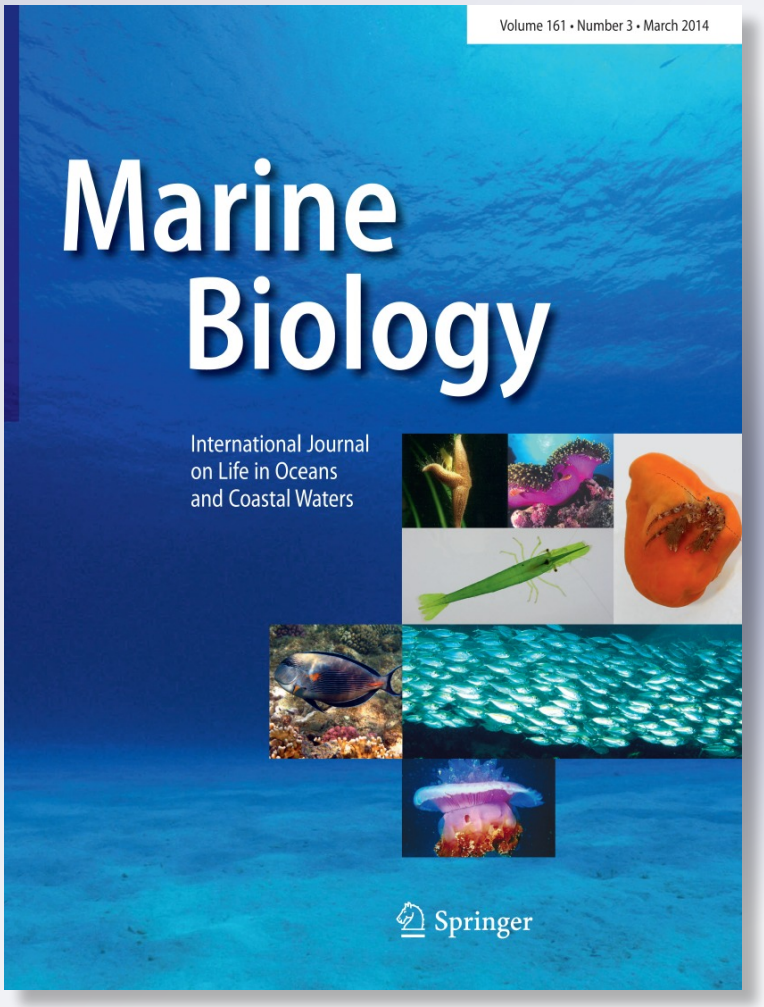
Foraging movements and habitat niche of two closely related seabirds breeding in sympatry

Isabel Afán, Joan Navarro, Laura Cardador, Francisco Ramírez, Akiko Kato, Beneharo Rodríguez, Yan Ropert-Coudert & Manuela G. Forero

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ORIGINAL PAPER

Foraging movements and habitat niche of two closely related seabirds breeding in sympatry

Isabel Afán · Joan Navarro · Laura Cardador · Francisco Ramírez · Akiko Kato · Beneharo Rodríguez · Yan Ropert-Coudert · Manuela G. Forero

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Abstract As central-place foragers, pelagic seabirds are constrained by spatiotemporal heterogeneity to find productive marine areas and compete for prey. We analysed 97 foraging trips to study the movement and oceanographic characteristics of foraging habitats of two different—yet closely related—species of shearwaters (Scopoli's shearwater *Calonectris diomedea* and Cory's shearwater *C. borealis*) breeding in sympatry in the Mediterranean. We combined various methodological approaches (GPS-tracking, species distribution modelling and stable isotope analysis) to explore the foraging strategies of these two species. Isotopic results suggested that trophic habits of both shearwater species were similar, mainly based on pelagic fish consumption. Foraging areas of both species were characterized by shallow waters near the colony. Both shearwater species exploited persistent productive marine areas. The foraging areas of the two species broadly overlapped during the incubation period, but during chick-rearing period, Scopoli's shearwaters apparently foraged in different areas than Cory's shearwaters.

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I. Afán (✉)
Laboratorio de SIG y Teledetección (LAST-EBD), Estación Biológica de Doñana (EBD-CSIC), C/Américo Vespucio s/n, 41092 Sevilla, Spain
e-mail: isabelafan@ebd.csic.es

J. Navarro
Institut de Ciències del Mar (ICM-CSIC), Passeig Marítim de la Barceloneta 37-49, 08003 Barcelona, Spain

L. Cardador
Forest Sciences Center of Catalonia (CTFC), Crta. de Sant Llorenç de Morunys km 2, 25280 Solsona, Spain

F. Ramírez · M. G. Forero
Departamento de Biología de la Conservación, Estación Biológica de Doñana (EBD-CSIC), C/Américo Vespucio s/n, 41092 Sevilla, Spain

A. Kato · Y. Ropert-Coudert
IPHC, Université de Strasbourg, 23 rue Becquerel, 67087 Strasbourg, France

A. Kato · Y. Ropert-Coudert
CNRS, UMR7178, 67037 Strasbourg, France

B. Rodríguez
SEO/BirdLife, Delegación de Canarias, C/Libertad 22, 38296 La Laguna, Tenerife, Islas Canarias, Spain

Introduction

The niche theory predicts some degrees of divergent feeding strategies between co-existing species to avoid competition for similar resources (Hutchinson 1959; Pianka 2002). Among marine predators, seabirds offer examples of ecologically similar species that coexist spatially, particularly during the breeding season when they breed in sympatry and forage within restricted ranges from their breeding places (Weimerskirch et al. 1986). In this situation, competition for food resources is expected to be particularly

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intense. Segregation in foraging area or trophic resources have been proposed as main mechanisms to reduce the degree of competition between coexisting seabird species (Hyrenbach et al. 2002; Weimerskirch et al. 2009; Navarro et al. 2013). Rapid advances in animal-tracking technology over the past 40 years have led to a proliferation of tracking data, thus providing the scientific community with new insights into animal habitat preferences and their spatial distribution (Ropert-Coudert and Wilson 2005). The use of bio-logging revealed that the at-sea distribution of seabirds are frequently associated with particular oceanographic features, such as frontal systems, gyres, shelf edges or upwellings, that all correspond to highly productive marine areas (Bost et al. 2009; Wakefield et al. 2009). In addition, bio-logging studies showed that seabirds adjust their foraging effort to the persistence and predictability of potential prey patches (Arcos et al. 2012; Louzao et al. 2012; Sigler et al. 2012). Anthropogenic activities, like fisheries, can also affect the foraging strategies of seabirds (Bertrand et al. 2007; Bartumeus et al. 2010). Seabirds may enhance the detection of prey aggregations by spotting and following fishing vessels, or scavenge on fishery discards (Navarro et al. 2009a; Bartumeus et al. 2010). Bio-logging is thus particularly adapted to the study of niche segregation in sympatrically breeding seabirds.

Scopoli's and Cory's shearwaters (*Calonectris diomedea* and *C. borealis* respectively) are closely related seabirds that, although currently being debated, have been recently recognized as different species based on genetic, morphological and ecological differences (Sangster et al. 2012; but see Genovart et al. 2013). These species breed in sympatry in some locations within the Alboran Sea in the Mediterranean (Martinez-Abrain et al. 2002; Gómez-Díaz et al. 2006), thus providing a unique scenario for investigating the nature and extent of foraging niche segregation. In accordance with niche theory predictions, previous studies on these species indicated that satellite-tracked Scopoli's and Cory's shearwaters breeding in Chafarinas Archipelago segregated their main foraging grounds during the chick-rearing stage (Navarro et al. 2009b). However, spatial data in Navarro et al. (2009b) were collected on a few individuals ($n = 7$) tracked during the chick-rearing period, and no information on spatial distribution during the incubation was provided. Here, we present a study of the foraging strategies of both Cory's and Scopoli's shearwaters breeding in sympatry at Chafarinas Archipelago during both incubation and chick-rearing period. In particular, we combined GPS-tracking, spatial distribution modelling and stable isotope approaches to explore the differential response (in terms of foraging behaviour, habitat use and trophic habits) of these central-place foragers to heterogeneity in marine resources availability.

