



Commercial fisheries, inter-colony competition and sea depth affect foraging location of breeding Scopoli's Shearwaters *Calonectris diomedea*

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The distribution of seabirds at sea is influenced by physical, ecological and anthropogenic factors such as sea depth, prey distribution, intra-specific competition and commercial fishing activities. We quantified the foraging habitat preferences of Scopoli's Shearwater *Calonectris diomedea* in the Mediterranean Sea. We analysed habitat preferences in relation to a suite of physical and ecological variables including sea depth, net primary production and distance to other colonies (as a proxy of intra-specific competition). Since the Mediterranean is heavily impacted by commercial fisheries, we also incorporated the distance to fishing harbours in our analyses as a proxy of the availability of discards which are a potential feeding source for Scopoli's Shearwater. Foraging birds preferred shallower waters and avoided areas close to other colonies, thereby reducing interactions with conspecifics. We also found that long-distance trips were undertaken to areas close to fishing harbours, suggesting that these represented particularly profitable locations to compensate for the greater travelling costs involved. No differences in foraging between the sexes were recorded. This study improves our understanding of the at-sea distribution and habitat preference of a seabird inhabiting the over-exploited Mediterranean Sea. Our results support growing evidence that seabirds exhibit complex relationships with commercial fishing activities, which must be considered when planning conservation programmes.

Keywords: colony, Cory's Shearwater, discard, fishery, GPS, habitat preference, harbour, seabirds.

Seabirds exploit a highly heterogeneous environment for food resources. Currents, stratifications, fronts and other physical processes produce a marked temporal and spatial heterogeneity in pelagic environments. Such heterogeneity affects primary production patterns and thus resource distribution and availability for upper trophic levels (Haury *et al.* 1978, Hunt *et al.* 1999). Patchy resource distribution can lead to a scale-dependent dispersion of marine predators (Pinaud &

Weimerskirch 2007). At large and medium scales, seabirds may be able to target profitable foraging areas such as shelf edges, frontal zones and upwellings when foraging away from their colony (Weimerskirch 2007). However, within these habitats, they normally use area-restricted search behaviours to seek prey (Kareiva & Odell 1987, Weimerskirch 2007, Paiva *et al.* 2010a).

Generally, studies of foraging area preferences by pelagic birds have focused on habitat features that are correlated with the distribution of prey species (for a review see Wakefield *et al.* 2009). These areas are of course exploited not only by

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seabirds but also by fishing fleets. Fisheries that catch pelagic fish are particularly widespread, and many of them process fish at sea, generating a large quantity of discards. Approximately 7.3 million tonnes of discards are returned to the sea annually by fisheries worldwide (Catchpol *et al.* 2006). Fish discards, including offal, undersized fish and non-target species, are a huge trophic resource that several species of seabirds such as gulls (Laridae), gannets (Sulidae) and shearwaters (Procellariidae) are able to exploit (Montevecchi 2002, Furness 2003, Grémillet *et al.* 2008a, Bartumeus *et al.* 2010). The availability of fishery discards can even strongly influence the demography and dispersal of seabirds (Oro *et al.* 2004).

Most seabirds exhibit colonial behaviour, which can result in depletions or disturbances of prey around the breeding sites, forcing birds to forage farther away from their breeding colony (Ashmole 1963, Furness & Birkhead 1984). Besides intra-colonial competition, the foraging distribution of seabirds is also generally influenced by the need to avoid competition with adjacent colonies, so birds from a colony may avoid foraging areas of conspecifics from other breeding sites (Wakefield *et al.* 2013). Theoretically, seabird colonies should be distributed in such a way as to minimize the overlap of foraging areas and consequently intra-specific competition (Cairns 1989). However, geomorphology may constrain an optimal distribution of colonies, as islands often occur in clusters (Forbes *et al.* 2000). In the case of colonies located on neighbouring sites, seabirds often show between-colony segregation of foraging areas in order to minimize the inter-colony competition (Grémillet *et al.* 2004, Wakefield *et al.* 2013).

The distribution of food resources may also force birds to forage far from the colony during the breeding season (Matthiopoulos 2003). Seabirds, and Procellariiformes in particular, have evolved adaptations to travel long distances to feed in more distant areas that are more profitable than those located closer to the colony (del Hoyo *et al.* 1992, Weimerskirch *et al.* 2000, Weimerskirch 2007). However, long foraging trips entail larger costs both due to increased energy consumption and, indirectly, due to the forced prolonged fasting of the partner attending the nest at the colony.

Furthermore, as well as physical, ecological and anthropogenic factors affecting the distribution of foraging seabirds, habitat use can differ between

the sexes even in seabird species in which morphological sexual dimorphism is small or absent. Sexual differences in diet and distribution can be related to different nutritional requirements of the two sexes during the breeding period, as has been shown in Audouin's Gull *Larus audouinii* (Navarro *et al.* 2010). In some cases, the sexual segregation of foraging areas and niche divergences can be mediated by differences in flight performance between the sexes, as has been suggested for Black-browed Albatross *Thalassarche melanophrys* and Grey-headed Albatross *Thalassarche chrysostroma*, two species with only slight sexual differences in body size (Phillips *et al.* 2004).

Although considerable progress has been made in understanding the extrinsic and intrinsic determinants of at-sea distributions of seabirds, much of the focus has been on a small number of species. However, it is not clear how representative these species are of the wider seabird community. Studies of closely related, less well studied species are therefore useful in testing this question. Cory's Shearwater *Calonectris borealis* has been the subject of several studies about at-sea distribution and habitat preference, which have shown that the species mainly forages in shallower waters (Paiva *et al.* 2010b) and in areas characterized by both high concentrations of chlorophyll *a* (Navarro & González-Solís 2009) and low sea-surface temperatures (Paiva *et al.* 2010c). It is well known that all these environmental characteristics increase the abundance of small pelagic fish schools (Agostini & Bakun 2002). Cory's Shearwaters can travel up to 1800 km from the colony (Magalhães *et al.* 2008) to reach profitable feeding areas (Navarro & González-Solís 2009, Paiva *et al.* 2010b). Here, we present an analysis of at-sea distribution and habitat preferences of the closely related Scopoli's Shearwater *Calonectris diomedea*, which has recently been separated taxonomically from Cory's Shearwater. We analysed, for the first time to our knowledge, the habitat selection of a seabird in the over-exploited Mediterranean Sea, and include both human-related and environmental factors. Besides primary productivity and sea depth, widely considered in studies on movement analysis of seabirds, we also analysed the potential influences of inter-colony competition and human fishery activity.

