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Home range and foraging habitat preference of Scopoli's shearwater *Calonectris diomedea* during the early chick-rearing phase in the eastern Mediterranean

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Pelagic seabirds that breed colonially are central-place foragers; their spatial distribution is restricted to marine areas around their colonies during the chick-rearing period, when attendance and food provision to their chicks has to be intense. In this study we analyzed the foraging trips of 11 Scopoli's shearwater *Calonectris diomedea* breeders that were tagged with GPS data loggers during 2014 in oligotrophic waters (Ionian Sea, western Greece), and assessed the range and oceanographic parameters of their foraging habitat. Contrary to previous findings suggesting a varying foraging strategy depending on the breeding stage, the tracked shearwaters made short trips, less than 4 days long, in the vicinity of the colony. By applying the Adaptive Kernel method, their 50% and 95% foraging range was estimated at 6871 km^2 and 23 014 km^2 respectively. In addition, generalized additive models showed that sea surface temperature (<25.5°C), minimum distance from the colony (<100 km), fishing pressure index from small scale fisheries (medium values) along with a two-dimensional soap film smoother for space (easting, northing) were the most significant factors affecting at-sea distribution of this marine top predator during the early chick-rearing period (i.e. 99.9% of the final model deviance). Our study will contribute to the revision of the boundaries of the local Special Protection Area (SPA) of Strofades. It will also address the implementation of specific conservation measures for the species at regional and national scale, and the development of a management plan for the protection of the study area.

The Mediterranean Sea is a highly dynamic ecosystem, influenced by different oceanographic parameters (e.g. primary productivity, sea surface temperature, sea level anomaly, seafloor depth, etc.) and human activities (e.g. fisheries), which may constrain prey availability for top marine predators ultimately affecting their foraging behaviour (FAO 2016, Piroddi et al. 2017). For example, marine productivity plays a crucial role for the foraging behaviour of seabirds and the adoption of a relevant strategy throughout their breeding cycle (Weimerskirch 2007, Cecere et al. 2014). Consequently, seabirds belonging to the upper trophic level must cope with marked spatio-temporal fluctuations of these ecogeographical and human-induced factors and are expected to congregate and feed in areas of high prey availability (Erikstad et al. 1990, Mehlum et al. 1996, Bost et al. 2009, Rayner et al. 2010; but see Fauchald 2009). Nevertheless, the Ideal free distribution theory, which predicts a strong aggregative response of seabirds to concentrations of prey has been disputed due to the assumption of a nonresponsive prey trying to avoid areas with predator high density and, consequently, high rates of mortality (Fauchald 2009).

In general, both physical oceanographic incidents and biotic activity are responsible for seabird prey concentrations over a variety of spatial and temporal scales (Shealer 2002). Recent studies have examined factors responsible for concentrating aggregations of prey and consequently of seabirds in the Atlantic Ocean and the Mediterranean Sea so as to determine whether these aggregations are random or predictable (Navarro and González-Solís 2009, Navarro et al. 2009, Olivar et al. 2010, Somarakis et al. 2011, Davoren 2013).

Monitoring the movements of breeding shearwaters in Mediterranean colonies has revealed significant variations in their foraging behaviour patterns throughout the breeding season (Dell' Ariccia et al. 2010, Arcos et al. 2012, Cecere et al. 2014). In particular, flights recorded using different miniaturized tracking equipment have shown that Scopoli's shearwater *Calonectris diomedea* breeders

may employ a dual foraging strategy (Louzao et al. 2009, Cecere et al. 2013) (but see Grémillet et al. 2014). This strategy, which is also followed by the closely-related Cory's shearwater *Calonectris borealis* over the north-east Atlantic Ocean (Magalhães et al. 2008, Paiva et al. 2010a) involves short trips in terms of both duration (1–4 days) and distance (ranging within a few dozen kilometres from the colony), as well as trips of 7–18 days, over routes of several hundred km long. The two different types of trips are believed to serve different needs, since the shorter ones are mainly observed during the first days after hatching, when chicks are relatively small and must be fed daily (Dell' Ariccia et al. 2010, Cecere et al. 2014). On the other hand, longer and more distant trips are recorded with increasing frequency as chick growth progresses, their body mass increases and fledging approaches. This has been interpreted as a response by the adults to meeting their own energy requirements following an arduous period as breeders, since chicks can then survive with less frequent nest visits for food provisioning (Granadeiro et al. 1998, Magalhães et al. 2008).

