, to best assess the use of the Canary Current, we first selected those positions between 0 and 80 km from the African coastline (see Fig. 2) and calculated the 95% Utilization Distributions (95% UD; in km^2; 'kernelUD' function in the ADEHABITAT package in R; Calenge *et al.*, 2006)

for each trip, and secondly, we calculated the percentage of all fixes (reflecting percentage of utilization time) of each trip that were at <80 km from the coast.

Normality checks for distributions of the first four trip parameters (partitioned by our eleven breeding events, i.e. colony × year) were made using Q-Q plots. Using model information criteria, we evaluated independently the effects of the breeding event and colony in foraging trip characteristics. Due to the nature of our data, year effect could not be properly tested; however, we could test for either breeding event or locality variation in foraging behaviour by fitting a set of candidate generalized linear mixed models (GLMMs), where each of the five foraging parameters was the response variable, and breeding event or locality was the main (fixed) explanatory variable. We chose link functions in the models following the nature of dependent variables: when modelling trip length, trip duration, maximum distance from the colony and area in the CC, we assumed a Gaussian distribution of error terms and used log-link function, while when modelling time in the CC (i.e. a proportion), logit-link function was applied instead, assuming a binomial distribution of error terms. To account for potential individual heterogeneity in trip parameters, the individual was included in all the GLMMs as a random term. Model selection was carried out using the Akaike information criteria corrected for small sample sizes (AICc) and the corresponding AICc weights (Johnson & Omland, 2004). GLMMs were conducted in R with additional functions provided by the R packages LME4 ('lmer'; Bates *et al.*, 2008) and MUMIN ('dredge'; Bartoń, 2009).

To quantify spatial sharing among colonies in the Canary Current but also to assess the annual effect within a colony, we calculated the space overlap between the eleven breeding events. Overlap indices between every pair of breeding events 95% UD were calculated using the 'kerneloverlap' function in the ADEHABITAT package (VI method; Fieberg & Kochanny, 2005).

Table 2 Foraging trip characteristics (mean ± SD and range) of Cory's shearwaters breeding on six colonies in the Macaronesian Archipelagos of Madeira, Salvages and Canaries; CC refers to Canary Current.

Breeding location	Sampling period	Tracking device	Tracked individuals (trips)	Interpolated positions	Characteristics of foraging trips					
					Trip length (km)	Trip duration (hours)	Max. distance from colony (km)	Trips in the CC	Area in the CC (km^2)	Time in the CC (%)
Alegranza Islet	06 Aug 2006 to 12 Sept 2006	PTT	20 (53)	5502	844.2 ± 545.1 (245.2–3020.9)	102.8 ± 89.4 (17–558.0)	270.6 ± 150.6 (105.8–625.9)	40	37,819.0 ± 50,993.9 (450.6–178,275.9)	67.7 ± 20.5 (9.5–95.8)
	10 Aug 2010 to 08 Sept 2010	GPS	26 (74)	5329	829.4 ± 730.7 (83.6–3351.6)	71.0 ± 60.1 (13–281.0)	297.9 ± 242.7 (32.9–959.5)	52	81,926.5 ± 116,995.3 (151.5–467,338.5)	77.1 ± 14.6 (30.0–97.9)
El Hierro Is.	22 Aug 2007 to 14 Sept 2007	PTT	10 (15)	2031	1422.8 ± 814.4 (224.5–2956.1)	134.4 ± 91.6 (20–287.0)	461.2 ± 235.3 (43.4–845.7)	11	26,623.5 ± 20,053.3 (8661.0–72,385.4)	65.6 ± 15.1 (40.6–89.5)
La Palma Is.	01 Aug 2007 to 21 Aug 2007	PTT	10 (22)	2672	1357.6 ± 1086.0 (165.5–3615.7)	120.5 ± 123.2 (16–427.0)	453.5 ± 283.3 (69.2–987.0)	13	86,155.7 ± 125,430.7 (7530.8–464,885.5)	61.9 ± 19.8 (22.2–87.3)
Porto Santo Is.	05 Aug 2011 to 17 Aug 2011	GPS	8 (9)	1166	2241.4 ± 534.0 (1505.1–3135.2)	128.6 ± 53.4 (57–205.0)	777.8 ± 163.8 (645.5–1125.5)	9	53,039.6 ± 76,989.5 (9642.1–253,659.3)	62.2 ± 23.1 (20.7–86.3)
Selvagem Is.	08 Aug 2008 to 16 Aug 2008	GPS	10 (15)	1249	1031.5 ± 656.5 (205.5–2213.1)	82.3 ± 61.0 (9–184.0)	415.0 ± 239.4 (88.6–907.6)	10	69,830.1 ± 70,062.3 (1694.7–201,233.7)	74.7 ± 18.0 (48.8–93.3)
	05 Aug 2009 to 24 Aug 2009	GPS	10 (15)	1645	1102.8 ± 578.8 (206.0–1988.7)	108.7 ± 81.1 (8–276.0)	420.9 ± 181.9 (113.9–676.2)	9	53,846.2 ± 51,174.7 (1451.1–140,219.1)	59.4 ± 20.9 (26.3–79.7)
	15 Aug 2010 to 24 Aug 2010	GPS	20 (28)	1894	1118.7 ± 549.4 (316.1–2630.3)	66.6 ± 40.4 (13–186.0)	485.0 ± 160.7 (146.9–891.6)	22	44,006.2 ± 70,925.9 (2695.9–303,479.5)	62.6 ± 13.6 (34.2–87.6)
	07 Aug 2011 to 20 Aug 2011	GPS	37 (42)	2786	1117.5 ± 629.9 (338.6–2520.3)	65.3 ± 42.2 (18–170.0)	451.3 ± 238.2 (132.7–1010.6)	24	65,820.9 ± 75,342.3 (649.0–268,933.5)	72.0 ± 14.5 (46.7–91.6)
Gran Canaria Is.	03 Aug 2005 to 27 Aug 2005	PTT	19 (26)	4041	1276.6 ± 793.1 (234.4–3161.4)	145.4 ± 127.7 (46–574.0)	367.4 ± 135.1 (96.2–769.4)	25	37,552.1 ± 39,860.2 (1571.7–153,745.5)	71.2 ± 19.5 (11.5–97.0)
	24 July 2011 to 04 Aug 2011	GPS	4 (7)	1099	1517.9 ± 591.2 (496.5–2055.1)	161.2 ± 75.6 (49–253.0)	427.2 ± 141.2 (211.2–656.6)	7	41,874.6 ± 45,491.3 (2393.5–141,861.9)	71.1 ± 19.9 (39.1–93.2)