Like Cory's Shearwater, Scopoli's Shearwater can undertake long foraging trips (1–18 days; Cecere *et al.* 2013) during the breeding period,

particularly when the waters surrounding the colony are characterized by a lower quality (Cecere *et al.* 2014). The behavioural plasticity of the species is also supported by the evidence that Scopoli's Shearwaters can adopt different movement strategies in relation to different biological constraints. Accordingly, Focardi and Cecere (2014) have shown that the probability of undertaking movements with Lévy flight properties is higher for trips during chick provisioning, when shearwaters were forced to forage in suboptimal areas.

Our study had two aims. First, we investigated habitat preferences during incubation of Scopoli's Shearwaters breeding in the Mediterranean, and for the first time analysed foraging behaviour of birds breeding in two different seascapes: the Tunisian Plateau, characterized by lower primary production (Bosc *et al.* 2004) and marine canyons, and the shallower and flat Adriatic Sea. Investigating the foraging behaviour of birds inhabiting different seascapes allows us better to understand the ecology and the plasticity of the species and to assess whether particular extrinsic or intrinsic factors are important to breeding birds irrespective of the ecological context. We assessed whether the foraging distribution of Scopoli's Shearwaters was affected by environmental characteristics and human fishery activities by comparing habitat characteristics related to foraging locations of GPS-tagged birds with habitat availability. More specifically, our goal was to assess whether Scopoli's Shearwaters preferred to forage in areas characterized by a higher primary productivity (Grémillet *et al.* 2008b) and shallower waters, as is the case for Cory's Shearwaters (Paiva *et al.* 2010b). In addition, we predicted that Scopoli's Shearwaters avoided areas located within the foraging distance of other conspecific colonies (Wakefield *et al.* 2013) and that their foraging areas would be associated with areas of high concentrations of fishing vessels. Moreover, given the differences in size between the sexes of Scopoli's Shearwater, with males generally being slightly larger than females (Massa & Lo Valvo 1986), we expected a diversification in habitat preferences between the sexes.

The second aim of the study was to test the prediction that birds use long foraging trips to reach further and more profitable areas than those located near the colony. We thus analysed the habitat characteristics of actual foraging locations in relation to the distance from the breeding site.

METHODS

Study colonies

The study was carried out during the breeding seasons of 2008–2010 in two colonies in the Mediterranean: Linosa Island and Tremiti Archipelago, Italy (Fig. 1). Linosa, located in the Tunisian Plateau/Gulf of Sidra region (35°51'33"N, 12°51'34"E) between Sicily, Tunisia and Libya, hosts one of the biggest colonies of Scopoli's Shearwaters in the Mediterranean with an estimated 10 000 breeding pairs (Baccetti *et al.* 2009). The Tremiti Archipelago (42°08'19"N, 15°30'52"E) hosts approximately 400 pairs (Baccetti *et al.* 2009), making it one of the largest breeding colonies of the species in the Adriatic; all the fieldwork in this archipelago was carried out on the small island of Capraia. The tracking activity was conducted during incubation during June–July 2008 on Linosa and during June–July 2009 and June 2010 on Capraia.

Subjects, GPS devices and foraging locations

We located Shearwater nests by inspecting crevices and burrows. Once a nest was found, the adult bird was captured by hand. After ringing, a GPS logger was attached to the back feathers using Tesa® marine cloth tape (Tesa SE, Hamburg, Germany); for more details see Cecere *et al.* (2013). To check for the presence of the tagged bird in the nest without further handling, we coloured a part of its breast feathers with a non-toxic and odourless animal crayon. Birds never showed any sign of distress due to the colour marking. Furthermore, coloration faded away naturally within a few days of contact with seawater. After the departure of the focal bird for a foraging trip, we captured its partner and ringed it for a long-term monitoring programme. In addition, we coloured its breast feathers with a different colour from that used for the tagged bird in order to check its presence in the nest without further handling until the return of the focal bird. Total handling time was kept below 10 min, and birds were returned to their nests immediately after handling. We monitored all nests once a day. Once a bird with a GPS logger returned to the nest, we captured it again by hand and removed the logger by peeling away the tape from the feathers. Each tagged bird was