Materials and methods

Study area and species

This study was conducted at the Chafarinas Archipelago (SW Mediterranean; Alboran Sea; North Moroccan Coast; 135°11′N, 2°26′E; Fig. 1). Although the Mediterranean Sea is characterized by a severe oligotrophy, hydrodynamic processes occurring at the Alboran Basin turn this area into a highly productive sub-basin (Huertas et al. 2012). In particular, the Alboran Basin supports the Almeria-Oran oceanographic front, which is characterized by the presence of two anticyclonic eddies formed by the superficial inflow of Atlantic waters entering the Strait of Gibraltar and mixing with resident Mediterranean waters. Such frontal system, which constitutes the real boundary between the Atlantic and Mediterranean waters, causes intermittent upwelling in the North-western coastal sector of the basin, thus enhancing marine productivity and supporting an important fishery industry (trawlers, longlines, purse seining) (Beckers et al. 1997; Arin et al. 2002).

Chafarinas Archipelago holds a sympatric population of Scopoli's and Cory's shearwaters estimated at ca. 850 breeding pairs, with Cory's shearwater representing less than 10 % of total breeding pairs. These species are long-lived seabirds with delayed maturity, high reproductive investment, long incubation (around 50 days) and chick-rearing (90 days) periods, 1-egg clutches, and slow postnatal growth (Thibault et al. 1997). Individuals were identified by a metallic band around the leg (as part of a long-term monitoring project, 2000–2011), and species and sex were determined using morphological and molecular information (Igual et al. 2009; Navarro et al. 2009b; Genovart et al. 2012). Although no diet study has been carried out at the Chafarinas colony, information from other breeding places, mainly focused on Cory's shearwater, indicates that the species feeds mainly on epipelagic and mesopelagic fish, obtained from active catch or opportunistically from fishery discards, and also a minor proportion of crustaceans and cephalopods (Xavier et al. 2011; Alonso et al. 2012).

GPS deployment and data processing

GPS were deployed and recovered during June (incubation stage) and October 2011 (chick-rearing stage). We instrumented a total of 53 individuals of both shearwater species with GPS-devices (CatTraQ™, Catnip Technologies, USA). The initial package was removed and put in a heat-shrink tube for water proofing. The final size was 27 × 55 × 12 mm and weighed 17 g, which represented less than 3 % of the body mass of the tracked individuals (Scopoli's shearwater mean body mass = 657 g; Cory's

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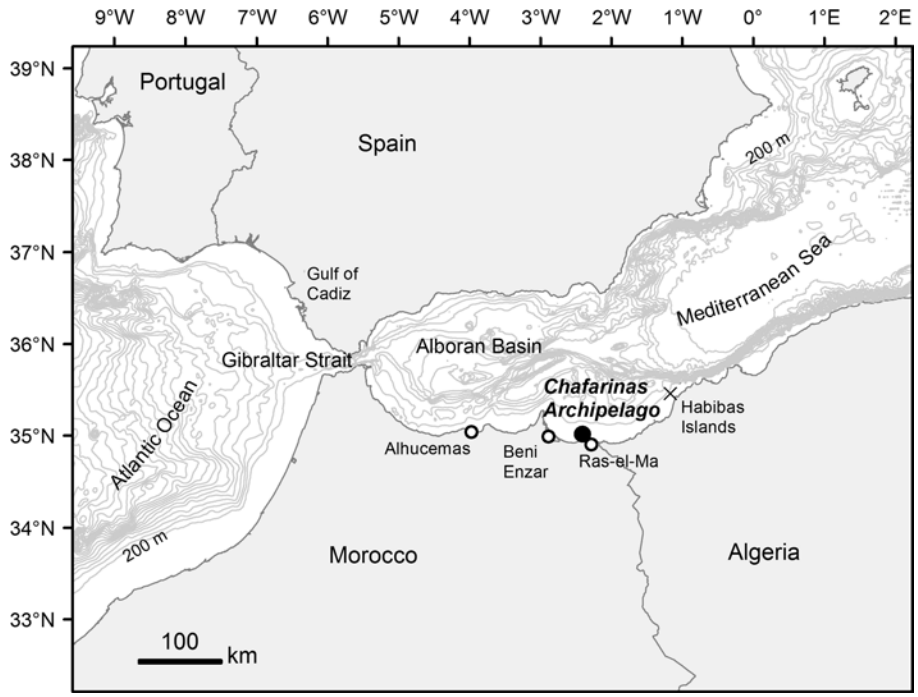


Fig. 1 Study area and breeding location (Chafarinas Archipelago) of Scopoli's and Cory's shearwaters. *White circles* indicate main fishing ports near the colony (Alhucemas, Beni Enzar and Ras-el-Ma). *Cross* indicates the nearby shearwater breeding colony of Habibas Islands (Algeria)

shearwater mean body mass = 770.6 g), i.e. the threshold under which no modification of the behaviour due to the presence of the device is observed (Phillips et al. 2003; Igual et al. 2005; Passos et al. 2010; Villard et al. 2011; but see Vandenabeele et al. 2012 and the need for future assessment of the relevance of this threshold for shearwaters). GPS-devices were attached to the mid-dorsal feathers using TESA® tape (Wilson et al. 1997). We instrumented individuals during the incubation (22 Scopoli's and 13 Cory's shearwaters) and chick-rearing period (15 Scopoli's and 3 Cory's shearwaters). GPSs were programmed to collect data every 5 min, and information was downloaded to a computer and saved as csv and gpx files with the @ trip PC software (http://www.a-trip.com/). Travelling distances were computed as geodetic distances (in m) based on Haversine algorithm. Speed (km h^{-1}), bearing (°) and distance (m) between successive raw positions were computed in ArcGIS10 (ESRI, Redland, USA) implemented in a python script.

For each complete foraging trip, we calculated trip distance (total distance travelled in one foraging trip), trip duration and maximum distance from the breeding colony. Bird behaviour (resting vs. active) at each location was estimated on the basis of speed and bearing rates between successive positions for all locations (complete and incomplete trips). Threshold limit of resting positions was calculated by inferring the lower limit of the bimodal ln (speed +1) (Supplementary material; Fig. S1) and following an exploratory analysis of bearing frequencies and visual inspection of successive bearing rate histograms from resting positions, which showed a linear pattern of consecutive positions in a predominant direction (locations with speeds lower than 6.3 km h^{-1} and bearing rates lower than |50°| were considered as resting positions). Main foraging areas were defined as the area encompassing 50 % isopleths of bivariate normal kernel analysis with ArcGIS10 (ESRI, Redland, USA), once resting positions were excluded (Seaman and Powell 1996). Then, active locations were classified as either foraging or travelling depending on whether they fall within or outside foraging areas of each foraging trip. Mean speeds at foraging and travelling locations were calculated. The proportions of time spent and distance covered in foraging areas were calculated for each foraging trip (Table 1).

Differences in foraging trip parameters were tested by using linear mixed models following a backward procedure. Sex (male or female), species (Scopoli's or Cory's shearwater) and breeding stage (incubation or chick-rearing), along with all potential interactions were included as fixed factors in the models. Individual identity was also included as a random factor to account for the dependence among different foraging trips from the same GPS-tracked individual. Normality (Shapiro–Wilk test) and homoscedasticity (Levene's test) of the data were verified before statistical analysis. All statistical analyses were performed using SPSS 18 (SPSS Inc., Chicago, Illinois, USA).