In the Mediterranean, studies on the foraging ecology of Scopoli's shearwaters describing their breeding range, feeding areas, movements and habitat use have focused on the colonies in the western and central part of the basin (Vaughan 1980, Massa and Lo Valvo 1986, Louzao et al. 2009, Arcos et al. 2012, Grémillet et al. 2014, Cecere et al. 2015). These areas constitute the most productive part compared to the eastern Mediterranean Basin (Turley et al. 2000, Lazzari et al. 2012), which is a contrasting ecological regime characterized by low concentrations of annual primary productivity (C 116–126 g m^{-2} $year^{-1}$) (Bosc et al. 2004) and annual chlorophyll concentration (chl-a 0.13–0.27 mg m^{-3}) (Gotsis-Skretas et al. 1999). In general, the Mediterranean Sea is characterized by evident eastward decline in primary production and increase of sea surface temperature (Coll et al. 2010). Sea surface temperature influences the productivity of marine ecosystems at low trophic levels (e.g. phytoplankton and zooplankton), and thus the foraging success of top predators such as marine birds (Peck et al. 2004, Erwin and Congdon 2007, Ramos et al. 2013, Weeks et al. 2013). Consequently, a decreasing longitudinal trend towards the east in fish species richness (Ben Rais Lasram et al. 2009, Coll et al. 2010; but see Keller et al. 2016 for cephalopod diversity) as well as in biometrical measures of shearwaters (Massa and Lo Valvo 1986) has been pointed out. This trend may have an impact on foraging behaviour and the population dynamics of seabirds in the eastern Mediterranean, suggesting that marine areas of enhanced food availability serve as highly profitable foraging grounds and important breeding sites for marine birds (Ramos et al. 2013, Grémillet et al. 2014).

To date, few studies have been carried out in the eastern Mediterranean to determine important sea areas for marine birds during the breeding season (Fric et al. 2012, Karris 2014). More specifically and until recently, no systematic telemetric studies had been carried out on the foraging patterns employed by the Greek colonies of Scopoli's shearwater breeders in either the Aegean or the Ionian Sea. For example, Karris (2014) collected a non statistically significant multi-year GPS tracking data set (2009–2013) from 12 adult breeders of an Ionian colony during the early stage of chick provision so as to examine their foraging distribution at-sea. The average foraging trip for the tracked birds was 1.6 ± 0.99 days (range: range: 1–4 days). Utilization distribution of 50% (core foraging areas) and 95% (home range) generated by the kernel density estimator covered an area of 830 km^2 and 8630 km^2 respectively.

It is expected that extreme low values of primary productivity around seabird colonies in the eastern Mediterranean will force breeders to perform a high proportion of long trips in their effort to reach the most profitable areas for food provision to chicks but also for their own energy demands (Cecere et al. 2014). Here we present the first data obtained from tracked breeding Scopoli's shearwaters under strong oligotrophic conditions in the Ionian Sea, eastern Mediterranean (Allen et al. 2002, Moutin and Raimbault 2002), where information on species distribution and more specifically its main foraging areas are scarce and patchy. We also assessed the predictability of high-use areas for foraging and the key environmental factors as well as human fishery activities that may affect foraging habitat preference.

Material and methods

Study area and species

The Strofades Island complex (37°15′N, 21°00′E) is a remote group of two small low islets (22 m a.s.l.) and several rocks, located in the southern Ionian Sea, 32 nm south of Zakynthos Island and 26 nm west of the Peloponnese (Fig. 1). The two main islets (Stamfani and Arpyia), which host about 5550 Scopoli's shearwater breeding pairs (Karris et al. 2017), cover an area of 4 km^2 and constitute part of the National Marine Park of Zakynthos. The target seabird species is a long-lived migrant Procellariid species, well-known for nest site tenacity, mate fidelity and its pelagic and wide-ranging distribution. The breeding sites of this species are located in the Mediterranean basin whereas its wintering grounds are located in the pelagic and coastal equatorial areas of the eastern Atlantic.

GPS transmitter deployment

The appropriate way of attaching tags on seabirds is still being debated (Bodey et al. 2017). Back attachment seems to be a better method in terms of balance/centre of gravity considerations, but there are other considerations that have not been formally considered. One thing that has not been investigated is pain, due to twisting and pulling of smaller back feathers as the bird banks during dynamic soaring. Another aspect is water intrusion, as the attachment breaks the insulating barrier. For the above reasons, we preferred to follow tail deployments as other authors have done for relevant studies (Wilson et al. 2009, Paiva et al. 2010b, Ramos et al. 2013).

Data collection was implemented during the breeding season of 2014. The tracked birds were removed from their breeding burrows between 23–29 July, when the majority of the chicks had hatched and were about 1–2 weeks old. We ringed and weighed all tagged breeders with a Pesola spring balance readable to 10 g, just before tag deployment (mean ± SE: 680.0 ± 27.47 g) and after tag retrieval

Figure 1. GPS tracks of Scopoli's shearwaters during recorded foraging trips in July 2014. The blue circle indicates the breeding colony on Strofades.

(mean ± SE: 628.2 ± 26.10 g). Global positioning system-GPS loggers storing tracking information were used on 20 different breeders. The waterproofed GPS data loggers were attached to the four central tail feathers using TESA tape and configured to record positions every 10 min. Weighing a total of 20–23 g, the loggers (45 × 32 × 18 mm) comprised slightly more than 3% of the mean body mass (range: 2.9–3.3%), which constitutes the recommended threshold for ensuring the elimination of any possible effect on their movement behaviour (Phillips et al. 2003, Passos et al. 2010). However, we assumed that deploying tags for short periods (here <4 days) would minimise the impact of loggers on seabird behaviour as Louzao et al. (2009) argued in a relevant study. Indeed, we found an average of 51.8 g decrease of shearwater weight after tag retrieval but this was not significant (paired t-test, $t = 2.1489$, $df = 10$, p-value > 0.05). Additionally, we monitored the breeding performance of the tagged birds so as to determine any possible effects of tag deployment on chick growth and as a consequence to breeding success. The data obtained by monitoring 14 nests, corresponding to the group of tagged birds, showed a breeding success of up to 0.93%. This score is much higher than the respective result (0.65%) obtained by monitoring 516 nests during five consecutive years (2008–2012) in the Strofades colony (Karris 2014). Furthermore, even if we tagged mates in six nests, there was no significant effect on their breeding success. These findings may serve evidences of lack of detrimental effects by tags deployment on central tail feathers. On returning to their nests over the following days, the birds fitted with GPS loggers were recaptured after food provision to chicks; the loggers were removed and data were downloaded and stored.