GPS, global positioning system; PTT, platform terminal transmitter.
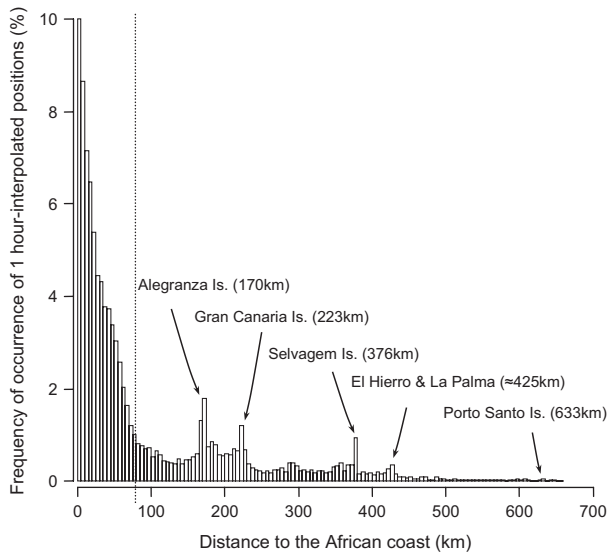
Figure 2 Frequency distribution of the minimum distance to the African coast (in km) for 29,414 1-h interpolated positions obtained from 306 foraging trips. Cory's shearwater (174 different individuals) were tracked during the chick-rearing period from 2005 to 2011 on six breeding colonies spread along three Macaronesian Archipelagos. Distribution shows most of the positions are at <80 km of the African coast (denoted by the dotted line), but also further peaks at a greater distance that can be attributed to the six breeding colonies (showed by arrows; exact minimum distances from the colony site to the continental coast in brackets).

Bird directionality while entering the area under the influence of the Canary Current (i.e. at 80 km off the African coast) was evaluated using circular statistics according to Batschelet (Batschelet, 1981). Rayleigh uniformity tests were first used to test whether the direction of a sample (breeding event in our case) differed significantly from that direction resulting from the minimum distance between the coast and the colony of origin.

Finally, we estimated the importance of specific areas along the Canary Current to each colony. Residence time was defined as the number of interpolated 1-hour positions spent by each bird within a $0.2° \times 0.2°$ cell. These counts of positions were weighed by considering the total numbers of interpolated positions in each breeding event, that is, the sampling effort per colony site. Additionally, these proportions of positions were also multiplied by the size of the population of origin (estimated as $2 \times$ number of breeding pairs; Table 1). By these means, we obtained an absolute estimate of the foraging intensity by breeding birds along the Canary Current.

Environmental data

NOAA CoastWatch (http://coastwatch.pfeg.noaa.gov/) provides accurate measurements of primary productivity (mg C m^{-2} day^{-1}; 0.1° spatial resolution, approximately 9 km) based on satellite measurements of chlorophyll-a concentration (AQUA MODIS sensor) and sea surface temperature (NOAA

PATHFINDER Project). Eight-day composites of these remote sensing data were downloaded for the summer season (July-September) of every sampled year and converted to raster data by interpolation. To estimate primary productivity along the Canary Current, we averaged, for every chick-rearing season, those values within 80 km off the African coast (i.e. bathymetry = 0; bathymetry data retrieved from http://ngdc.noaa.gov/mgg/bathymetry/relief.html at 0.01° spatial resolution, approximately 1 km). Additionally, oceanic wind intensity (m s^{-1}) and direction were extracted from the SeaWinds database (QuikSCAT; http://winds.jpl.nasa.gov; 0.125° spatial resolution, approximately 11 km) and averaged for every chick-rearing season. Environmental data were extracted for a grid including breeding colonies and the main Canary Current between 20 and 5°W, and 15 and 35°N.