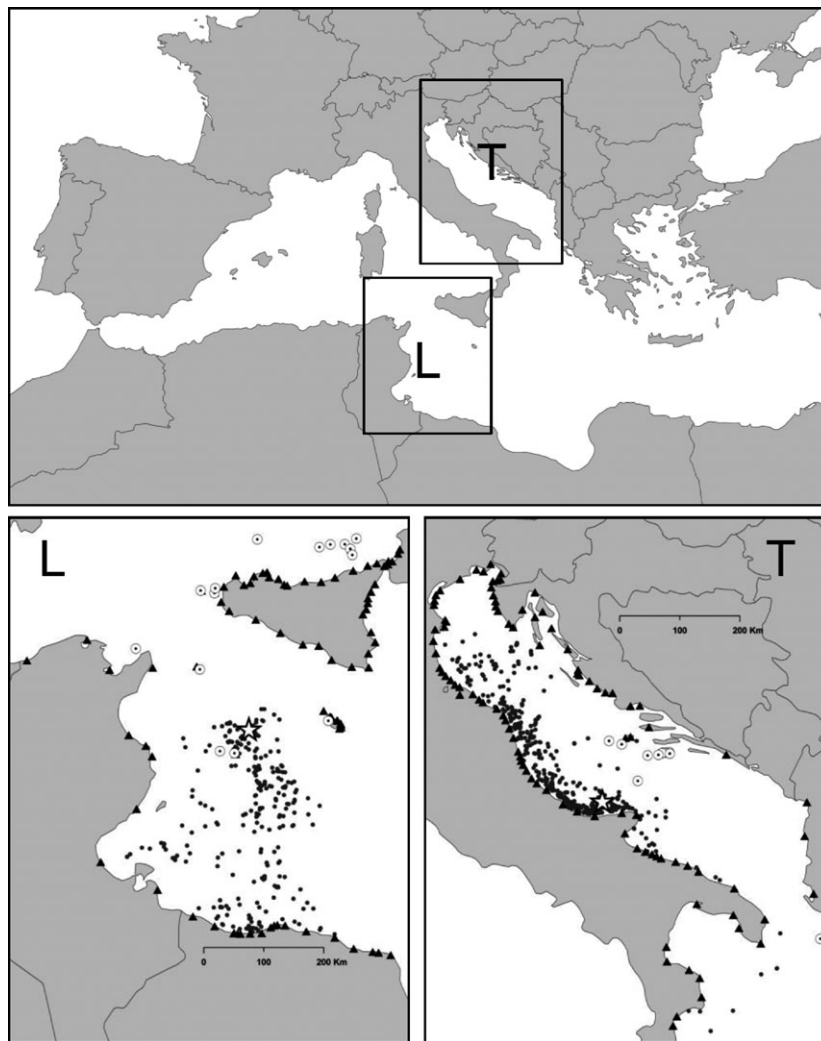


Figure 1. Foraging locations (grey dots) of Scopoli's Shearwater *Calonectris diomedea* breeding on Linosa (L) and the Tremiti Archipelago (T). Star = breeding colony; circles = other Scopoli's Shearwater colonies; triangles = fishing harbours.

sexed during handling by using its or its partner's sex-specific vocalization (Robb & Mullarney 2008).

Bird mass was taken at GPS logger deployment, and devices were chosen accordingly. We used three types of GPS devices: in 2008 on Linosa we used GPS loggers from Earth & Ocean Technologies (Kiel, Germany) weighing 19.4 g; in 2009 and 2010 we also deployed GPS loggers from Techno-smart (Guidonia, Italy) powered by two battery models: 500 and 250 mA weighing 11.9 and 9.8 g, respectively. The deployment of the lightest type of GPS allowed us to track birds too light for the other types of devices, despite having the drawback of a shorter battery life. The average

ratio between the weight of the heavier device type and the body mass of tagged birds was 3.04% (range 2.6–3.9%); that with the medium weight device was 2.1% (range 2–2.3%); and that with lighter type of device was 1.8% (range 1.7–1.9%). For all tagged birds, the ratio was lower than the threshold beyond which an extra mass could affect the movement behaviour of Cory's Shearwaters (Passos *et al.* 2010).

GPS loggers were configured to record the position and the instantaneous speed of the bird every 10 min. To investigate habitat preference, we first identified short landings on the sea surface as proxies of foraging events following Paiva *et al.* (2010a), who used this method to investigate the

foraging strategies of Cory's Shearwaters in the Atlantic Ocean. We first retrieved those fixes where flight speed was less than 9 km/h from all GPS data (Guilford *et al.* 2008). Among these fixes, we considered potential foraging positions to be those that lasted shorter than two consecutive fixes (i.e. 10 min). In this way we could exclude longer periods in the water due to resting or preening. To assess whether Scopoli's Shearwaters prefer particular environmental characteristics (see below for variable explanation) to forage, we compared actual foraging positions with 1000 control points at each colony. These were generated within the circular buffer centred on the colony with a radius equal to the maximum distance recorded by the individuals carrying GPS loggers. We consider this area to be representative of marine habitat available to individuals breeding at the colony. All land areas were removed from buffers. As breeding shearwaters are central-place foragers, foraging areas are not equally available with respect to the distance from the colony. Therefore, control points were located with the same distribution of distances from the colony as actual foraging locations (Matthiopoulos 2003, Aarts *et al.* 2008, Fig. S1). We used this approach to make the availability of habitats dependent upon both their spatial extent and their distance from the breeding site (Wakefield *et al.* 2009). Twenty-three control points of 1000 related to the Linosa colony and 81 related to Tremiti had missing primary production values (see below) and so were discarded from the analyses.

Anthropogenic and environmental variables

We selected four variables to characterize the environment at foraging and control locations: (1) sea depth and (2) net primary productivity, which both might be relevant for determining the availability of small pelagic fish (Agostini & Bakun 2002), the main prey of Scopoli's Shearwaters (Sarà 1993); (3) an index of proximity to other Scopoli's Shearwater colonies as a proxy of intra-specific competition (Wakefield *et al.* 2013); and (4) an index of proximity to fishing harbours as a proxy of proximity to discards which are exploited by shearwaters (Bartumeus *et al.* 2010). As vessels and discarding location behave like central-place foragers, with low speeds (typically 10–12 knots) and thus a relatively limited range, we considered

the density of boats discarding fish to be inversely proportional to the distance from harbours. Furthermore, because most Mediterranean boats fish in mixed grounds (Bellido *et al.* 2008), i.e. where target and non-target fish are mixed, it is necessary for fishing personnel carefully to check their catch before discarding the fish (European Commission 2011). Therefore, fish need to be boarded and are usually discarded at sea after each fishing operation, particularly between the last haul and the harbour (Dr Francesco Colloca, IAMC-CNR, Mazzara del Vallo, Italy, pers. comm.) where the boats are already converging. Thus, we would expect discard availability to increase with proximity to harbours.