Home range analysis

Estimation of utilization distribution is of great importance in home range studies (Worton 1989), as it represents the probability density of relocating an animal at any place on the basis of geographical coordinates (van Winkle 1975). GPS locations in the vicinity (within 2 nm) of the Strofades colony were not included in the spatial analysis, assuming that the birds would congregate in large rafts just before visiting their nests to feed the chicks during the night. According to Louzao et al. (2009), we also excluded consecutive GPS locations from the spatial analysis, on the basis of low speed flight (<2 km h^{-1}) assuming that this behaviour may be defined as resting or floating with the sea current. Given that the majority of the breeders seems to have similar behaviour in this particular time of the year (also confirmed from the data in this particular period), we have decided to map a more general home range for all birds (Supplementary material Appendix 1 Table A1, Fig. A1). The 95% and 50% (core foraging areas) home ranges of breeding shearwaters were then estimated using a bivariate normal fixed kernel. The reference bandwidth (href = 18 500 in the currents study) plays the role of a smoothing parameter, which controls the "width" of the kernel functions placed over each point. The scaling factor (multiplier) was set at 1 000 000 and the cell size of kernel output was defined at 100 m. Spatial analyses and mapping were implemented using ESRI's ArcGIS ver. 9.2 GIS software (ESRI 2007). More specifically, kernel density estimator for generating the utilization distribution was implemented using the Home Range tool (Rodgers et al. 2007). Prior to spatial analyses and map production, the GPS locations were projected to WGS 84/UTM zone 34N.

Environmental and fishing effort parameters

Satellite environmental parameters, bathymetry, distance from the coastline, distance from the Strofades colony and fishing effort (Table 1), were used as independent variables in order to model the distribution of foraging intensity. The kernel density outcome based on the abovementioned home range analysis was considered as a proxy of the distribution of foraging intensity. As long as the areas have higher kernel density values; there is a greater potential that these areas belong to an intense foraging location. Details on the relevant analyses are provided in the next paragraph. Monthly satellite images of sea surface temperature (SST), sea surface chlorophyll (CHL) and sea level anomaly (SLA) were used for modelling (Table 1). We followed the classification scheme of Kavadas et al. (2015) for characterizing the productivity level in terms of CHL concentrations (mg m^{-3}) within the study area: oligotrophic waters (<0.084), lower mesotrophic waters (0.084–0.23), medium mesotrophic waters (0.23–0.46), upper mesotrophic waters (0.46–0.793) and eutrophic waters (>0.793). Spatial distribution of bathymetry was estimated using a composition of

Table 1. General characteristics of independent variables

Variable	Abbreviation	Sensor/model	Resolution	Source
Sea surface temperature (C°)	SST	AVHRR	0.013 dd*	<www.eoweb.dlr.de:8080>
Sea surface chlorophyll	CHL	MODIS AQUA	0.41 dd (interpolated to 0.013 dd using ArcGIS topo to raster method)	<www.oceancolour.gfc.nasa.gov>
Sea level anomaly	SLA	AVHRR	0.41 dd (interpolated to 0.013 dd using ArcGIS topo to raster method)	<www.aviso.altimetry.fr>
Bathymetry	Depth	Estimated by a composition of interpolation methods	0.013 dd	Kavadas et al. 2013
Fishing effort from purse seiners	PS	Estimated by VMS data	5*5 km² (a resampling algorithm is used using nearest neighbour assignment to transform the cell size to 0.013 dd)	Kavadas and Maina 2012
Fishing pressure index from small scale fisheries	SSC	Estimated by MCDA method	0.013 dd	Kavadas et al. 2015

*dd: decimal degrees, 0.013 dd is ~ 1.5 km.

spatial interpolation methods within the framework of the IMAS-Fish research project (Kavadas et al. 2013). Minimum distances from the coastline and the Strofades colony were estimated using the 'near' proximity tool, which forms part of ESRI's ArcGIS toolboxes (ESRI 2007). Parameters such as SST, CHL, depth and distance from coastline are considered important due to the influence on marine species such as small pelagic fish (Agostini and Bakun 2002, Giannoulaki et al. 2011, Cecere et al. 2015), which mainly affect the foraging pattern of Scopoli's shearwaters (Sarà 1993). Also, SLA varies with ocean processes such as gyres, meanders and eddies that enhance productivity and often function as physical barriers differentiating the distribution of species (Larnicol et al. 2002).