Finally, to investigate the spatial structure of Cory's shearwaters and relevant environmental data (primary productivity), we used simple and partial Mantel tests (Mantel, 1967; Legendre & Legendre, 1998). Standard statistical tests assume independence between data points but because of spatial autocorrelation, locations that are close to each other have more similar characteristics than those further apart. Mantel tests differ from standard regression techniques in that the dependent variables are dissimilarity matrices, the test measures the degree of pairwise similarity between sets of data and significance is evaluated via permutation procedures (Mantel, 1967). Distance matrices were based on Euclidean metrics calculated between every pair of locations in the respective data set (i.e. seabird abundance, primary production and geographical positions). Because primary productivity variable exhibited high degrees of spatial autocorrelation, we used partial Mantel tests to specifically explore the relationship between seabird abundance and primary productivity, while controlling for spatial structure (Legendre & Legendre, 1998). This procedure was carried out both at regional scale (i.e. considering all grids) and in the Canary Current (i.e. within 80 km from the coast). The significance value for each test was determined using 10,000 permutations, and confidence intervals were obtained using 1000 bootstrapping events. The Mantel r are based on the normalized value r of the Mantel statistic z, which bounds on $[-1, 1]$ after standardization.

RESULTS

We obtained 306 complete foraging trips from 174 individual Cory's shearwaters sampled at six different colonies (Table 2). After conducting filter and interpolation procedures, we obtained 29,414 hourly positions. Of these positions, 68.0% were <80 km from the African coast, most of them over the continental shelf or on the shelf break and immediately adjacent waters (Fig. 2).

Our analysis of trip characteristics showed a substantial heterogeneity among the sampled colonies (Table 2). When modelling foraging trip characteristics using information criteria, colony effect was often stronger than that of breeding

event (Table 3). The best-supported models for trip length, trip duration, maximum distance from the colony and area exploited in the Canary Current included colony as fixed effect, while the best model for time spent in the Canary Current was the constant model. The random individual component accounted for a relatively small amount of the total variability in all cases. Trip length and maximum distance from the colony tended to be higher in those remote colonies such as Porto Santo, and lower in colonies closer to the coast, such as Alegranza and Gran Canaria (Tables 2 & 3). However, neither trip duration nor the area and time spent in the Canary Current showed such a relationship between colonies and proximity to the coast.

Bird directionality towards the coast, evaluated as the direction of each bird at 80 km from the African coast, was not statistically different from the direction of the vector originating at the colony and linking it to the coast by the shortest distance (Rayleigh tests; Table S1). However, the direction of the prevailing wind at 80 km from the African coast was significantly different to each bird direction (Watson-Williams tests, all $P < 0.001$; Fig. S1; Table S1).

Most of the birds foraged within the core of the northern Canary upwelling zone (Figs 1 & 3). Cory's shearwaters breeding at Porto Santo foraged mostly north of Cape Rhir where they moderately overlapped with other colonies located at midlatitudes such as Selvagem and Alegranza (mean of 22.2% of overlap; Table 4). These birds breeding at Porto Santo overlapped very little with those breeding in the southernmost colonies, that is, La Palma, El Hierro and Gran Canaria (5.2%). Birds from colonies of Selvagem and Alegranza tended to forage in large numbers at midlatitudes in the Canary Current (around and north of Cape Juby), although they also used significantly northern and southern

locations. These two large colonies showed a relatively high overlap (59.2%), but this overlap tended to be lower with the southernmost colonies (24.8%). Birds from the southernmost colonies, that is, La Palma, El Hierro and Gran Canaria, mostly foraged in latitudes between Cape Bojador and Cape Blanc (Fig. 3), with an abundance peak north of Cape Dakhla. These three colonies highly overlapped among themselves (50.4%; Table 4). Additionally, areas exploited from birds from those colonies sampled in different years showed a relatively high overlap rate (mean of 57.8%, 56.8% and 62.7% for Selvagem, Alegranza and Gran Canaria Islands, respectively; Fig. 3 and Table 4).

During the study period, active upwelling occurred along the length of the coast, being most intense in three dynamic upwelling nuclei (Fig. 4a): two of them in a relatively restricted area north of Cape Rhir (at about 31°N) and around Cape Juby (between 29 and 27°N), and another larger one, centred on Cape Blanc, but extending north to Cape Dakhla (between 24.5 and 19.5°N). Water boundaries with high primary production were clearly coincident with the bathymetric relief. Maximum primary production occurred within 10–20 km of the African continent, although active upwelling extended 100-km offshore around Cape Blanc. Annual variability of primary productivity throughout July, August and September was relatively low along the northern Canary Current, and it was only substantial offshore from Cape Blanc (Fig. 4b).