Bathymetry, expressed in negative values, was obtained from the General Bathymetric Chart of the Oceans (GEBCO 08) of the British Oceanographic Data Centre (https://www.bodc.ac.uk/data/online_delivery/gebco/) as a 30 arc-second (approximately 1 km) grid. Net primary production data (standard Vertically Generalized Production Model (VGPM)) was downloaded from the Ocean Productivity site (<http://www.science.oregonstate.edu/ocean.productivity/index.php>) for a spatial resolution of 10 min (approximately 18 km). VGPM data are based on monthly MODIS-aqua r2009.1 input data including sea surface temperature, chlorophyll and photosynthetically active radiation values (Behrenfeld & Falkowski 1997). For each location, we extracted the primary productivity value of the month (Linosa: June and July 2008; Tremiti: June and July 2009 and June 2010) in which tracking was performed. We assigned a primary productivity value to each control point by randomly selecting a value from the different months in which tracking was performed in the same proportion as actual foraging locations (control points in Linosa buffer: 60.5% of control points with primary production values from June 2008, 39.5% July 2008; control points in Tremiti buffer: 13.6% June 2009, 21.1% July 2009, 65.3% June 2010).

We obtained the locations and sizes of Scopoli's Shearwater colonies of the Central Mediterranean from experts in Italy (Baccetti *et al.* 2009; database of LIPU BirdLife Italy), Malta (BirdLife Malta), Tunisia (Les Amis des Oiseaux), Greece (HOS Hellenic Ornithological Society) and Croatia (BIOM Association for Biological Research). We are therefore confident that we identified all important breeding colonies in the study regions.

We then calculated a distance index to other conspecific colonies (DC), similarly to the previous index:

$$DC = - \sum \frac{w_c}{d_c^2}$$

where d_c is the distance (km) of the foraging/control location from each colony weighted for the approximate size ($w_c = 10$ for colonies with 10–100 estimated pairs, $w_c = 100$ for colonies with 101–1000 estimated pairs, $w_c = 1000$ for colonies with >1000 estimated pairs). The lower the value of DC, the closer the foraging/control location to a high number of conspecific colonies and/or to large colonies.

The positions of fishing harbours and their capacity were retrieved from several sources (Table S2). For EU countries (Italy, Slovenia and Malta), we downloaded the data from the Community Fishing Fleet Register (http://ec.europa.eu/fisheries/index_en.htm) using the vessels active in 2009 as the search query (mean date of the study period). EU technical documents also provided information on main harbours in Croatia (Iborra Martín & Kekez 2009) and Montenegro (AA.VV. 2006), and data on fishing harbours in Albania were obtained from an FAO report (Albanian Fishery Policies Directorate 2006). Information from Libyan fishing harbours and fleets is described on the FAO website (http://www.fao.org/fishery/countrysector/FI-CP_LY/en). The Tunisian Ministry of Agriculture provided data and statistics on fisheries in its country (DGPA 2009).

The index of proximity to fishing harbours (DH) was calculated for each foraging and control location as:

$$DH = - \sum \frac{w_h}{d_h^2}$$

where d_h is the distance (km) of the foraging/control location from each fishing harbour (raised to the second power to account for the probability of encounter decreasing non-linearly with distance because of the relationship between distance and area) weighted for the corresponding fleet size (w_h , i.e. the number of fishing boats; we considered only harbours with a capacity of at least 15 fishing boats). As shearwaters, in general, do not fly over land, we also considered for the

Tremiti study site the additional circumnavigation distance of Apulia (i.e. in each distance calculation between foraging/control locations in the Adriatic Sea and harbours in the Ionian Sea), and for the Linosa study site, we considered the additional circumnavigation distance of Sicily or North Tunisia, when necessary, using a set of intermediate turning points placed along the coast to calculate distances between foraging/control locations and harbours. The lower the value of DH, the closer the foraging/control locations were to a high number of harbours or to harbours with a high capacity.

The extraction of raster values for each point was obtained using the Spatial Analyst Tools package for ARCGIS 9.2 (ESRI® Inc., Redlands, CA, USA), and all the distances were calculated using the ET GEOWIZARDS package (Spatial Techniques, www.ian-ko.com).

Habitat preference analysis

Analysis of habitat preference was performed using binary generalized linear mixed models (GLMMs) with individual birds fitted as random grouping factors. We adopted an information-theoretic approach, testing all linear combinations of variables, and then used Akaike's information criterion (AIC) to select the best performing model. Models with $\Delta AIC \leq 2$ were used to undertake model averaging with the corresponding Akaike weights (Burnham & Anderson 2002). To avoid problems with parameter estimations, we first checked for pair-wise correlations between variables (Zuur *et al.* 2007).

Environmental variables (sea depth, net primary productivity, DC and DH) were entered in the models as both linear and quadratic terms to account for possible non-linear relations, e.g. preference (or avoidance) by birds of intermediate values of the variables (Myers 1990). Gender and study area were included both as fixed factors and as interaction terms with the other factors.

As the foraging locations of each bird were likely to be autocorrelated, we followed the approach of Kaczensky *et al.* (2008) and assigned a weight lower than 1 ($0 < w_i < 1$) to locations separated by less than 12 h (720 min) from the previous one. The relationship between distance covered and time interval (less than 720 min) was fitted by a power function whose exponents were estimated to be 0.6181 for Linosa and 0.6322 for

Tremi. Weights were then assigned proportional to the time interval according to the following formula: $w_i = \Delta t^{ce}/720^{ce}$, where Δt is the interval in minutes since the last foraging location and ce is the exponent specific for the colony. Locations separated by more than 12 h were considered independent ($w_i = 1$), as covered distance was not correlated to the time interval between successive locations over this time interval in any of the colonies.

Differences in preference for foraging locations between the two study years (2009 and 2010) of birds from Tremi were investigated with a Poisson GLMM for each environmental variable, fitting year as a fixed factor, individual identity as a random grouping factor, and weights for foraging locations as described before. The bird-logger mass ratio did not significantly differ between the two study years in Tremi birds (Wilcoxon test: $W = 99.5$, $n = 26$, $P = 0.39$), so we excluded an effect of bird-logger mass ratio on possible differences in foraging behaviour.