The spatial distribution of purse seiner (PS) fishing effort was estimated on the basis of vessel monitoring system (VMS) data. According to Commission Regulation (EC 2003) no. 2244/2003, fishing vessels over 15 m long are legally required to be equipped with a VMS, which provides data on each vessel's location, heading and speed to the fisheries authorities at two-hour intervals. In Greece, 225 purse seiners are 15 m long or more and are therefore fitted with a VMS. The basic methodological steps for the estimation of fishing effort based on VMS data are further described by Kavadas and Maina (2012) and Maina et al. (2016).

In addition, a small scale fisheries fishing pressure index (SSC) was estimated by means of the multi criteria decision analysis (MCDA) methodology. The estimation was conducted through a stepwise procedure, based on influential components affecting coastal fishing in terms of its distribution and intensity such as fishing capacity, bathymetry etc. (see more details in Kavadas et al. 2015).

Habitat preference analysis

Modelling the distribution of foraging intensity was based on generalized additive models (GAMs), which employ non-linear and non-parametric techniques for regression modelling (Hastie and Tibshirani 1990, Wood 2006). The spatial grid of the kernel density values was used to describe the distribution of foraging intensity (the higher values the more intensive foraging location and non-intensive otherwise). The analysis was performed in predefined geographical locations (points) expressed as a grid with a spatial resolution of 10 × 10 km. Subsequently, each point was linked with environmental and fishing effort parameters prevailing during the sampling season.

The detection of collinearity problems between independent variables was based on variance inflation factor (VIF) analysis, using the USDM library in R statistical software (<www.r-project.org>). A stepwise procedure, based on a VIF threshold value (i.e. VIF value = 3 proposed by Zuur et al. (2010)), was performed to drop collinear covariates.

A GAM, incorporating a tensor product of a soap film smoother for space (for details see Wood et al. 2008, Wood 2017) was implemented to avoid any model misspecifications, inherent in inappropriately imposing smoothness across boundary features (e.g. islands, peninsulas) which can result in various problems such as over-smoothing. In that account, the two-dimensional soap film smoother was constructed within the spatial domain (boundary) covered by the kernel density outcome (see Fig. 2 for the boundary of home range). Modelling was performed through the MGCV library of R. Foraging activity data were modelled using a Tweedie error distribution (Tweedie 1984), with a Tweedie index parameter set to 1.78 (considered as the most appropriate parameter value based on the residual validation plots), and a logit link function. A thin plate regression spline was applied as a smoother for the main effects. To avoid over-fitting and to simplify the interpretation of the results, the maximum degrees of freedom allowed for the smoothing functions were limited at k = 5 for the main effects (Wood 2017). Additionally, a two-dimensional soap film smoother for space (easting, northing), was included in the models (Wood 2017). The geographic coordinates, easting and northing, are longitude and latitude expressed in meters using the projected system WGS 84/UTM zone 34N. The degree of smoothing of each predictor was chosen based on the restricted maximum likelihood (REML); a method able to protect against bias in variance component estimates (Wood 2011). The original values for the fishing pressure from small-scale vessels were log-transformed in order to achieve normal distributions (Hastie and Tibshirani 1990).

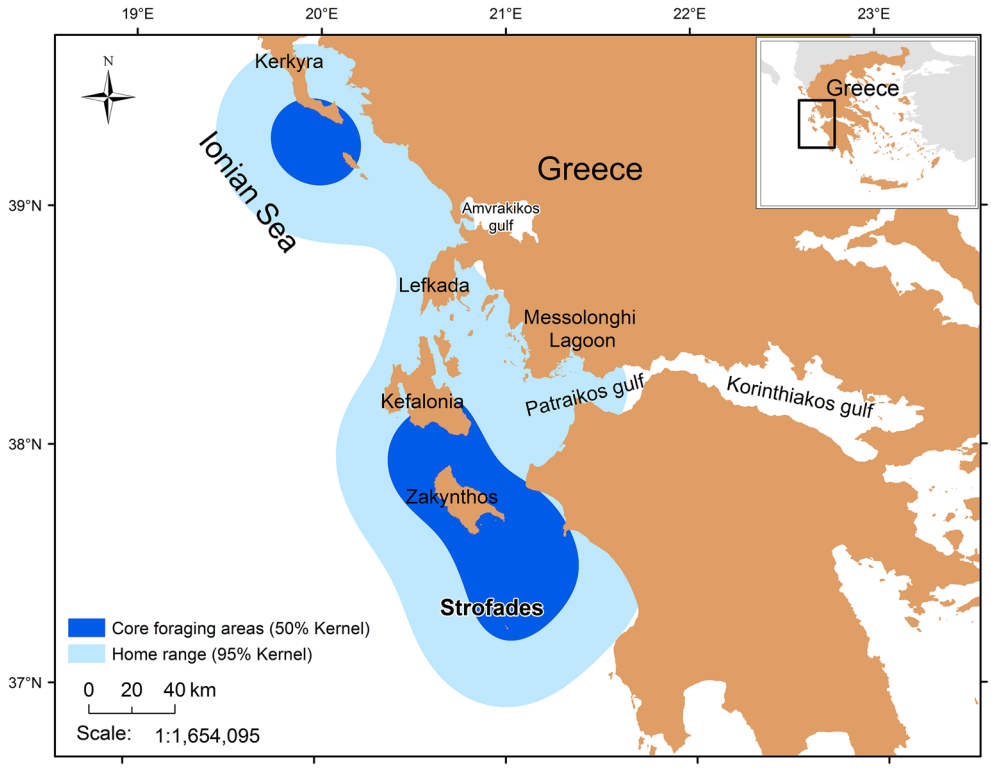

Figure 2. Home range and foraging areas of Scopoli's shearwater breeders of the Strofades colony during the 2014 early chick-rearing phase.