Stable isotope determination

For dietary reconstructions with isotopic approaches, we collected blood samples (0.5 ml) from 31 GPS-tracked individuals (26 Scopoli's and 5 Cory's shearwaters) at

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Table 1 Mean and standard deviation of foraging trip, foraging area and habitat parameters of GPS-tracked Scopoli's and Cory's shearwater during incubation and chick-rearing period 2011 in Chafarinas Archipelago (SW Mediterranean)

	INCUBATION		CHICK-REARING	
	Scopoli's shearwater	Cory's shearwater	Scopoli's shearwater	Cory's shearwater
Foraging trips	$n = 18$	$n = 10$	$n = 8$	$n = 1$
Number of complete/incomplete trips	27/7	20/6	36/0	1/0
Trip duration (days)	3.8 ± 2.8	4.7 ± 3.6	2.2 ± 2.7	5.1
Trip distance (km)	385.2 ± 463.4	322.2 ± 290.6	210.8 ± 414.05	1,021.7
Maximum distance (km)	77.9 ± 111.9	48.4 ± 85.4	36.5 ± 28.2	134.3 ± 95.0
Speed at foraging locations ($m \cdot s^{-1}$)	9.6 ± 9.9	9.4 ± 10.3	9.3 ± 10.1	8.9 ± 9.0
Speed at travelling locations ($m \cdot s^{-1}$)	19.4 ± 12.7	22.2 ± 15.4	17.2 ± 13.1	26.8 ± 8.9
Foraging areas				
Number of foraging areas	190	148	192	23
Area (ha)	2.5 ± 3.8	2.1 ± 3.1	2.2 ± 2.7	1.4 ± 2.4
Proportion of time spent in foraging areas (%)	24.7 ± 7.2*	19.4 ± 7.9*	26.6 ± 7.1*	26.5
Proportion of distance covered in foraging areas (%)	32.5 ± 7.7	32.4 ± 9.4	33.9 ± 6.8	28.0
Habitat of foraging areas				
Bathymetry (m)	−114.6 ± 147.5	−125.1 ± 157.9	−72.8 ± 49.2	−144.7 ± 224.8
Sea surface temperature (°C)	21.8 ± 0.6	21.7 ± 0.6	24.1 ± 0.6	23.1 ± 0.9
Chlorophyll-*a* ($mg \cdot C\ m^{-3}$)	0.22 ± 0.30	0.27 ± 0.48	0.20 ± 0.08	0.42 ± 0.44
Isotopic values	$n = 14$	$n = 4$	$n = 8$	$n = 1$
$\delta^{13}C$ (‰)	−19.2 ± 0.4	−19.4 ± 0.3	−18.9 ± 0.3	−19.3
$\delta^{15}N$ (‰)	12.2 ± 0.4	11.9 ± 0.1	12.2 ± 0.2	12.49

Statistical differences found between groups using linear mixed models are indicated with an asterisk

the end of the foraging trip. Serum was separated from the cellular fraction of the blood by centrifugation after approximately 3 h from the extraction and stored in a freezer (–20 °C) until the stable isotopic determination. In a medium size bird species, stable isotopic values in serum represent the food intake of the 3–5 days prior to blood extraction (Hobson and Clark 1992; Dalerum and Angerbjorn 2005). To interpret the functional significance of shearwaters' isotopic values, we obtained samples of their main potential prey species (pelagic fish: *Boops boops, Sardina pilchardus, Trachurus trachurus*; benthic fish: *Buglossidium luteum, Gobius cruentatus, Lophius piscatorius, Mullus barbatus, Solea solea*; squid: *Loligo vulgaris*) that were collected from the main fishing ports occurring within the foraging range used by the blood-sampled individuals: Ras-el-Ma (35°08′, 2°25′, 4 km far from the colony), Beni Enzar (35°16′, 2°55′, 45 km), and Alhucemas (35°14′, 3°55′, 134 km, Fig. 1) during October 2011. All prey samples were frozen (−20 °C) until stable isotope analyses. This selection of prey was based on previous published diet information for these species, collected elsewhere than Chafarinas (Paiva et al. 2010a; Xavier et al. 2011; Alonso et al. 2012). Serum from shearwater blood samples and muscle from prey samples were freeze-dried, ground to a powder and lipid-extracted before isotopic analysis with several rinses of chloroform–methanol (2:1) solution in order to reduce isotope variability due to a differential content of lipids (Logan et al. 2008). Subsamples of powdered materials were weighed to the nearest μg and placed into tin capsules for $\delta^{13}C$ and $\delta^{15}N$ determinations. Isotopic analyses were performed at the Laboratory of Stable Isotopes at the Estación Biológica de Doñana (www.ebd.csic.es/lie/index.html). All samples were combusted at 1,020 °C using a continuous flow isotope ratio mass spectrometry system (Thermo Electron) by means of a Flash HT Plus elemental analyser interfaced with a Delta V Advantage mass spectrometer. Stable isotope ratios are expressed in the standard δ-notation (‰) relative to Vienna Pee Dee Belemnite ($\delta^{13}C$) and atmospheric N_2 ($\delta^{15}N$). Based on laboratory standards, the measurement error was ±0.1 and ±0.2 for $\delta^{13}C$ and $\delta^{15}N$, respectively.

Dietary composition of Cory's and Scopoli's shearwaters was estimated based on their isotopic values and those of their potential prey groups by using a Bayesian multisource stable isotope mixing model, SIAR (Parnell et al. 2008). Based on previous dietary reports for Cory's shearwater (Paiva et al. 2010a; Xavier et al. 2011; Alonso et al. 2012), we defined three different dietary endpoints (pelagic fish, benthic fish and squids). However, since the isotopic signatures of benthic fish and squids were similar ($P > 0.5$), we grouped these two categories into a single one and defined two dietary endpoints: pelagic fish and non-pelagic

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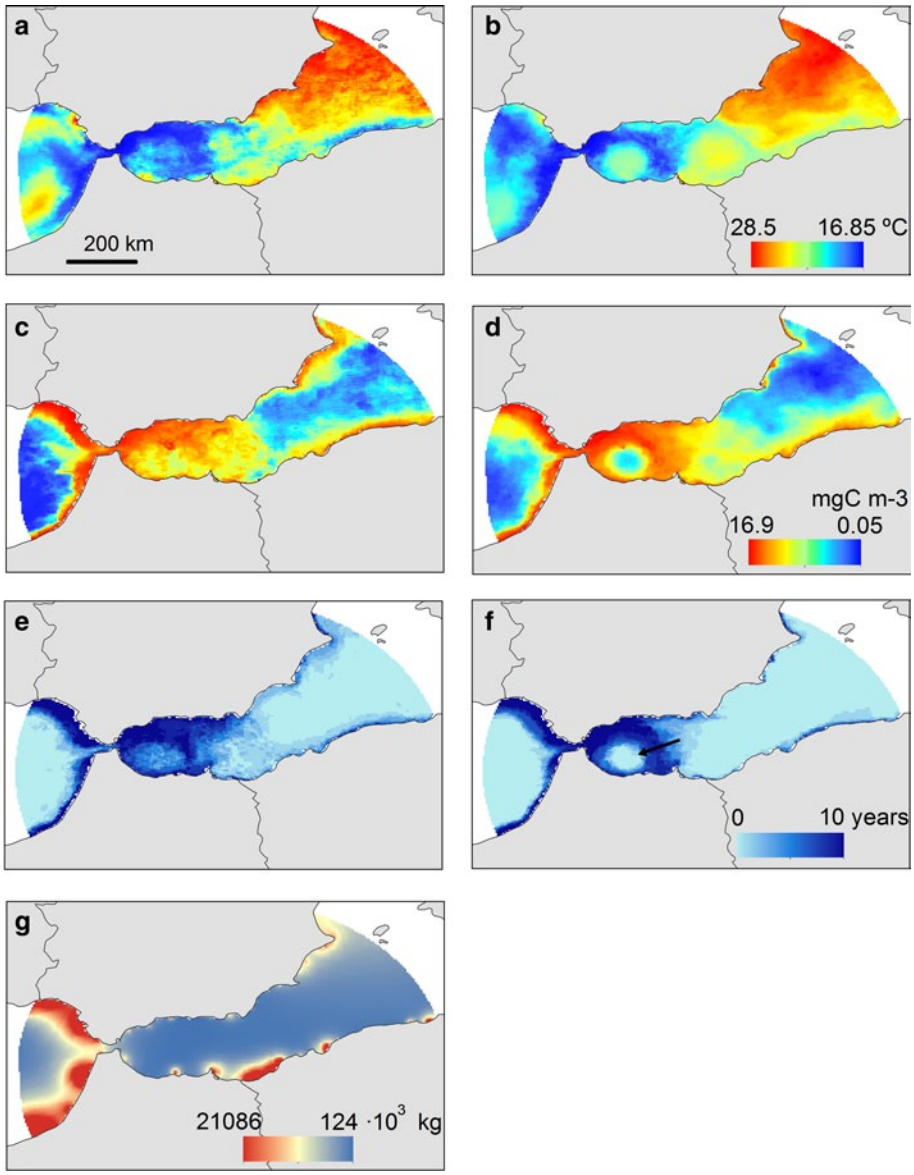