Simple Mantel tests showed strong spatial autocorrelations in primary productivity at both global breeding area and the Canary Current scales (Table 5). However, autocorrelation in seabird abundance was found at neither global breeding area nor the Canary Current scales. Partial Mantel tests showed that there was a significant effect of the distribution of primary productivity on seabird abundance, when spatial autocorrelation was accounted for. This effect was significant

Table 3 Parameter estimates (±SE) from generalized linear mixed models fitted to five trip characteristics of Cory's shearwater from six Macaronesian colonies (selected models in bold). In the first four features (trip length, trip duration, maximum distance to colony and area in the Canary Current), the best-supported model included colony as fixed effect, while in the last one (i.e. percentage of time spent in the Canary Current) the constant model was preferred. All evaluated models included the individual as a random effect. AICc refers to the corrected (c) Akaike's information criterion (AIC) increments and CC to Canary Current.

|	Trip length (km)	Trip duration (hours)	Max. distance from colony (km)	Area in the CC (km²)	Time in the CC (%)
AICc					
Breeding event (colony × year)	62,895,337	671,029.0	5,781,557	578,527,405,819	264.0
Colony	**62,895,328**	**671,025.6**	**578,1550**	**578,527,405,775**	241.0
Constant	62,895,353	671,048.8	5,781,586	578,527,406,930	**234.2**
Fixed effects (estimate ± SE)					
Alegranza (Intercept)	835.6 ± 61.7	89.1 ± 8.8	286.5 ± 18.5	47,705.2 ± 7211.5	51.1 ± 2.0
El Hierro	587.2 ± 189.7	47.6 ± 24.0	174.7 ± 56.8	−28,230.1 ± 20,910.2	
La Palma	522.0 ± 160.4	41.2 ± 22.0	167.0 ± 48.0	5342.2 ± 18,361.7	
Porto Santo	1405.8 ± 239.6	40.5 ± 28.9	491.3 ± 71.8	5754.7 ± 25,915.8	
Selvagem	267.2 ± 92.9	−12.5 ± 12.2	164.2 ± 27.8	−9388.6 ± 10,438.1	
Gran Canaria	490.0 ± 127.2	63.4 ± 16.4	92.2 ± 38.1	−9762.5 ± 14,143.2	
Random effect (variance ± SE)					
Individual	55,287.0 ± 235.1	893.4 ± 29.9	3809.6 ± 61.7	460,251,692 ± 21,453	0.4 ± 6.0
Residual	201,580.1 ± 449.0	2145.9 ± 46.3	18,524.4 ± 136.1	5,020,942,317 ± 70,859	11.6 ± 34.0
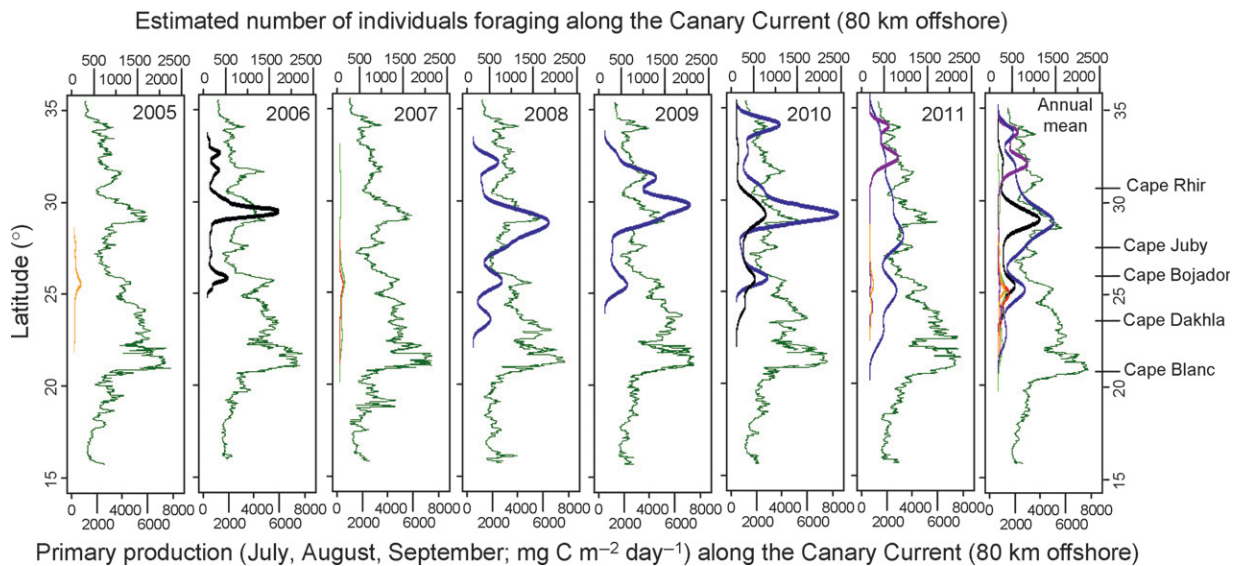
Figure 3 Estimated primary production (in dark green; mg C m^{-2} day^{-1}) throughout July, August and September along the African coast. Latitudinal mean of the closest 80 km along the continental coast is depicted in each subplot, from left to right, from 2005 to 2011. Similarly, estimated numbers of individuals (every 0.2° latitudinally) foraging in that 80-km corridor along the continental coast are shown annually (annual mean in the right most plot) for breeding populations of Gran Canaria (orange), Alegranza (black), La Palma (light green), El Hierro (red), Selvagem (blue) and Porto Santo (magenta).