Minimization of the Bayesian information criterion (BIC) across a set of candidate models and the level of deviance explained (DE) led to the selection of the model best fitting the response data. To examine whether the final selected model has eliminated spatial autocorrelation in residuals, semivariograms of the Pearson residuals (detecting spatial autocorrelation) were considered.

Results

Foraging activity

Overall, we recovered 11 out of 20 GPS devices from which complete foraging trips were obtained (Table 2), showing a success rate of up to 55% per deployment. Five GPS tags failed to yield complete recorded data due to technical problems and were not included in the final analysis. Two of the 20 birds fitted with GPS loggers were not recaptured before the departure of the fieldwork team from Strofades, while two of the devices fell off. The majority of individuals (90.9%) showed similar spatial distribution in their foraging activity; their track positions with respect to the breeding site were moved N-NE-NW (Fig. 1). For the 11 tracked birds, the average foraging trip lasted 1.6 ± 1.03 days (range: 1–4). Scopoli's shearwaters covered a maximum recorded distance of 248.2 ± 257.62 km and spent 28.2 ± 24.82 h in the sea during a foraging trip. The duration of foraging trips was correlated with the respective maximum distance covered by tracked individuals (Pearson 2-tailed; $r = 0.977$; $p = 0.01$). The average speed of tracked individuals was 8.9 ± 2.75 km h^{-1} and the total area used during recorded activity was 1371.8 ± 1677.15 km^2.

Table 2. GPS loggers mount and track information of equipped Scopoli's shearwaters. Positions: number of recorded positions, Trel: releasing time of tracked bird, P: track position respect to the colony, MD: maximum recorded distance, TGP: total time to reach maximum recorded distance, Av Sp: average speed, Area: foraging area, Days: trip duration.

N	Year	Date	Positions	Trel	P	MD (km)	TGP (h)	Av sp (km h^{-1})	Area (km^2)	Days
1	2014	23 Jul	61	23:20	N-NW	110.3	9.4	12.0	124.0	1
2	2014	23 Jul	111	22:50	N-NW	193.6	19.7	9.5	1286.0	3
3	2014	24 Jul	96	02:30	N-NE	178.0	20.5	9.0	1308.0	1
4	2014	24 Jul	31	01:15	N	44.1	5.1	9.0	5.3	1
5	2014	24 Jul	46	05:00	N-NE	119.0	10.4	11.0	1428.0	1
6	2014	24 Jul	93	03:45	S	43.4	18.8	2.0	9.1	1
7	2014	24 Jul	187	02:57	N-NE	396.0	39.0	10.0	1677.0	2
8	2014	24 Jul	260	00:40	N-NE	387.0	46.4	8.5	2747.0	2
9	2014	25 Jul	135	22:25	N	137.3	24.7	6.0	25.0	1
10	2014	25 Jul	562	23:20	N-NE	940.0	93.4	10.5	5695.0	4
11	2014	27 Jul	134	01:40	N-NE	181.2	23.2	10.0	785.0	1

Utilization distribution

On analyzing each foraging trip using the adaptive kernel method, we found that the 50% (core foraging areas) and 95% (home range) distribution range of breeding shearwaters was about 6871 km^2 and 23 014 km^2, respectively. More specifically, spatial analysis of all recordings showed that breeders use mainly two different core areas for foraging activities (Fig. 2). Generally, these foraging grounds are located in coastal areas around Zakynthos Island and off the western Peloponnese. GPS tracking of actively breeding Scopoli's shearwaters also confirmed that birds stopped for some hours in front of the breeding area, southwest of Stamfani Island, before departing for foraging trips. The same behaviour was recorded when the tracked individuals returned to the colony and raft adjacent to their breeding sites.

Habitat preference

The final model exploring the distribution of foraging intensity of Scopoli's shearwater included the variables: SST, the minimum distance from the colony (colony_dist) and the natural logarithm of the variable SSC+1 (lnSSC) (Table 3). These variables along with easting and northing were found to be significant, explaining 99.9% of the final model deviance. VIF analysis did not show any collinearity problems between the variables included in the final model. As shown in Fig. 3, SST had a positive effect at temperatures <25.5°C; a positive effect was found for the variable colony_dist at distances <100 km, and lnSSC had a positive effect on fishing pressure values between 12 and 35 units, which are relatively medium values according to the SSC in the Ionian Sea (Kavadas et al. 2015). The variables CHL, depth, distance from the coastline and fishing effort from PS did not reveal a significant effect on the presence of core foraging areas.