GLMMs were performed in R ver. 2.15.2 (R Core Team 2012) with the *lme4* package (Bates et al. 2012). We used a binomial error distribution and a logit model link function. The *MuMIn* package (Barton 2012) was used for model averaging.

Foraging locations and distance from the colony

Long foraging trips imply higher costs for the breeding pair, and as a trade-off they are predicted to be used to exploit more profitable areas. To assess whether longer foraging excursions were used to feed in more distant locations or to spend more time around the colony, we first assessed whether the distance of the furthest foraging location of each bird from the colony was related to trip duration and whether this differed between colonies and sexes, using a generalized linear model (GLM). We also considered the first-order interactions between trip duration and the other two explanatory variables. Then, to identify the environmental variables that predicted travelling distance, we used GLMMs with the distance of each foraging location from the colony as the dependent variable and environmental characteristics, sex and study area as fixed effects. As before, bird identity was used as a random grouping factor. For temporal autocorrelation of locations and

model selection, we followed the approach used in the habitat preference analysis.

GLMMs were performed in R ver. 2.15.2 (R Core Team 2012) with the *lme4* package (Bates et al. 2012). We used a Gaussian error distribution, and P -values for the fixed effects were computed using the *car* package (Fox & Weisberg 2011). No model averaging was undertaken in this case, as there was a single preferred model.

RESULTS

On Linosa, we equipped 19 birds with GPS loggers, of which four birds lost the device and one bird returned without data. On Tremi Archipelago, we equipped 16 birds in 2009 (five came back without data) and 22 birds in 2010 (one device lost and six without data). In total, 40 birds were tracked in the two colonies (Linosa: 5 females, 8 males, 1 unsexed; Tremi: 13 females, 11 males, 2 unsexed) providing a total of 11 957 fixes for Linosa including 266 foraging locations, and 18 416 fixes for Tremi including 456 foraging locations (Fig. 1). Unsexed birds were excluded from analyses that included sex as a fixed factor. Weighting of locations to account for temporal autocorrelation reduced the effective sample size to $n = 149$ (148 without the unsexed bird) for Linosa and $n = 244$ (228 without unsexed birds) for Tremi.

Habitat preference analysis

None of the pairs of anthropogenic and environmental variables was highly correlated ($|r| \leq 0.52$), either considering the whole dataset or considering data separately from the two study areas (Table S1).

The analysis of the habitat preference of sexed birds performed using GLMM identified six models with $\Delta AIC < 2$ (Table 1). The averaged model (Table 2) showed that, compared with availability, birds from both colonies preferred areas further from other conspecific colonies characterized by the lowest values of primary productivity. The positive coefficient of sea depth represents a preference of birds for shallower waters (Table 2), as the variable is expressed as negative values. Moreover, birds from Tremi preferred shallower waters than birds from Linosa. Foraging preferences of tagged birds did not differ between the sexes.

Table 1. Selected logistic GLMMs (models within $\Delta AIC \leq 2$; all other models had $\Delta AIC > 3$ from the best model) performed between actual foraging locations (Use) and control points (Availability). AIC and Akaike weights (W) are also shown for each model. Foraging locations were weighted to account for temporal autocorrelation. Variables used for the analysis are: Sea depth (m); InPP: log-transformed net primary productivity (mg C/m²/day); DH: index of distance to fishing harbours (km⁻²); DC: index of distance to conspecific colonies (km⁻²); Area: study area of Linosa and Tremiti; Sex. The last two factors were also included as interaction terms (:) with the other factors. Individual identity (1 | RING) was entered as a random effect.

Model no.	Model (Use/Availability)	Fixed factors (n)	AIC	W
1	Area + Depth + DC + InPP + Area:Depth + (1 RING)	5	1529.3	0.30
2	Area + Sex + Depth + DC + InPP + Area:Depth + (1 RING)	6	1530.5	0.16
3	Area + Depth + Depth ² + DC + InPP + Area:Depth + (1 RING)	6	1530.6	0.15
4	Area + Depth + DC + InPP + DH + Area:Depth + (1 RING)	6	1530.7	0.15
5	Area + Depth + Depth ² + DC + InPP + Area:Depth + Area:Depth ² + Area:InPP + (1 RING)	9	1531.0	0.13
6	Area + Sex + Depth + Depth ² + DC + InPP + Area:Depth + Area:Depth ² + Area:InPP + Sex:Depth + (1 RING)	10	1531.0	0.12

Table 2. Model averaging performed between actual foraging locations (Use) and control points (Availability). The averaged parameter estimates of all variables included in the models with $\Delta AIC \leq 2$ (Table 1) are weighted with the corresponding Akaike weight (see Table 1). Z-values and probability values (P) refer to Z-tests of the difference of each parameter estimate from zero. Foraging locations were weighted to account for temporal autocorrelation. Variables used for the analysis are: Depth (m); DC: index of distance to conspecific colonies (km⁻²); DH: index of distance to fishing harbours (km⁻²); InPP: log-transformed net primary production (mg C/m²/day); Area: study area of Linosa and Tremiti; Sex. The last two factors were also included as interaction terms (:) with the other factors. Individual identity (1 | RING) was entered as a random effect.