Fig. 2 Sea surface temperature during **a** incubation period (June 2011) and **b** chick-rearing period (September 2011). Chlorophyll-*a* concentration during **c** incubation period (spring 2011) and **d** chick-rearing period (summer 2011). Persistent chlorophyll-*a* level during **e** incubation (spring 2002–2011) and **f** chick-rearing period (summer 2002–2011). *Black arrow* shows the anticyclonic gyre in Alboran Sea. Fishing activity influence (g) in terms of annual fish landings (see "Materials and methods" for the details)

prey (benthic fish and squids). To build the SIAR mixing model, we used diet-serum isotopic fractionation values between prey and blood of 2.83 ‰ for $\delta^{15}N$ and −0.8 ‰ for $\delta^{13}C$ (Caut et al. 2009).

Environmental data

We used a total of six environmental variables: (1) sea surface temperature (SST, °C) (Fig. 2a, b) and (2) bathymetry (BAT, m) as proxies for physical processes or features driving prey distribution. (3) Chlorophyll-*a* concentration (CHL, mg C m^{-3}) was considered as an index of marine productivity (Fig. 2c, d). Given that areas of persistent marine productivity might be visited by seabirds from 1 year to the next (Arcos et al. 2012), we additionally estimated the spatiotemporal component of marine productivity. We extracted the longest time series of seasonal composite products of spring and summer of chlorophyll-*a* (2002-2012). (4) Key productive marine areas (PCHL, i.e. highly persistent and productive marine areas) (Louzao et al. 2012) were then identified as those areas which present at least 50 % of the time series a high-productive category, defined by the values within the upper quartile (75th percentile). We also used this variable to explore the spatiotemporal distribution of key marine areas surrounding the Chafarinas Archipelago (Fig. 2e, f). (5) We calculated the distance between each grid cell and the colony (COLONY, km), to account for the potential influence of central-place foraging. For this calculation we did not include landmasses, assuming an infinite flight cost over the land. (6) Finally, we included a variable describing fishing activity in the study areas (FISHERY, 10^3 kg) using

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a modified version of an isolation function (Hanski 1998) $F_i = \sum \exp(-d_{ij} \cdot B_j) \cdot P_j$, where d_{ij} is the distance from each grid cell i to the harbour j, and P_j is the annual fish landings (10^3 kg) of harbour j. B_j is the inverse of the minimum Euclidean distance from each harbour to 200 m isobaths, which determines the spatial influence threshold of fishing fleet operability (Fig. 2g). Fish landings were obtained from different sources: Spain (Galisteo et al. 2010), www.agricultura.gva.es, www.portsib.es; Portugal (Carvalho 2010); Algeria (Sahi and Bouaicha 2003); and Morocco (ONP 2011).

SST and CHL were obtained from Aqua MODIS sensor (http://oceancolor.gsfc.nasa.gov/), as level 3 HDF products at a spatial resolution of 0.0467° (approx. 4 × 4 km). SST was extracted from the monthly composites corresponding to the breeding stages (June and September 2011 for incubation and chick-rearing periods, respectively). Seasonal spring and summer composites (21 March–20 June 2011 for incubation and 21 June–20 September 2011 for chick-rearing period) were extracted for CHL, to account for the lag of time between current marine productivity and features, such as food availability, that could attract seabirds (Wakefield et al. 2009). BAT was downloaded from ETOPO web site (www.ngdc.noaa.gov/mgg/global/global.htm) as a binary product at a spatial resolution of 0.01° (approx. 1 km). All variables were processed and converted to raster images using the Marine Geospatial Ecology Tools for ArcGIS10 (Roberts et al. 2010).

All environmental variables were resampled to match the spatial resolution of remote sensing environmental data (0.04667° cell size) in a 514 km radius extent of the breeding colony, defined by the maximum distance of the kernel 50 reached by the GPS-tracked birds during the study period.

Habitat niche modelling

Habitat suitability models were developed by means of Maximum Entropy modelling approach (Maxent; Phillips et al. 2006; Elith et al. 2011). Maximum entropy is a presence-only generative modelling approach that models species distribution directly by estimating the density of environmental covariates conditioned to only species' presence (Elith et al. 2011). Three different models were performed, one for each species and breeding stage, except for Cory's shearwater during chick-rearing stage since we only have GPS-tracking data from one individual. We used the raw foraging locations (i.e. those locations that overlap with the 50 % foraging kernels, see above in section GPS deployment and data processing) for model construction. To minimize the influence of any particular individual on the population-wide model, we randomly selected an equal number of locations for each bird (i.e. the minimum number of foraging locations registered for an individual, $n = 33$) to be included in models. Maxent does not require absence data point for the modelled distribution; instead Maxent uses pseudoabsences generated automatically by the program (10,000 background samples). Pseudoabsences are randomly drawn within the spatial extent of the environmental data (i.e. the area encompassed by a radius of 514 km around the colony, see methods) (Phillips et al. 2006). Before modelling, all six predictor variables for each breeding stage (SST, BAT, CHL, PCHL, COLONY and FISHERY) were checked for collinearity by calculating all pairwise Spearman's rank correlation coefficients. When pairs of predictor variables were strongly correlated ($|r_s| > 0.6$), we excluded one of the redundant variables, in order to obtain a set of proximate rather than exhaustive and correlated variables (Barry and Elith 2006). As a result, PCHL was excluded from the four models to avoid collinearity with CHL, and in order to preserve environmental predictors with a temporal correspondence with localities of the two breeding stages.

Models were constructed with the interface of the standalone Maxent program v. 3.3.3 k (www.cs.princeton.edu/~schapire/maxent/; default parameters were used). Model performance was assessed by randomly dividing the species occurrence data into training (70 %) and tests (30 %) datasets by using the option "random test percentage" in Maxent program. A given model was calibrated on the training data and evaluated on the test data using the area under the receiver operating characteristics curve (AUC) as a threshold-independent assessment measure. To reduce uncertainty caused by sampling artefacts (generated during the random resampling of presence occurrence localities), we conducted 15 replicate models for each of the four datasets. We evaluated the contribution of the environmental variables to the Maxent model based on a jackknife procedure. For each species in each stage, the differences between predictors relative contribution (in terms of regularized training gain) according to jackknife procedure were tested using analysis of variance (ANOVA). Tukey's multiple comparison tests was used to evaluate for differences between pairs of values.

Spatial autocorrelation in model residuals (i.e. observed occurrence minus probability of occurrence given by Maxent) was investigated by examining Moran's correlogram of residuals, which plots the Moran's Index coefficients against distances between localities. Twenty distance classes for the correlogram were defined by equal number of pairs. To test the significance of Moran's Index, each lag distance was evaluated separately after Bonferroni correction (here $P < 0.025$). Moran's Index and Moran's correlogram of residuals were built using SAM (Spatial Analysis in Macroecology v4.0) (Rangel et al. 2010). Similarity in distribution predictions between species and periods were

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tested by *I* statistics (Warren et al. 2008) using ENM Tools 1.3, a modified Hellinger distance by computing the differences between those predictions, cell by cell. *I* statistical values range from 0, indicating that the two predictions are completely different, to 1, suggesting that they are equal. Following Monk et al. (2012), we consider *I* statistics values >0.8 to be indicative of high degree of spatial distribution overlap, values between 0.7 and 0.8 to indicate moderate overlap and values <0.7 to indicate low similarity.