Furthermore, no patterns were observed in the residual plots and in the semivariogram of Pearson residuals, suggesting that the final model adequately described the underlying data (Fig. 4).

Discussion

Attaching GPS loggers to adult Scopoli's shearwaters from the largest seabird colony in the eastern Mediterranean yielded the first data on the foraging areas used by the birds in the Ionian Sea during the early chick-rearing phase, in the first two weeks after hatching, which generally occurs in mid-July. According to our results, we rejected the hypothesis about forcing of breeders to perform a high proportion of long lasting foraging trips under extreme low values of primary productivity around colony. The tracks revealed that Scopoli's shearwater breeders made short foraging movements just after egg hatching and they did not employ a dual trip duration (short–long) even though strong oligotrophic conditions, such as the ones prevailing around the Strofades colony (Fig. 5a) may promote long lasting trips as shown by Cecere et al. (2014) in three Mediterranean colonies, i.e. the island of Linosa, the Tuscan Archipelago and the La Maddalena Archipelago. The lack of long foraging trips (>4 days) was also observed during the early chick-rearing phase of the 2009–2013 breeding seasons, revealing a constant unimodal foraging strategy followed by Strofades breeders within their home range (Karris 2014). Although the recorded mean distance covered in the 2014 breeding season was about 250 km, corresponding to a mean foraging sortie of 28 h, the distance from the Strofades colony to the furthest main foraging area (located between the western Peloponnese and southeastern Zakynthos) was approximately 50–60 km. One exception involved a tracked bird leaving the Strofades for four days. Among other areas, this specific individual visited a foraging ground near Kerkyra Island, i.e. 250 km from the colony. In general, the relatively short distance from the colony to the main foraging grounds during the chick-rearing phase is comparable with the findings for the Zembra colony, off Tunis, in the central Mediterranean, and for a Cory's shearwater colony in the Azores, where the average distance covered to approach the core foraging grounds at the same breeding stage was 90–105 km and 75 km, respectively (Magalhães et al. 2008, Grémillet et al. 2014). These results of strict central-place foraging around the colony are also in accordance with recent studies of other populations in the central and western Mediterranean (Navarro et al. 2009, Dell' Ariccia et al. 2010, Cecere et al. 2013), where tracked birds commute between foraging areas around the breeding colonies during the first stages of chick-rearing.

Taking into consideration the overall range of the core foraging areas (50% kernel contour: 6871 km^2) of Scopoli's shearwater breeders of the Strofades and their total breeding population (5550 pairs), we found that the at-sea area per breeding pair was 1.24 km^2. This score is lower compared

Table 3. Results for factors affecting the distribution of foraging intensity based on the best generalized additive model (GAM); s: smooth function represented using penalized regression splines, edf: estimated degrees of freedom, REML score: restricted maximum likelihood score.

Model for the presence of core foraging areas	Variable	edf	p-value
Approximate significance of smooth terms of the final GAM	s(SST)	3.834	0.000103
	s(colony_dis)	3.012	0.044426
	s(lnSSC)	3.006	0.004557
	s(easting, northing)	61.627	< 2e-16
Deviance explained (%):99.9%			
REML score: –388.44			
Number of observations: 180			

Final model formula: distribution of foraging intensity ~ s(SST, k=5)+s(colony_dis, k=5)+s(lnSSC, k=5)+s(easting, northing, bs ="so", k=25, xt=list(bnd=fsb)), knots=soap_knots, data=mydata, family=Tweedie (p=1.78, link=log), method ="REML").