Table 4 95% kernelUD overlap computed with those foraging locations of Cory's shearwaters situated at <80 km from the African coast. Comparisons include the eleven breeding events considered in the study.

Breeding event	Porto Santo 2011	Selvagem 2008	Selvagem 2009	Selvagem 2010	Selvagem 2011	Alegranza 2006	Alegranza 2010	La Palma 2007	El Hierro 2007	Gran Canaria 2005
Selvagem 2008	17.1									
Selvagem 2009	24.1	53.5								
Selvagem 2010	32.9	54.7	63.2							
Selvagem 2011	21.3	72.2	51.7	51.6						
Alegranza 2006	27.3	57.4	76.9	68.1	52.2					
Alegranza 2010	10.5	65.6	51.0	51.0	61.8	56.8				
La Palma 2007	10.5	39.3	28.1	26.8	49.0	32.2	51.2			
El Hierro 2007	3.6	14.6	8.9	6.8	17.2	11.5	24.9	40.2		
Gran Canaria 2005	3.2	26.4	12.7	10.2	25.3	18.2	41.5	40.7	53.2	
Gran Canaria 2011	3.6	28.8	16.1	14.7	28.6	21.6	41.1	41.8	63.9	62.7

when considering both the global breeding area (Mantel partial $r^2 = 0.080$, $P < 0.001$) and the restricted Canary Current (Mantel partial $r^2 = 0.002$, $P = 0.041$).

The northern Canary Current is characterized by prevailing north-easterly winds during summer, which were clearly dominant throughout the study period (Fig. 4c). Wind speeds recorded on the Canary Current coast differed considerably depending on the area we considered. The northernmost and southernmost productive areas, around Cape Rhir and Cape Blanc respectively, were exposed to relatively strong winds averaging 8–10 m s^{-1}. On the other hand, the productive area around Cape Juby experienced lower wind intensity, averaging 4–6 m s^{-1}. Annual variability in wind intensity during summer was only high in the locally restricted area off Cape Rhir (Fig. 4d).

Finally, at a meta-population scale, Cory's shearwaters breeding in Central Macaronesia spent most time foraging within the core of the northern Canary upwelling zone: all birds rearing chicks rapidly headed straight towards the coast edge and then concentrated their foraging effort in different patches between 20 and 35°N (Fig. 5). The core area where birds spent maximum time corresponded to inshore waters (isobath < −100 m), located within 20 km from the coastline.

DISCUSSION

Cory's shearwaters foraging in the Canary Current

As previously reported, our study confirmed that foraging strategies of Cory's shearwaters breeding in the Central
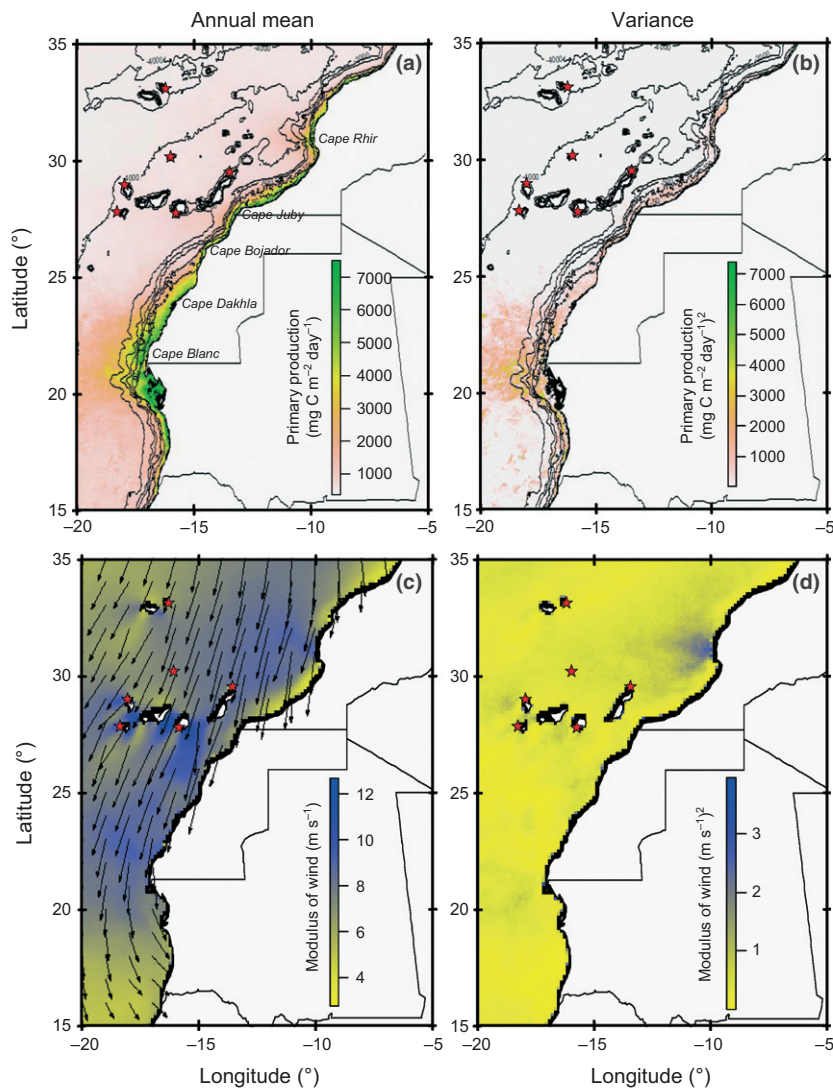
Figure 4 Mean (a, c) and variance (b, d) of summer primary productivity (mg C m^{-2} day^{-1}; top) and wind direction and intensity (m s^{-1}; bottom) along the African coast during the study period (July-September from 2005 to 2011). Red stars show the location of the breeding colonies evaluated. −50, −100, −500, −1000, −2000 and −4000 isobaths (in metres) are depicted in solid black lines in a) and b).