Results

We recovered 28 GPS-devices during incubation and 9 during the chick-rearing period, accounting for a total of 97 foraging trips (84 complete trips and 13 incomplete trips) of 37 different individuals (Table 1). A total of thirteen devices recorded no data or were not retrieved during the fieldwork period. On average (mean and standard deviation), we recorded 2.1 ± 1.8 trips per individual on Scopoli's shearwater during incubation ($n = 34$ trips in total) and 4.6 ± 2.2 trips per individual during chick-rearing ($n = 26$ trips in total). The average trip number recorded in Cory's shearwater during incubation was 2.6 ± 2.2 ($n = 36$ trips in total), and only one trip was recorded during chick-rearing period. Foraging areas of both species were mainly distributed along the coast (92 % of foraging areas were in shelf areas with a bathymetry less than 200 m depth) and essentially confined within 2°–4° W westward of the colony, with an important overlap during incubation stage (Fig. 3a–d). However, during incubation, some individuals of both species reached farther foraging areas located in the Atlantic (one Scopoli's shearwater and two Cory's shearwaters) and Algerian Mediterranean waters (four Scopoli's shearwaters) (Fig. 3a, b). Cory's shearwater rarely foraged eastward of the colony (only one individual in each period), though Scopoli's shearwater did it more often (eight individuals in incubation and seven in chick-rearing stage). One Cory's shearwater explored exceptionally distant zones during the incubation period, reaching the coast of Mauritania in the Atlantic (21.5°N latitude), but foraging areas were identified only up to 33°N as the trip was incomplete because the battery exhausted during the return journey to the breeding colony (Supplementary material; Fig. S2).

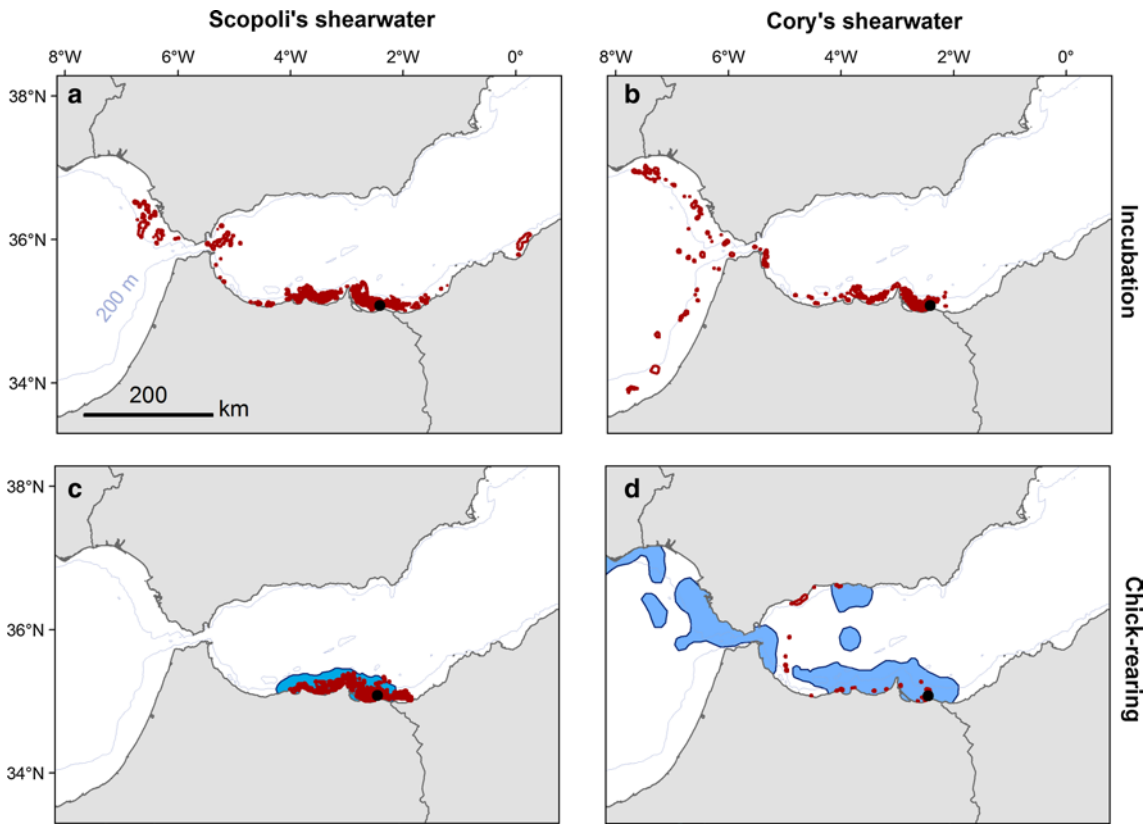


Fig. 3 Main foraging areas (*red colour*, 50 % individual fixed kernel density) of Scopoli's (**a**, **c**) and Cory's (**b**, **d**) shearwaters tracked with GPS during incubation (**a**, **b**) and chick-rearing (**c**, **d**) periods. The main foraging areas described in Navarro et al. (2009a) during chick-rearing in 2007 are represented in *blue colour*. Breeding location (Chafarinas Archipelago) is indicated with a *black dot*. *Grey line* denotes isobaths 200 m

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Foraging behaviour

No statistical differences in foraging trip duration, trip distance and average speed were found between species, sexes and breeding periods (in the case of Scopoli's shearwaters) (all $p > 0.05$, Table 1). Although only one individual was recovered for Cory's shearwater during chick-rearing stage, it is remarkable the greater trip distance covered for this tracked individual in comparison with the trip distance recorded during incubation. Foraging area covered during foraging trips and the foraging range did not differ between species, sexes and breeding periods (in the case of Scopoli's shearwater) (linear mixed models, $P > 0.05$ in all cases). The proportion of distance covered within foraging areas (50 % fixed kernel density) with respect to the total distance covered in a single trip was similar between species and between breeding stages in Scopoli's shearwater (Table 1). Only the proportion of time spent in foraging areas was significantly higher in Scopoli's shearwater, once removed the non-significant effect of sex and breeding stage (linear mixed model, $F_{(1,84)} = 4.23$, $P = 0.04$).

Persistence productive marine areas

We found several recurrent, highly productive marine areas that occurred consistently in the coastal upwellings in the western sector of the Mediterranean basin, strongly influenced by the circulation regimes of the Alboran Sea (Fig. 2e, f). The anticyclonic gyre in Alboran Sea (Fig. 2f) determines a strong gradient of productivity areas at the edges, at the expense of nutrient-poor waters of the centre of the gyre. The heavily exploited foraging areas along the coastal shelf at the west of the study area showed consistently high values of chlorophyll-*a*; greater than 0.66 mg m^{-3} in spring and 0.48 mg m^{-3} in summer between 2002 and 2012 (Fig. 2e, f).

Habitat niche modelling

Habitat niche models for Scopoli's shearwater during incubation and chick-rearing period and for Cory's shearwater during incubation period showed good ability to predict the observed foraging distributions (averaged values of AUC for all models >0.9). Habitat selection patterns were highly similar for both species and periods of the breeding season in Scopoli's shearwater ($I > 0.7$ for comparisons of all modelled distributions). Particularly, higher similarities were found between species in the incubation period ($I = 0.92$). Overall, environmental variables with the highest univariate contributions to species distribution were BAT and COLONY for both species and periods of the breeding cycle (Fig. 4). These variables also reduced the gain the most when they are omitted. Probability of occurrence of both the Cory's and Scopoli's shearwaters increased in the shallowest waters (lower values of bathymetry) closest to the colony. However, distance to the colony was significantly more important for the Scopoli's shearwater, particularly during the chick-rearing period (Fig. 4c). SST contributed only between 0.46 and 5.43 % to these models, with some differences between species and periods. CHL contributed between 0.24 and 0.44 %. The explanatory power of FISHERY range between 7.97 and 22.60 % and was significantly more important in the incubation period (Fig. 4a, b), when the species used areas with higher values of FISHERY, particularly for the Cory's shearwater. We found little evidence for spatial auto-correlation in the model residuals ($P > 0.01$ for all distance classes), which suggests that an adequate set of predictors was used.