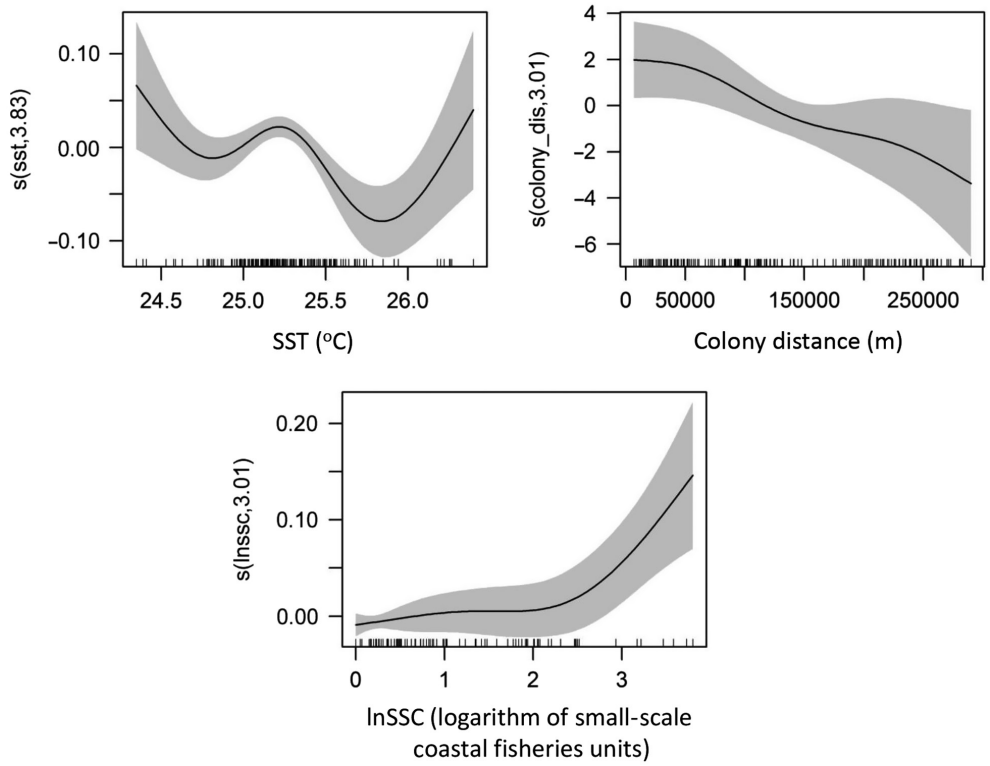

Figure 3. Coefficients of the generalized additive models (GAMs) for Scopoli's shearwater distribution of foraging intensity against SST, colony_dist and lnSSC. Black lines indicates the value of GAMs coefficient, the grey area represents the confidence intervals at p = 0.05. The rug under the single variable effects plots indicates the density of points for different variable values.

to the smaller colonies of French Mediterranean islands (2–16 km^2; 40–400 pairs) and higher than the colony of Zembra Island (0.04 km^2; 141 000 pairs), which is in agreement with Grémillet et al. (2014) who argued that the range of core foraging areas per breeding pair is considerably lower to larger than to smaller colonies.

Contrary to expectations, the main foraging areas in the Ionian Sea during the early chick-rearing phase are not particularly productive and are characterized as lower mesotrophic to oligotrophic (Fig. 5a), with CHL levels of less than 0.10 mg m^{-3} (Kalaroni et al. 2016). These results are in accordance with Cecere et al. (2013) who showed that, during chick-rearing, Scopoli's shearwater breeders forage in less profitable areas, closer to their colonies in the central Mediterranean Sea. This foraging behaviour may be explained by the fact that breeders are forced to cope with the increasing demand for food provision to chicks. Consequently, they choose to use sub-optimal foraging sites near the colony (distance <100 km) in order to ensure direct, rapid access to food resources for regular chick-feeding. Additionally, the resulting exploited site and the core foraging areas around the Strofades colony (e.g. coastal zones of the western Peloponnese and southeastern Zakynthos) compared to the relevant findings of Karris (2014), revealed a substantial degree of fidelity to specific feeding grounds, thus ensuring their importance for the conservation of the species. This persistent use of the same feeding grounds may be explained by the fact that these areas: 1) constitute continental and insular shelves where resources are highly predictable (Weimerskirch 2007), and 2) are distant from other known colonies of shearwater species with common diet habits, resulting in low interspecific and intraspecific competition and, as a consequence, optimization of foraging success, as Cecere et al. (2015) argued for the shearwater colonies of Linosa Island and Tremiti Archipelago in Italy.

The depth of marine habitats is a fundamental oceanographic factor determining major foraging grounds for Shearwaters, and thus indirectly their spatial dispersal (Paiva et al. 2010b, Cecere et al. 2015). The retrieved GPS data points from breeders of the Strofades colony showed no significant correlation between the main foraging grounds of the birds and the depth. Nevertheless the core foraging areas were mainly in water less than 250 m deep. These results are in accordance with relevant findings during the chick-rearing phase, which showed that shearwaters from the colonies in the western and central Mediterranean (Louzao et al. 2009, Grémillet et al. 2014) as well as the north-eastern Atlantic (Navarro and González-Solís 2009, Ramos et al. 2013), mainly foraged in waters from <200 m to <100 m in depth. More specifically, one of the most important foraging areas is located in the coastal zone around the Katakolo Peninsula in the western Peloponnese; it extends from median low-tide level to a depth of 200 m, roughly corresponding to the continental shelf (Fig. 5b). Similar depths were also typical at the foraging ground around Cape Gerakas in south-eastern Zakynthos and in a marine zone extending 3 nm from the Strofades Islands where raft aggregations take place.

Surface temperature in the study area showed that waters in the main foraging grounds are typically colder than the corresponding pelagic waters in the distribution range of shearwaters (Fig. 5c), as observed for other seabird colonies in the Mediterranean (Louzao et al. 2009) and Atlantic