	Fixed effects		
	Coeff. estimate $\pm$ se	Z	P
(Intercept)	2.11 $\pm$ 1.01	2.07	0.04
Depth	2.73 $\times 10^{-3} \pm 9.66 \times 10^{-4}$	2.82	<0.01
Depth ²	-6.68 $\times 10^{-7} \pm 1.36 \times 10^{-6}$	0.49	0.62
DC	6.22 $\times 10^3 \pm 1.29 \times 10^3$	4.83	<0.0001
DH	-45.21 $\pm$ 83.02	0.54	0.59
InPP	-0.42 $\pm$ 0.17	2.48	0.01
Area (Tremiti)	1.59 $\pm$ 1.41	1.13	0.26
Sex (female)	0.18 $\pm$ 0.17	1.08	0.28
Area(Tremiti):Depth	2.29 $\times 10^{-2} \pm 1.06 \times 10^{-2}$	2.16	0.03
Area(Tremiti):Depth ²	-1.35 $\times 10^{-4} \pm 6.36 \times 10^{-5}$	2.13	0.03
Area(Tremiti):InPP	0.23 $\pm$ 0.28	0.81	0.42
Sex(female):Depth	1.37 $\times 10^{-3} \pm 9.35 \times 10^{-4}$	1.47	0.14

No difference in foraging habitat preference by birds from the Tremiti colony was detected between the two study years (Table S3).

Foraging locations and distance from the breeding site

The most distant foraging location reached by birds breeding on Linosa and Tremiti was 369 km and 387 km from the colony (Euclidean distances), respectively. The furthest foraging location

(km) reached by each sexed bird was correlated with the duration of foraging trips (days) ($r = 0.75$, $P < 0.0001$; Fig. S2); colony and sex had no influence ($P > 0.09$).

The model (GLMM) of foraging distance from the colony that had the lowest AIC included all the anthropogenic and environmental variables and all their interactions with study area and gender (Table 3). This model indicated that the distance of foraging locations from the colony was positively related to the index of distance to other

Table 3. Selected GLMMs (five models with the lowest AIC values) of the foraging distance from the colony. Foraging locations were weighted to account for temporal auto-correlation. Variables used for the analysis are: Depth (m); lnPP: log-transformed net primary production (mg C/m²/day); DH: index of distance to fishing harbours (km⁻²); DC: index of distance to conspecific colonies (km⁻²); Area: study area of Linosa and Tremiti; Sex. The last two factors were also included as interaction terms (:) with the other factors. Individual identity (1 | RING) was entered as a random effect.

Model no.	Model (Distance from the breeding colony)	AIC
1	Area + Sex + Depth + DC + DC ² + DH + DH ² + lnPP + Area:Depth + Area:DC + Area:DC ² + Area:DH + Area:DH ² + Area:lnPP + Sex:Depth + Sex:DC + Sex:DC ² + Sex:DH + Sex:DH ² + Sex:lnPP + (1 RING)	15 966
2	Area + Sex + Depth + DC + DC ² + DH + DH ² + lnPP + Area:Depth + Area:DC + Area:DH + Area:DH ² + Area:lnPP + Sex:Depth + Sex:DC + Sex:DC ² + Sex:DH + Sex:DH ² + Sex:lnPP + (1 RING)	16 032
3	Area + Sex + Depth + DC + DC ² + DH + DH ² + lnPP + Area:Depth + Area:DC + Area:DC ² + Area:DH + Area:DH ² + Area:lnPP + Sex:Depth + Sex:DC + Sex:DH + Sex:lnPP + (1 RING)	16 098
4	Area + Sex + Depth + DC + DC ² + DH + DH ² + lnPP + Area:Depth + Area:DC + Area:DC ² + Area:DH + Area:DH ² + Area:lnPP + Sex:Depth + Sex:DC + Sex:DH + Sex:lnPP + (1 RING)	16 199
5	Area + Sex + Depth + DC + DC ² + DH + DH ² + lnPP + Area:Depth + Area:DC + Area:DH + Area:lnPP + Sex:Depth + Sex:DC + Sex:DH + Sex:lnPP + (1 RING)	16 308

colonies of Scopoli's Shearwaters and negatively correlated to the index of distance to fishing harbours. The negative effects of the quadratic effect of distance to fishing harbours indicate a non-linear relationship between the distance of foraging locations from the colony and distance to fishing harbours. At least for Linosa birds, the distance to fishing harbours seemed to decrease markedly only when the foraging location was more than 200 km from the colony; the effect seems negligible for shorter distances. In addition, the model shows that females foraged closer both to other colonies and to harbours compared with males. Linosa birds foraged further from other colonies, closer to fishing harbours and in shallower waters than Tremiti birds (Table 4, Fig. S3).

DISCUSSION

We investigated the foraging habitat preferences of Scopoli's Shearwaters breeding in two different and widely separated colonies in the central Mediterranean. Breeding birds preferred foraging areas characterized by shallower waters and located further from other Scopoli's Shearwater colonies. Moreover, birds did not disperse indiscriminately from their colony towards the open sea, but performed longer trips to forage further from other colonies and closer to fishing harbours. Overall, the study highlighted the complex relationship between pelagic birds and human activities and

supported the suggestion that intra-specific competition plays an important role in the foraging distribution of seabirds. Our study highlights the value of working on new species that are closely related to well-studied ones (Cory's Shearwater in this case), which allows one to explore the representativeness of findings in other species.

Habitat preferences

Birds from the two colonies inhabited different seascapes (Cecere *et al.* 2013). Compared with the relatively shallow and flat Adriatic, the Tunisian Plateau has much lower primary productivity (Bosc *et al.* 2004) and higher mean sea surface temperature (Coll *et al.* 2010), is surrounded by marine canyons, and is crossed by the Atlantic cold current, which creates upwellings near the coast of Tunisia and Libya (Agostini & Bakun 2002). However, despite differences in seascape, birds from both colonies showed similar preferences for foraging locations. The comparison between the two study areas could theoretically be complicated by the fact that the birds of the two colonies were tracked in different years. Nevertheless, the lack of differences between the two sampling years at Tremiti suggests that patterns of foraging habitat preferences are consistent among years.

In accordance with previous studies showing that the closely related Cory's Shearwater mainly feeds in neritic habitats (Paiva *et al.* 2010b), we

Table 4. Coefficient estimates of fixed effects of the best performing model for the foraging distance from the colony. Foraging locations were weighted to account for temporal autocorrelation. Variables used for the analysis are: Depth (m); DC: index of distance to conspecific colonies (km^{-2}); DH: index of distance to fishing harbours (km^{-2}); InPP: log-transformed net primary production ($\text{mg C/m}^2/\text{day}$); Area: study area (1 Linosa, 2 Tremiti); Sex (1 male, 2 female). The two latter factors were also included as interaction terms (:) with the other factors. Individual identity (1 | RING) was entered as a random effect.