Stable isotopes values and dietary estimation

There was no significant effect of species and breeding period on $\delta^{13}C$ and $\delta^{15}N$ values of serum (MANOVA tests, Wilks' lambda = 0.73, $F_{(4,\ 52)} = 2.26$, $P = 0.08$, Table 1). Pelagic fish differed significantly from non-pelagic prey in both N and C isotopic values (Wilks' lambda = 0.27, $F_{(2,\ 160)} = 216.9$, $P < 0.001$). Pelagic fish: $\delta^{13}C = -18.9 \pm 0.4$ ‰; $\delta^{15}N = 10.1 \pm 0.85$ ‰. Non-pelagic prey: $\delta^{13}C = -17.4 \pm 0.4$ ‰; $\delta^{15}N = 11.4 \pm 1.1$ ‰. According to dietary estimates provided by isotopic mixing models, the diet of both species consisted mainly of pelagic fish (mean relative contribution ranged 88–97 %; Fig. 5), with a lesser contribution of non-pelagic prey (mean ranged 2–11 %; Fig. 5).

Discussion

In the present study, we investigated the foraging strategies of two closely related pelagic seabirds, the Cory's and the Scopoli's shearwaters, breeding in sympatry in the south western Mediterranean Sea. Overall, foraging trip parameters (trip duration, trip distance and average foraging speed) were similar between species and were consistent with those reported for Scopoli's shearwaters in central Mediterranean colonies of Italy and for Cory's shearwater in Atlantic colonies (Navarro and González-Solís 2009; Alonso et al. 2012; Cecere et al. 2012). The similar foraging behaviour found in the two species is probably explained by the proximity of the productive waters of the Alboran Basin to the breeding colony (Renault et al. 2012). However, Cory's and Scopoli's shearwaters significantly differed in the relative time spent inside foraging areas, which was higher for Scopoli's suggesting potential differences in efficiency in the exploitation of resources between the two species.

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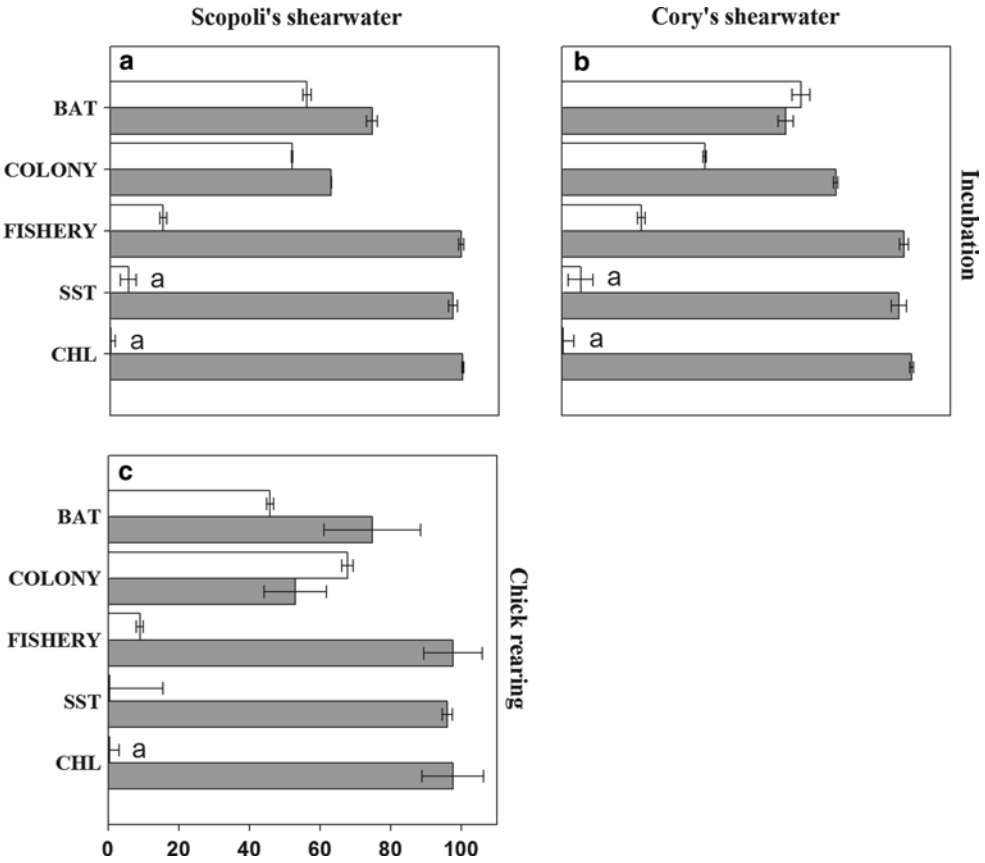


Fig. 4 *Bars* indicate average and 95 % confidence intervals over replicate runs for the importance of each habitat variable as estimated by the Jackknife test. The *white bar* indicates the explanatory power (in terms of regularized training gain) of the model when the environmental variable is used in isolation, and the *grey bar* indicates the explanatory power of the model when the single environmental variable is omitted from a model containing all the other environmental variables. The indexes are calculated so that training gain for the global model (i.e. the model including all the environmental variables) averages 100. Groups with "a" letter are not significantly different (Tukey's multiple comparison, $p < 0.05$)

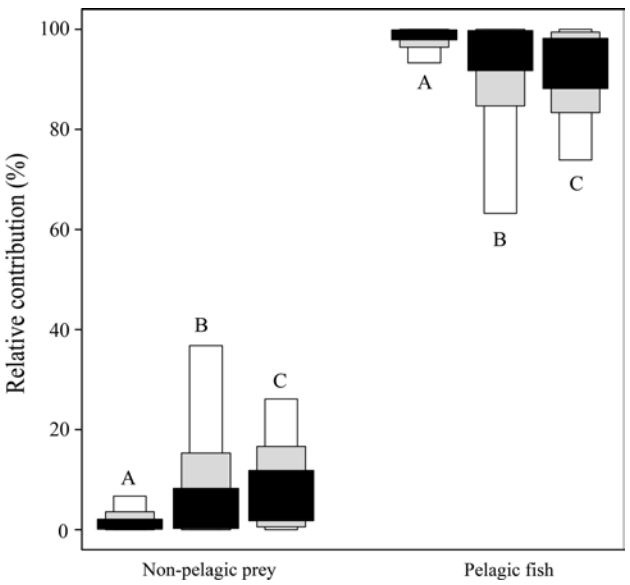


Fig. 5 Results of SIAR (95, 75 and 50 % Bayesian credibility intervals) showing estimated contribution of non-pelagic prey and pelagic fish in the diet of Scopoli's shearwaters during incubation (a), Cory's shearwaters during incubation (b) and Scopoli's shearwaters during chick-rearing period (c)

Habitat modelling also revealed that similar factors influenced the foraging habitat used for both species. Scopoli's and Cory's shearwaters selected the shallowest waters as foraging areas that were also the closest to the breeding places, which is in accordance with previously published data (Navarro and González-Solís 2009; Paiva et al. 2010b; Cecere et al. 2012). The selection of shallow waters for foraging was related to the higher availability of food resources in such areas (Louzao et al. 2012). Accordingly, the use of the areas closest to the colony may be related to the energy and time restrictions posed by the central-place foraging behaviour (Weimerskirch et al. 2005). The repercussions of these constraints become particularly important during the chick-rearing period for Scopoli's shearwater, when adults need to visit more frequently the nest to feed their offspring and attend increased food demands (Shaffer et al. 2006; Fauchald 2009).