Table 5 Mantel *r* statistics and *P*-values of simple and partial Mantel tests between dissimilarity matrices representing space, primary production and Cory's shearwater abundance (estimated number of birds per 0.2° × 0.2° cell) during the chick-rearing period both in the entire study area and in the restricted area of the Canary Current (within 80 km from the African continental coast). Simple Mantel tests were used to examine any spatial autocorrelation of the considered variables, while partial Mantel tests were used to assess the correlation between these variables while taking into account the spatial autocorrelation.

Mantel tests	Entire breeding area	Canary current
Simple tests		
Spatial structure in Cory's shearwater abundance	r = 0.019; P = 0.109	r = −0.053; P = 0.999
Spatial structure in Primary Production	r = 0.324; P < 0.001	r = 0.302; P < 0.001
Partial tests		
Cory's shearwater abundance-Primary Production (after controlling for spatial dependency)	r = 0.282; P < 0.001	r = 0.041; P = 0.0409

Macaronesian archipelagos are closely linked to this Canary Current system (Ramírez *et al.*, 2008; Arcos *et al.*, 2009). Based on six representative breeding colonies around the area, our findings show that shearwaters oriented most of

their foraging trips towards the closest and highly productive waters over the African continental shelf (at <80 km from the coast and in waters <100 m in depth). Despite a certain degree of inter-population segregation, different colonies

Figure 5 Habitat utilization by Cory's shearwaters from six different colonies indicated by stars based on (a) the number of interpolated locations that fall in each 0.2° × 0.2° cell (positions/cell) and (b) that number magnified by the size of the population of origin (birds/cell). The number of interpolated locations is relative to the sampling effort, that is, to the total number of interpolated positions per tracked population.
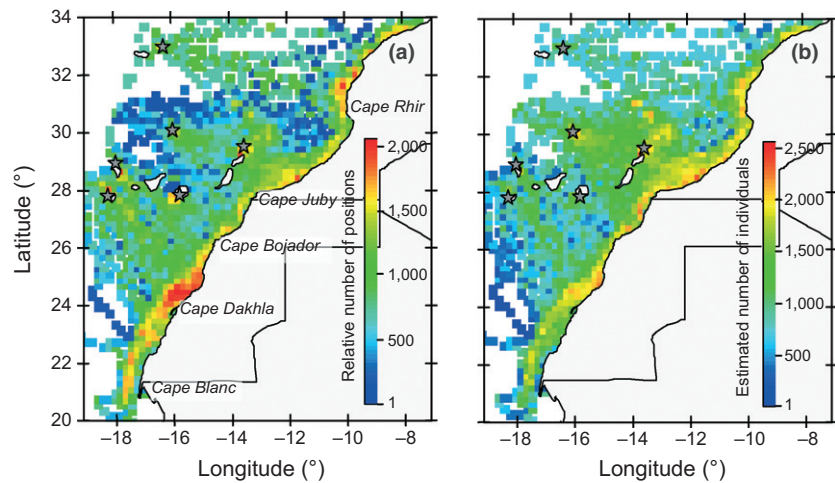
largely overlapped in two highly profitable foraging areas within the Canary Current. These two core foraging grounds, located at ~25 and ~28°N, matched geographically with two peaks of primary productivity and are known to be the coldest nutrient-enriched waters along that part of the north-west African coast (Machu et al., 2009). Although a third large peak in marine productivity occurred around Cape Blanc (likely to be intensively used by the endemic Cape Verde shearwaters Calonectris edwardsii during breeding; J. González-Solís' unpublished data), this remote area is likely to be beyond geographical range of those Cory's shearwaters with rearing duties. Hence, we found that Cory's shearwaters were predictably associated with high primary production concentrations close to the continental coast.

The relatively narrow continental shelf off north-west Africa is characterized by intense upwelling of nutrient-rich deep waters, associated with strong winds from north–north-east and complex current systems (Machu et al., 2009). This upwelling enhances primary and secondary production, and supports high abundances of epipelagic fish, notably anchovies (Engraulis encrasicolus), pilchards (Sardina pilchardus, Sardinella aurita and S. maderensis), mackerels (Scomber scombrus, S. colias, Trachurus trachurus and T. picturatus) and epipelagic cephalopod species (Arístegui et al., 2009), which are important prey of Cory's shearwaters (Paiva et al., 2010b; Xavier et al., 2011; Alonso et al., 2012) and other marine predators. The inter-annual stability in oceanographical parameters in the study area might make these prey concentrations relatively predictable in space and time, as they are unavoidably tied to seasonally forced cold, upwelling waters. Such prey predictability would explain the consistency of the general foraging areas used by each colony in different years. The association between the feeding locations and primary production suggests that birds mainly used feeding grounds according to their prey availability, which would increase their foraging success and promote fidelity to specific feeding patches (Weimerskirch, 2007; Louzao et al., 2011a).