	Fixed effects		
	Coeff. estimate $\pm$ 1 se	<i>t</i>	<i>P</i>
(Intercept)	$3.94 \times 10^5 \pm 1.37 \times 10^5$	2.88	0.004
Depth	-32.5 ± 35.78	-0.9	0.63
DC	$4.59 \times 10^9 \pm 4.81 \times 10^8$	9.55	<0.0001
DC ²	$1.45 \times 10^{13} \pm 2.35 \times 10^{12}$	6.19	0.07
DH	$-1.16 \times 10^8 \pm 4.81 \times 10^7$	-2.42	0.009
DH ²	$-5.47 \times 10^{10} \pm 2.14 \times 10^{10}$	-2.55	0.02
InPP	$-9.33 \times 10^3 \pm 2.31 \times 10^4$	-0.4	0.25
Sex(female)	$-1.65 \times 10^5 \pm 9.76 \times 10^4$	-1.69	0.37
Area(Tremiti)	$-6.64 \times 10^4 \pm 1.41 \times 10^5$	-0.47	<0.0001
Sex(female):Depth	$59.16 \times 10^2 \pm 77.14$	0.76	0.44
Sex(female):DC	$-2.23 \times 10^9 \pm 5.51 \times 10^8$	-4.05	<0.0001
Sex(female):DC ²	$-1.09 \times 10^{13} \pm 2.57 \times 10^{12}$	-4.23	<0.0001
Sex(female):DH	$-3.91 \times 10^7 \pm 1.75 \times 10^7$	-2.24	0.02
Sex(female):DH ²	$-4.25 \times 10^9 \pm 2.08 \times 10^9$	-2.36	0.04
Sex(female):InPP	$1.72 \times 10^4 \pm 1.39 \times 10^4$	1.23	0.21
Area(Tremiti):Depth	$8.14 \times 10^2 \pm 1.66 \times 10^2$	4.91	<0.0001
Area(Tremiti):DC	$-2.13 \times 10^9 \pm 4.01 \times 10^8$	-5.3	<0.0001
Area(Tremiti):DC ²	$-3.65 \times 10^{12} \pm 1.5 \times 10^{12}$	-2.43	0.01
Area(Tremiti):DH	$1.74 \times 10^8 \pm 4.96 \times 10^7$	3.5	<0.001
Area(Tremiti):DH ²	$6.02 \times 10^{10} \pm 2.16 \times 10^{10}$	2.78	0.005
Area(Tremiti):InPP	$-8.48 \times 10^3 \pm 2.31 \times 10^4$	-0.36	0.71

found that breeding Scopoli's Shearwaters also preferred to forage in shallow waters. The preference for these habitats could be due to a generally higher prey availability in shallow waters.

In addition, we found a strong preference for areas more distant from other breeding colonies. Scopoli's Shearwaters, like other colonial seabirds, are central-place foragers and exploit resources within a given range of the central breeding colony set by food distribution and their travelling capabilities (Orians & Pearson 1979). A recent study based on the foraging trips of 184 chick-rearing Northern Gannets *Morus bassanus* tracked simultaneously from 12 colonies in the UK showed a marked segregation of foraging areas among birds from different colonies (Wakefield *et al.* 2013). A similar result was also previously recorded for other seabird species, such as Cape Gannets *Morus capensis* breeding in two neighbouring islands (Grémillet *et al.* 2004). This spatial segregation is likely to be determined by density-dependent competition (Wakefield *et al.* 2013). Scopoli's Shearwaters generally breed in large numbers and

often the same sites are used also by other seabird species, such as the Yelkouan Shearwater *Puffinus yelkouan* (Baccetti *et al.* 2009), the Mediterranean species most similar to the study species in food habits. As a result of both competition with adjacent conspecific colonies and perhaps inter-specific competition, Scopoli's Shearwaters optimize their feeding by avoiding areas closer to other shearwater colonies.

High net primary productivity is typically related to greater pelagic fish abundance (Agostini & Bakun 2002), and numerous studies have shown that seabirds prefer areas of high productivity (Wakefield *et al.* 2009). This is the case in two studies of Cory's Shearwater that show that breeding birds prefer foraging areas characterized by a high concentration of chlorophyll *a* and low sea-surface temperatures (Navarro & González-Solís 2009, Paiva *et al.* 2010c). However, we found the converse, with Scopoli's Shearwaters using areas of low primary productivity. This result might be affected by the generally higher primary productivity of the Western Adriatic (Agostini & Bakun

2002). Thus, birds from Tremiti could not seek areas characterized by higher values of primary production. Another possibility is that the relationship between primary productivity and seabirds is not immediate, and that there exists a temporal lag between primary production and prey abundance.

Contrary to our expectation, we did not find a preference for areas located closer to fishing harbours, our proxy of discard availability. When interpreting this result, we need to consider that preferences for any resource are affected by their accessibility, especially in central-place foragers (Matthiopoulos 2003). Thus, this result could be due to the large distance of fishing harbours from the breeding colonies. This conjecture is supported by the fact that birds used long-distance trips to forage closer to fishing harbours.

Lastly, despite the difference in size between males and females (Massa & Lo Valvo 1986), we found no differences in habitat use between the sexes, as has been found for other seabird species with minor morphological dimorphism (Phillips *et al.* 2004, Navarro *et al.* 2010). Sexual differences were also not found for Scopoli's Shearwaters in foraging trip duration during either incubation or chick-rearing (Cecere *et al.* 2013). On the whole, these results suggest an absence of sexual divergence in foraging strategies in Scopoli's Shearwaters.