Cory's shearwaters followed a different foraging strategy than Scopoli's shearwater during the chick-rearing period (Navarro et al. 2009b): they exploit more productive areas further away from the breeding colony. Although based on only one individual, our results seem to support this pattern: the single bird tracked during this period exploited a

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different foraging area than Scopoli's shearwaters further away from the colony. Cory's shearwaters, similar to other pelagic seabirds, may learn where and when their pelagic prey are distributed within their foraging range and return consistently to specific feeding areas (Weimerskirch 2007; Navarro and González-Solís 2009). In fact, Cory's shearwaters individuals breeding in Chafarinas have arrived in the Mediterranean Sea from the nearby Atlantic colonies (Berlengas and Selvagens Islands), where they probably foraged in Atlantic waters. Thus, it could be possible that, after moving to the Chafarinas Islands, they have remained faithful to their previous foraging area (Navarro et al. 2009b).

At regional scales, the foraging distribution of the two species might be the reflection of spatiotemporal patterns in the distribution of exploited trophic resources, which, in turn, may respond to several physical, biological, and anthropogenic features. Foraging areas matched with historically, highly predictable productive areas (persistent chlorophyll-*a* areas; Fig. 3) close to the south of Spain and the Mediterranean Moroccan coastal zones. Shelf waters western to 3ºW, mainly used as foraging areas by Scopoli's and Cory's shearwaters, appear as key marine areas to these predators, more productive than those areas located eastern from the colony. This situation is more apparent in persistent productive zones measured during the summer time. However, the Algerian waters, west from the colony, are also commonly exploited by other procellariiform species, such as the Balearic shearwaters *Puffinus mauretanicus* (Louzao et al. 2012). The proximity of the Algerian population of Scopoli's shearwaters, breeding in Habibas islands (300–450 pairs), 130 km east from Chafarinas Archipelago (Anselme and Durand 2012), with a substantial Algerian fishery activity may help explain the avoidance of Algerian waters by the shearwaters breeding in Chafarinas Archipelago.

Fisheries might also provide local enhancement of prey availability for seabirds by providing discards, which represent highly abundant and predictable food resources (Bugoni et al. 2009; Bartumeus et al. 2010; Cama et al. 2012). In our models, fishing activity had a relatively high explanatory power for foraging distribution of the two species during the incubation period. During incubation, both species performed foraging trips to the Atlantic and Algerian waters that sustain a high fishing activity. However, it is important to note that the FISHERY factor also showed spatial correlation with other environmental variables considered in our study (as indicated by the low reduction in model performance when this variable was omitted from models), which did not allow us to separate its independent contribution to species distribution.

Regarding the diet, isotopic mixing models indicated that no difference was found, at least in the main groups of prey consumed for both species during the incubation period and between the incubation and chick-rearing periods in the case of the Scopoli's shearwater. In particular, our results indicated that both species mainly consumed pelagic fish during the breeding period, whereas the importance of non-pelagic prey (benthic fish and squid) was very low, as has been reported in Atlantic colonies (Paiva et al. 2010a; Xavier et al. 2011; Alonso et al. 2012).

In conclusion, our study illustrates the similar feeding strategies and overlapping foraging niches of two closely related pelagic seabird species breeding in sympatry. We characterized environmental and anthropogenic factors driving the distribution of these birds at sea and highlighted the foraging core areas of both species throughout the incubation and chick-rearing periods. During incubation period, both species showed similar foraging strategies, with a preference for foraging areas located on the shelf waters close to the breeding colony. During the chick-rearing period when energy demand is very high, Scopoli's shearwater reduced their foraging areas, while Cory's shearwaters seemed to keep it broad (although more data are needed to confirm this). In addition, both species showed no differences in dietary preferences, feeding almost exclusively on pelagic prey. As niche differentiation is expected to be greater in restricted resource conditions, our results suggest that waters surrounding Chafarinas Archipelago hold prey availability high enough to support the feeding requirements of both species, at least during incubation stage.

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References

Alonso H, Granadeiro JP, Paiva VH, Dias AS, Ramos JA, Catry P (2012) Parent–offspring dietary segregation of Cory's shearwaters breeding in contrasting environments. Mar Biol 159:1197–1207

Anselme L, Durand J-P (2012) The Cory's Shearwater *Calonectris diomedea diomedea*, updated state of knowledge and conservation of the nesting populations of the small Mediterranean islands. Initiative PIM: 23

Arcos JM, Bécares J, Villero D, Brotons L, Rodríguez B, Ruiz A (2012) Assessing the location and stability of foraging hotspots

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for pelagic seabirds: an approach to identify marine important bird areas (IBAs) in Spain. Biol Conserv 156:30–42

Arin L, Anxelu X, Morán G, Estrada M (2002) Phytoplankton size distribution and growth rates in the Alboran Sea (SE Mediterranean): short term variability related to mesoscale hydrodynamics. J Plankton Res 24:1019–1033

Barry S, Elith J (2006) Error and uncertainty in habitat models. J Appl Ecol 43:413–423

Bartumeus F, Giuggioli L, Louzao M, Bretagnolle V, Oro D, Levin SA (2010) Fishery discards impact on seabird movement patterns at regional scales. Curr Biol 20:215–222

Beckers JM, Brasseur P, Nihoul JCJ (1997) Circulation of the western Mediterranean: from global to regional scales. Deep Sea Res Pt II:44:531–549

Bertrand S, Bertrand A, Guevara-Carrasco R, Gerlotto F (2007) Scale-invariant movements of fishermen: the same foraging strategy as natural predators. Ecol Appl 17:331–337

Bost C-A, Cotté C, Bailleul F, Cherel Y, Charrassin J-B, Guinet C, Ainley DG, Weimerskirch H (2009) The importance of oceanographic fronts to marine birds and mammals of the southern oceans. J Marine Syst 78:363–376

Bugoni L, D'Alba L, Furness RW (2009) Marine habitat use of wintering spectacled petrels P*rocellaria conspicillata*, and overlap with longline fishery. Mar Ecol Prog Ser 374:273–285

Cama A, Abellana R, Christel I, Ferrer X, Vieites DR (2012) Living on predictability: modelling the density distribution of efficient foraging seabirds. Ecography 35:912–921

Carvalho AC (2010) Estatísticas da Pesca 2010. In: Aquicultura DGdPe (ed). Instituto Nacional de Estatística, Lisboa

Caut S, Angulo E, Courchamp F (2009) Variation in discrimination factors (Δ^{15}N and Δ^{13}C): the effect of diet isotopic values and applications for diet reconstruction. J Appl Ecol 46:443–453

Cecere J, Catoni C, Maggini I, Imperio S, Gaibani G (2012) Movement patterns and habitat use during incubation and chick-rearing of Cory's shearwaters (*Calonectris diomedea diomedea*) (Aves: Vertebrata) from Central Mediterranean: influence of seascape and breeding stage. Ital J Zool 80:82–89

Dalerum F, Angerbjorn A (2005) Resolving temporal variation in vertebrate diets using naturally occurring stable isotopes. Oecologia 144:647–658

Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ (2011) A statistical explanation of MaxEnt for ecologists. Divers Distrib 17:43–57

Fauchald P (2009) Spatial interaction between seabirds and prey: review and synthesis. Mar Ecol Prog Ser 391:139–151

Galisteo A, González F, Naranjo S, Abreu L, Losa MT, Alonso C, Cobo R, Espinosa D (2010) Producción pesquera andaluza. Año 2010. In: Pesca CdAy (ed). Junta de Andalucía, pp 123

Genovart M, Sanz-Aguilar A, Fernández-Chacón A, Igual JM, Pradel R, Forero MG, Oro D (2012) Contrasting effects of climatic variability on the demography of a trans-equatorial migratory seabird. J Anim Ecol 82:121–130

Genovart M, Thibault J-C, Igual JM, Del Mar Bauzà-Ribot M, Rabouam C, Bretagnolle V (2013) Population structure and dispersal patterns within and between Atlantic and Mediterranean populations of a large-range pelagic seabird. PLoS ONE 8:e70711

Gómez-Díaz E, González-Solís J, Peinado M, Page RDM (2006) Phylogeography of the *Calonectris* shearwaters using molecular and morphometric data. Mol Phylogenet Evol 41:322–332