Directionality of foraging trips was not influenced by the prevailing winds of each area, and birds flew, in most cases, directly to the closest area on African continental shelf and then dispersed from there independently of wind direction (i.e. both clockwise and anticlockwise directions; but see Navarro & González-Solís, 2009). Thus, the geographical position of each breeding colony conditioned the resulting exploited area, resulting in a certain degree of fidelity to specific feeding grounds, and explains to a certain extent the relative high overlap among foraging areas of closer colonies and the low overlap among areas of colonies distant from one another (Grémillet et al., 2004; Louzao et al., 2011a). In addition to this, intra-specific and inter-population competition for trophic resources may induce individuals from peripheral colonies to move further while seeking feeding grounds with fewer conspecifics (e.g. Lewis et al., 2001). This could be, for instance, the case for the southernmost colonies of our study; instead of exploiting the close and highly productive area around Cape Juby (~28°N), shearwaters breeding at Gran Canaria foraged much more to the South, possibly avoiding the huge numbers of shearwaters from Alegranza and Salvages, which foraged at midlatitudes. Although Navarro & González-Solís (2009) suggested the north-east prevailing winds as the key feature in explaining Cory's shearwater distributions along the Canary Current, the present results suggest that intra-specific competition, in addition to optimal foraging ranges, may play a role in explaining the species distribution (Grémillet et al., 2004; Louzao et al., 2011b; Fort et al., 2012).

Potential MPAs and implications for marine conservation

MPAs are often criticized for aiming to protect unpredictable features due to the dynamic nature of productivity hotspots (such as those associated with specific thermal fronts, oceanic currents, sea surface winds, upwellings and eddies; Game et al., 2009; Kaplan et al., 2010). However, some of these physical phenomena are highly constant due to bathymetric features, and other processes are spatially predictable but temporally variable such as wind-driven upwelling phenomena

(Lombard *et al.*, 2007). This seems to be the case of the Canary Current where both primary productivity and wind direction and intensity are relatively constant year after year. Thus, these results provide some evidence that oceanographical features could reliably be represented in permanent and spatially fixed MPAs in the area, or alternatively in static MPAs that could be applied seasonally. In fact, foraging trips of Cory's shearwaters in the study region concentrate consistently throughout years in the same patches supporting the inter-annual consistency of the physical and biological processes involved.

By tracking at-sea distributions of several seabird populations, we have shown the relevance of considering population sizes when aiming to identify major foraging areas. While using simple positions of the tracked animals, one specific area appeared as the most relevant for the species, even after we corrected those positions for sampling effort. This core area located around ~25°N accounted for the greatest number of the positions and, indeed, it also accumulated the highest diversity regarding the origin of birds. However, when those positions were weighed by the size of their colonies of origin, a different map pattern was generated and the original core area was diluted all along the Canary Current, bringing up other patches of greater relevance. Particularly, latitudes between 27°N and 30°N in the Canary Current increased in importance, and a larger number of foraging individuals was estimated to forage there. Additionally, other offshore areas emerged as relevant for Cory's shearwaters, such as a series of seamounts north and north-east of Alegranza (the so-called Palaeo-Canaries; Fernández-Palacios *et al.*, 2011; Figs 1 & 5). Although in terms phytoplankton productivity such seamount areas may be relatively poor, they have abundant prey resources for seabirds by hosting some important Atlantic fish populations (Morato *et al.*, 2008). Thus, weighting the importance of foraging grounds defined by the tracks of a few individuals, using population size corrections, seems advisable for appropriate and effective MPA delimitation. This implies that accurate population size estimates for those studied populations become essential when assessing their relevance in a wider scale (i.e. at meta-population level).

Once the location and extent of key seabird areas are identified, governance efforts must be directed towards the establishment of long-term monitoring programmes for assessing significant threats affecting those seabirds and the development of appropriate management plans for the ultimate implementation of MPAs. In the European Union for instance, the Natura 2000 network provides tools for legal protection of wild birds by delimiting marine Important Bird Areas (IBAs) within the EC Bird Council Directive 79/409/EEC. However, in our case, the vast majority of waters exploited by Cory's shearwaters fall beyond the European legislation, and their eventual protection might rely exclusively on Morocco and Western Sahara administrations. Exclusive economic zone law provides states with special rights to manage marine resources over its jurisdictional waters. Therefore, African states could restrict access of commercial fisheries to a 50-km corridor along their continental coast and develop specific management regimes, which would ultimately preserve this marine environment in a permanent MPA. However, these governance challenges will probably be best dealt within a framework of international cooperation, to extend the protection of these marine areas beyond the jurisdictional borders of any particular party.