Foraging locations and distance from the breeding site

Theoretically, long foraging trips could be used by seabirds either to spend more time foraging close to the colony or to reach further and possibly more profitable locations such as areas of known high fish density (Weimerskirch 2007). Scopoli's Shearwaters from both study colonies used long foraging trips to reach foraging locations far from their breeding islands, reaching distances of up to 369 and 387 km from the colonies of Linosa and Tremiti Archipelago, respectively, during incubation. It is likely that the adoption of trips lasting several days requires larger costs both at an individual level, due to high energy demands, and at a breeding pair level, as it implies prolonged fasting of the partner attending the egg or lower feeding rates during chick-rearing. On the other hand, these trips enable birds to explore a heterogeneous environment, giving them the opportunity to for-

age in more profitable areas than those near the colony. This is the case for Cory's Shearwaters, which use long trips to forage in areas characterized by high values of chlorophyll *a* and low sea surface temperatures (Paiva *et al.* 2010c), suggesting that birds exploited areas according to prey availability.

We show that Scopoli's Shearwaters from both colonies used long-distance trips to forage in areas located further from other Scopoli's Shearwater colonies and closer to fishing harbours. As the density of fishing boats discarding fish should be higher close to fishing harbours, we suggest that a significant proportion of food may come from fishery discards, as has been demonstrated in other studies of shearwaters in the Mediterranean (Bartumeus *et al.* 2010). Fishery discards are an abundant and predictable source of food for seabirds, and in our study areas a high proportion of discards comprise small fish such as anchovies and sardines, which are potential prey for shearwaters (European Commission 2011). Furthermore, in the case of bottom trawlers, which are very common in both study areas (European Commission 2011), the discard makes available a large amount of demersal fish that otherwise would not be available for surface predators such as shearwaters (Arcos *et al.* 2007). The presence of such an abundant food source (Tsagarakis *et al.* 2013) in a heavily over-fished sea such as the Mediterranean (FAO 2005) means that pelagic birds may have many opportunities to exploit discards. The fact that fishing vessels are perceived as a food resource by Scopoli's Shearwaters has already been described by Sarà (1993), as has the well-documented mortality on the longline fisheries in the western Mediterranean (Belda & Sánchez 2001). The extensive use of fishery discards was also shown for Balearic Shearwaters foraging off the Ebro Delta (Arcos & Oro 2002), and we could expect similar results for the third Mediterranean shearwater, the Yelkouan Shearwater.

We did not directly analyse the exploitation of discards by seabirds, and it is reasonable to predict that areas with high productivity are used by both fishing vessels and shearwaters with, potentially, no direct association between the two. Nevertheless, we analysed the distance to fishing harbours whose locations do not coincide with commercial fishing areas. This supports the strength of our conclusions on the exploitation of discards by Scopoli's Shearwaters. However, fishery discards do

not necessarily benefit seabird populations. Bioenergetic models run on Cape Gannets show that consumption of low-energy fishery discards does not seem to compensate for the absence of natural prey (Pichegru *et al.* 2007). It has also been demonstrated that, although non-breeding Cape Gannets can survive when complementing their diet with fishery discards, chicks fed with fishery wastes have a lower probability of survival (Grémillet *et al.* 2008a). Hence, there may be advantages and disadvantages to feeding on discards due to the prolonged consumption of low-energy and low-quality food as well as by-catch risk.

It is not surprising that the model that best explained the distance of foraging locations from the breeding site showed an effect of the marine habitat where the colonies are located. In comparison with Linosa birds, those breeding in Tremiti did not need to perform such long trips to forage in shallower waters and nearby fishing harbours, as the breeding site is located closer to the coast and in shallower waters. In addition, the selected model showed that gender is related to foraging range, suggesting a difference in foraging behaviour between males and females. Navarro *et al.* (2010) found differences in the consumption of fish discards and small pelagic fish between sexes in the Audouin's Gull, a species characterized by slight sexual differences, with males being slightly bigger. However, we believe that more specific studies are needed properly to investigate this aspect in Scopoli's Shearwater.

Management implications

The results of the present study corroborate the current opinion (e.g. ACAP 2012) that the conservation of pelagic seabirds cannot be limited only to marine-protected areas around breeding sites. In addition to local scales related to both colonies and foraging areas, it is necessary that pelagic bird conservation programmes become part of transnational fishery policies.

Starting from 2015 in the Baltic Sea and 2017 in the Mediterranean Sea, the European Union is going to ban fishery discards by introducing a 'landing obligation' in all European seas. According to this new regulation, fishing boats are required to land all catches ideally to reduce catching non-target and small-sized individuals of target species (Bellido *et al.* 2014). However,

although this regulation will inevitably produce a large amount of very cheap raw material for other industries (e.g. the animal feed industry), it will probably result in a reduction of marine biomass, with possible, still unknown, negative consequences on the marine environment (Bellido *et al.* 2014). Fishery discards may represent more than half of the total energy intake of shearwaters in the Mediterranean (Arcos 2001), and thus the risk is that birds living in such a strongly depleted sea will lose this important food source with a consequent heavy reduction of their carrying capacities. Because of this, it will be interesting, if not mandatory from a conservation point of view, to repeat similar studies on seabirds after the enforcement of this regulation.

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SUPPORTING INFORMATION

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

Table S1. R-values for cross-correlation among anthropogenic and environmental variables related to foraging locations of all recorded birds.

Table S2. List of harbours considered in the analyses and related number of fishing boats.

Table S3. Mean values ($\pm$ se) of environmental variables and results of GLMM analyses investigating the effect of the sample year for Tremiti birds on

environmental characteristics of foraging locations.

Figure S1. Distribution of control points within the circular buffers around the colonies with a radius equal to the distance of the furthest recorded location of birds from Linosa and Tremiti.

Figure S2. Scatter plots of the duration of foraging trips vs. the distance of furthest reached foraging locations from the breeding colony.

Figure S3. Scatter plots of each anthropogenic and environmental variable vs. the distance from the breeding colony.