Hanski I (1998) Metapopulation dynamics. Nature 396:41–49

Hobson KA, Clark RG (1992) Assessing avian diets using stable isotopes 1. Turnover of ^{13}C in tissues. Condor 94:181–188

Huertas I, Ríos AF, García-Lafuente J, Navarro G, Makaoui A, Sánchez-Román A, Rodriguez-Galvez S, Orbi A, Ruíz J, Pérez FF (2012) Atlantic forcing of the Mediterranean oligotrophy. Global Biogeochem Cy 26:GB2022

Hutchinson GE (1959) Homage to Santa Rosalia or why are there so many kinds of animals? Am Nat 93:145–159

Hyrenbach KD, Fernández P, Anderson DJ (2002) Oceanographic habitats of two sympatric North Pacific albatrosses during the breeding season. Mar Ecol Prog Ser 233:283–301

Igual J, Forero M, Tavecchia G, González-Solis J, Martínez-Abraín A, Hobson K, Ruiz X, Oro D (2005) Short-term effects of data-loggers on Cory's shearwater (*Calonectris diomedea*). Mar Biol 146:619–624

Igual JM, Tavecchia G, Jenouvrier S, Forero MG, Oro D (2009) Buying years to extinction: is compensatory mitigation for marine bycatch a sufficient conservation measure for long-lived seabirds? PLoS ONE 4:e4826

Logan JM, Jardine TD, Miller TJ, Bunn SE, Cunjak RA (2008) Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and modelling methods. J Anim Ecol 77:838–846

Louzao M, Delord K, Garcia D, Boue A, Weimerskirch H (2012) Protecting persistent dynamic oceanographic features: transboundary conservation efforts are needed for the critically endangered balearic shearwater. PLoS ONE 7:e35728

Martinez-Abrain A, Sanchez A, Oro D (2002) Atlantic Cory's Shearwaters breeding in a colony of Mediterranean Cory's Shearwaters. Waterbirds 25:221–224

Monk J, Ierodiaconou D, Harvey E, Rattray A, Versace VL (2012) Are we predicting the actual or apparent distribution of temperate marine fishes? PLoS ONE 7:e34558

Navarro J, González-Solís J (2009) Environmental determinants of foraging strategies in Cory's shearwaters *Calonectris diomedea*. Mar Ecol Prog Ser 378:259–267

Navarro J, Louzao M, Igual JM, Oro D, Delgado A, Arcos JM, Genovart M, Hobson KA, Forero MG (2009a) Seasonal changes in the diet of a critically endangered seabird and the importance of trawling discards. Mar Biol 156:2571–2578

Navarro J, Forero MG, González-Solís J, Igual JM, Bécares J, Hobson KA (2009b) Foraging segregation between two closely related shearwaters breeding in sympatry. Biology Lett 5:545–548

Navarro J, Votier SC, Aguzzi J, Chiessa JJ, Forero MG, Phillips RA (2013) Ecological segregation in space, time and trophic niche of sympatric planktivorous petrels. PLoS ONE 8:e622897

ONP (2011) La pêche côtière et artisanale au Maroc. Rapport Statistiques 2011. ONP (Office National des Pêches) 22

Paiva VH, Xavier J, Geraldes P, Ramirez I, Garthe S, Ramos JA (2010a) Foraging ecology of Cory's shearwaters in different oceanic environments of the North Atlantic. Mar Ecol Prog Ser 410:257–268

Paiva VH, Geraldes P, Ramírez I, Meirinho A, Garthe S, Ramos JA (2010b) Oceanographic characteristics of areas used by Cory's shearwaters during short and long foraging trips in the North Atlantic. Mar Biol 157:1385–1399

Parnell A, Inger R, Bearhop S, Jackson AL (2008) Stable isotope analysis in R (SIAR). http://cran.r-project.org/web/packages/siar/. Accessed 19 Sept 2012

Passos C, Navarro J, Giudici A, González-Solís J (2010) Effects of an extra mass on the pelagic behaviour of a seabird. Auk 127:100–107

Phillips RA, Xavier JC, Croxall JP (2003) Effects of satellite transmitters on albatrosses and petrels. Auk 120:1082–1090

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Model 190:231–259

Pianka ER (2002) Evolutionary ecology. Addison-Wesley, San Francisco

Rangel TF, Alexandre J, Diniz-Filho F, Bini LM (2010) SAM: a comprehensive application for spatial analysis in macroecology. Ecography 33:46–50

Author's personal copy

Renault L, Oguz T, Pascual A, Vizoso G, Tintoré J (2012) Surface circulation in the Alborán Sea (western Mediterranean) inferred from remotely sensed data. J Geophys Res 117:C08009

Roberts JJ, Best BD, Dunn DC, Treml EA, Halpin PN (2010) Marine geospatial ecology tools: an integrated framework for ecological geoprocessing with ArcGIS, Python, R, MATLAB, and C++. Environ Modell Softw 25:1197–1207

Ropert-Coudert Y, Wilson RP (2005) Trends and perspectives in animal-attached remote sensing. Front Ecol Environ 3:437–444

Sahi M, Bouaicha M (2003) La pêche artisanale en Algérie. In: Halieutiques MdlPedR (ed). Document FAO Copemed, Alger, 23

Sangster G, Collinson JM, Crochet PA, Knox AG, Parkin DT, Votier SC (2012) Taxonomic recommendations for British birds: eighth report. Ibis 154:874–883

Seaman DE, Powell RA (1996) An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075–2085

Shaffer SA, Tremblay Y, Weimerskirch H, Scott D, Thompson DR, Sagar PM, Moller H, Taylor GA, Foley DG, Block BA (2006) Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. Proc Natl Acad Sci 103:12799–12802

Sigler MF, Kuletz KJ, Ressler PH, Friday NA, Wilson CD, Zerbini AN (2012) Marine predators and persistent prey in the southeast Bering Sea. Deep-Sea Research Part Ii-Topical Studies in Oceanography 65–70:292–303

Thibault JC, Bretagnolle V, Rabouam C (1997) Cory's Shearwater *Calonectris diomedea*. Birds of the Western Palearctic Update 12:75–98

Vandenabeele SP, Shepard EL, Grogan A, Wilson RP (2012) When three per cent may not be three per cent; device-equipped seabirds experience variable flight constraints. Mar Biol 159:1–14

Villard P, Bonenfant C, Bretagnolle V (2011) Effects of satellite transmitters fitted to breeding Cory's shearwaters. J Wildlife Manage 75:709–714

Wakefield ED, Phillips RA, Matthiopoulos J (2009) Quantifying habitat use and preferences of pelagic seabirds using individual movement data: a review. Mar Ecol Prog Ser 391:165–182

Warren DL, Glor RE, Turelli M (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62:2868–2883

Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? Deep Sea Res II 54:211–223

Weimerskirch H, Jouventin P, Stahl JC (1986) Comparative ecology of the six albatross species breeding on the Crozet Islands. Ibis 128:195–213

Weimerskirch H, Le Corre M, Jaquemet S, Marsac F (2005) Foraging strategy of a tropical seabird, the red-footed booby, in a dynamic marine environment. Mar Ecol Prog Ser 288:251–261

Weimerskirch H, Shaffer SA, Tremblay Y, Costa DP, Gadenne H, Kato A, Ropert-Coudert Y, Sato K, Aurioles D (2009) Species- and sex-specific differences in foraging behaviour and foraging zones in blue-footed and brown boobies in the Gulf of California. Mar Ecol Prog Ser 391:267–278

Wilson RP, Pütz K, Peters G, Culik BM, Scolaro JA, Charrassin JB, Ropert-Coudert Y (1997) Long-term attachment of transmitting and recording devices to penguins and others seabirds. Wildl Soc Bull 25:101–106

Xavier JC, Magalhaes MC, Mendonça AS, Antunes M, Carvalho N, Machete M, Santos RS, Paiva VH, Hamer KC (2011) Changes in diet of Cory's shearwaters *Calonectris diomedea* breeding in the Azores. Mar Ornithol 39:129–134