From the conservation point of view, the eventual establishment of MPAs in this less researched area would not only benefit breeding Cory's shearwaters, but also a large number of organisms that constitute one of the most complex trophic webs in marine ecosystems (Arístegui *et al.*, 2009). At the top of this trophic web, a vast community of seabirds (including shearwaters Procellariidae, storm-petrels Hydrobatidae, gannets Sulidae, phalaropes *Phalaropus* spp., skuas Stercorariidae, gulls Laridae and terns Sternidae; Oro & Martínez-Vilalta, 1994; Wynn & Knefelkamp, 2004; Camphuysen & Van der Meer, 2005; Stenhouse *et al.*, 2012), in addition to several predatory fish (Fonteneau *et al.*, 1993), sea turtles (Monzón-Argüello *et al.*, 2009) and endangered marine mammals (Forcada *et al.*, 1999) feed in these highly productive areas of the eastern Atlantic. The relevance of this potential MPA could slightly differ among its inhabitants as each species might display particular ecological requirements (McPherson & Jetz, 2007). In this regard, although this study is based on a ubiquitous and widespread top predator of the Canary Current, the extent and value of a potential MPA should be enhanced by complementary work involving other taxa.

Such productive shelf waters are also targeted by significant commercial fisheries from diverse nationalities (Karpouzi *et al.*, 2007), which congregate around the shelf break of Morocco, Western Sahara and Mauritania and involve annual catches of tens of 1000 tons of small pelagic fish (Alder & Sumaila, 2004; Charouki *et al.*, 2011). Any local depletion of food resources by fisheries, particularly that of anchovies, sardines and mackerels, may have dramatic effects on seabird populations (Cury *et al.*, 2011). In addition, Cory's shearwater is one of the seabirds most affected by longline vessels when scavenging on bait (García-Barcelona *et al.*, 2010; Ramos *et al.*, 2012). Fisheries operating in these highly productive zones may provide some complementary food source to some specific seabird populations (e.g. Barnes *et al.*, 1997), although this would probably not compensate for the detrimental effects of bycatch and stock depletion (Louzao *et al.*, 2011b; Ramos *et al.*, 2012). MPAs should prevent these deleterious effects by protecting those sensitive populations or species from any fishery competition or occasional bycatch. In this sense, although our primary focus is on the conservation of marine biodiversity and ecosystem functioning, fishery industries and commercial harvest of pelagic species should also benefit from these MPAs at large temporal scale, as they would make fisheries much more sustainable (Roberts *et al.*, 2005; Coll *et al.*, 2012).

CONCLUSIONS

As important components of marine environments, seabirds can be used to identify biologically and ecologically significant areas of the marine ecosystem. First of all, our results corroborate that pelagic seabirds breeding on remote islands can move long distances to forage in highly productive areas characterized by complex oceanographical processes. Second, our findings confirmed that seabirds from various colonies can target and aggregate in a few of these highly profitable areas during the key breeding period. The existence of these meta-population hotspots has important implications for seabird conservation and related studies, notably those aiming to define MPAs. Third, the relevance of considering accurate population size estimates in spatial distribution studies based on tracking several animals from different colonies is highlighted here as a requirement for more realistic MPAs delimitations. Fourth, our results validate the importance of studies conducted at meta-population scales and call for similar investigations to be performed on various other species to gain a more comprehensive understanding of sensitive marine areas that might require protection. In addition, because these meta-population hotspots varied in space along the Canary Current and extended into different jurisdictions, future MPAs necessarily have to rely on the capacity of countries to adopt collaborative management plans, independently of their geopolitical interests and in favour of the marine ecosystem sustainability. Finally, future work should be directed at confirming the stability of the core foraging grounds identified here in the long term and to address the development of management plans to make effective the protection of these sites. In this last regard, the extension and robustness of such potential MPA would ultimately depend on complementary work involving other marine top predators.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Circular distributions of the directions taken by Cory's shearwaters and circular histograms of the oceanic surface winds within 80 kilometres from the African coast, during the chick-rearing period (i.e. July, August and September).

Table S1 Circular statistics of directionality of Cory's shearwater foraging trips when entering the area under the influence of the Canary Current (i.e. within 80 km from the African coast).

BIOSKETCH

Raül Ramos is currently interested in the spatial and temporal responses of seabirds to the marine environment. He has combined several interdisciplinary approaches such as intrinsic biogeochemical markers (trace elements and stable isotope analysis), tracking devices and capture–mark–recapture data to ascertain the distribution, abundance and demography of seabirds in the marine environment. His previous work focussed on the trophic ecology of seabirds and their long-distance migratory strategies. More recently, his interests have expanded into several fields involving the epidemiology and the immune system acquisition of long-lived seabirds such as seagulls and shearwaters.

Author contributions: R.R, J.P.G. and P.C. conceived the ideas; R.R, J.P.G., B.R., J.N., V.H.P., J.B., J.M.R.-G., I.F., A.R., P.A., J.G.-S. and P.C. collected the data; R.R, J.P.G. and P.C. analysed the data; and R.R, J.P.G., B.R., J.N., V.H.P., P.A., J.G.-S. and P.C. led the writing.

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