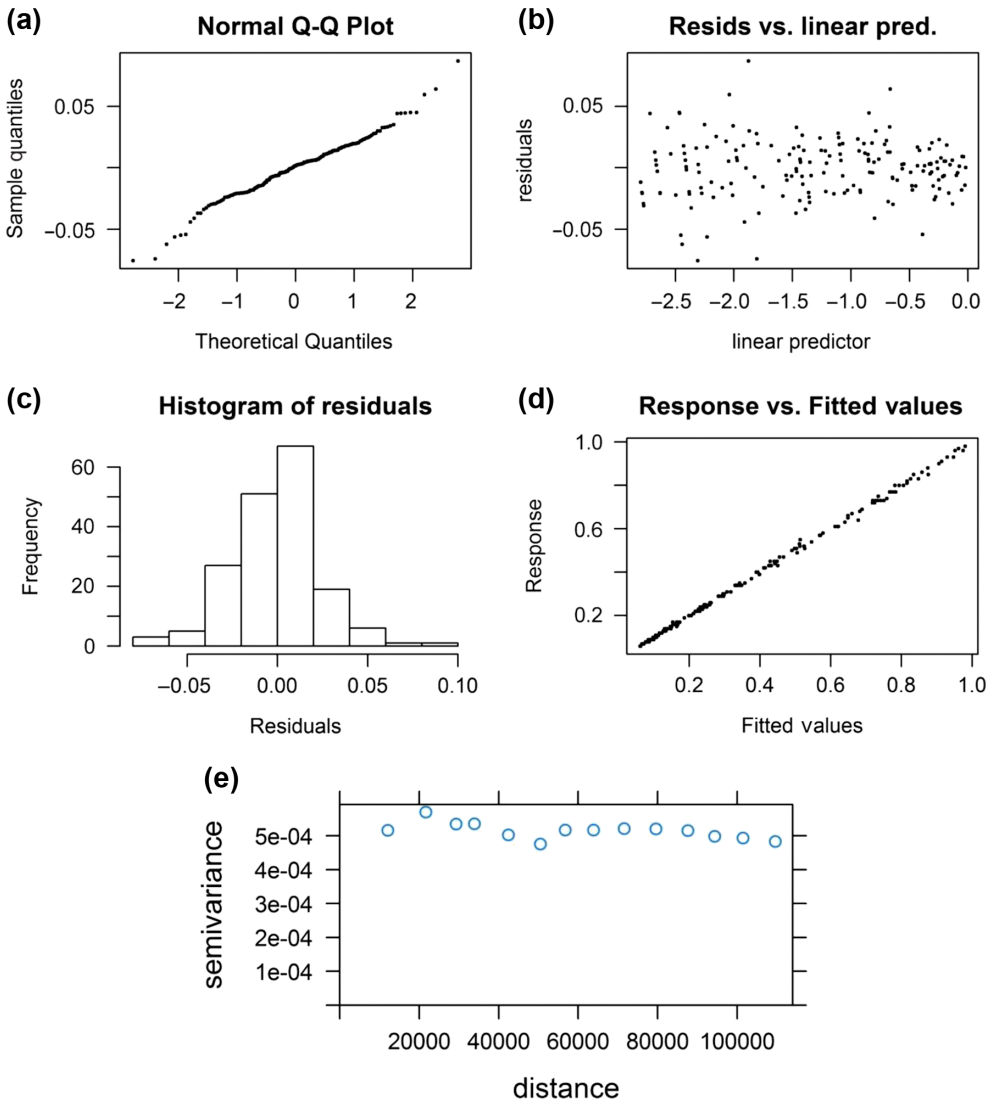

Figure 4. Standard diagnostic plots (residual plots) based on the final generalized additive model. (a): normal Q-Q plot; (b): residuals versus linear predictor; (c): histogram of residuals; (d): response versus fitted values and (e) is the semivariogram based on the Pearson residuals of the final GAM. The Pearson residuals are the raw residuals divided by the corresponding standard errors. If the semivariance is clearly increasing with distance (in meters) there is a confirmation that spatial autocorrelation is present in the residuals of the model. Thus, as there was no trend in the semivariogram, the residual spatial autocorrelation was properly accounted for.

(Ramos et al. 2013). The cold waters in the coastal zones of the western Peloponnese and south-eastern Zakynthos may favour primary productivity. Nevertheless, a recently noticeable increase in sea surface temperature throughout the Mediterranean has been observed, with potential consequences for the reproductive phenology and reproductive success of marine organisms such as the loggerhead sea turtle *Caretta caretta*, which nests on Zakynthos Island (Mazaris et al. 2009). This necessitates monitoring given that the phenomenon could impact shearwater foraging grounds.

Our study highlights that specific fishery gears may affect the foraging distribution pattern of Scopoli's shearwater breeders. The central and southern Ionian Sea is known for significant fishery–seabird interactions, including both detrimental effects on marine bird populations such as bycatch mortality (Karris et al. 2013), and potentially beneficial ones such as food provision via fishery discards (Machias et al. 2001, Karris et al. 2018). More than 35 small and larger fishing ports are distributed along the coastline of the sea area that extends north (towards the coast of Kefalonia) and east (towards the coast of the Peloponnese) of the Scopoli's shearwater colony. About 700 fishing vessels are registered in the area and the majority of them are small boats using trammel nets, gillnets and longlines as fishing gear (Kavadas et al. 2013). During the breeding season of Scopoli's shearwater, coastal vessels fish intensively due to good weather conditions and market needs for fresh fish during the peak tourism season. The fishing footprint of SSC is considered high (Kavadas et al. 2015) and our results highlighted a slight overlap between fishery operations and the foraging areas of shearwaters (Fig. 5d). SSC fishing activity around the fishing grounds provides feeding opportunities to Scopoli's shearwater, primarily during the discarding process as shown also by Cecere et al. (2015). Additionally, it should be mentioned that a small number of Italian and Greek trawlers operate in the international

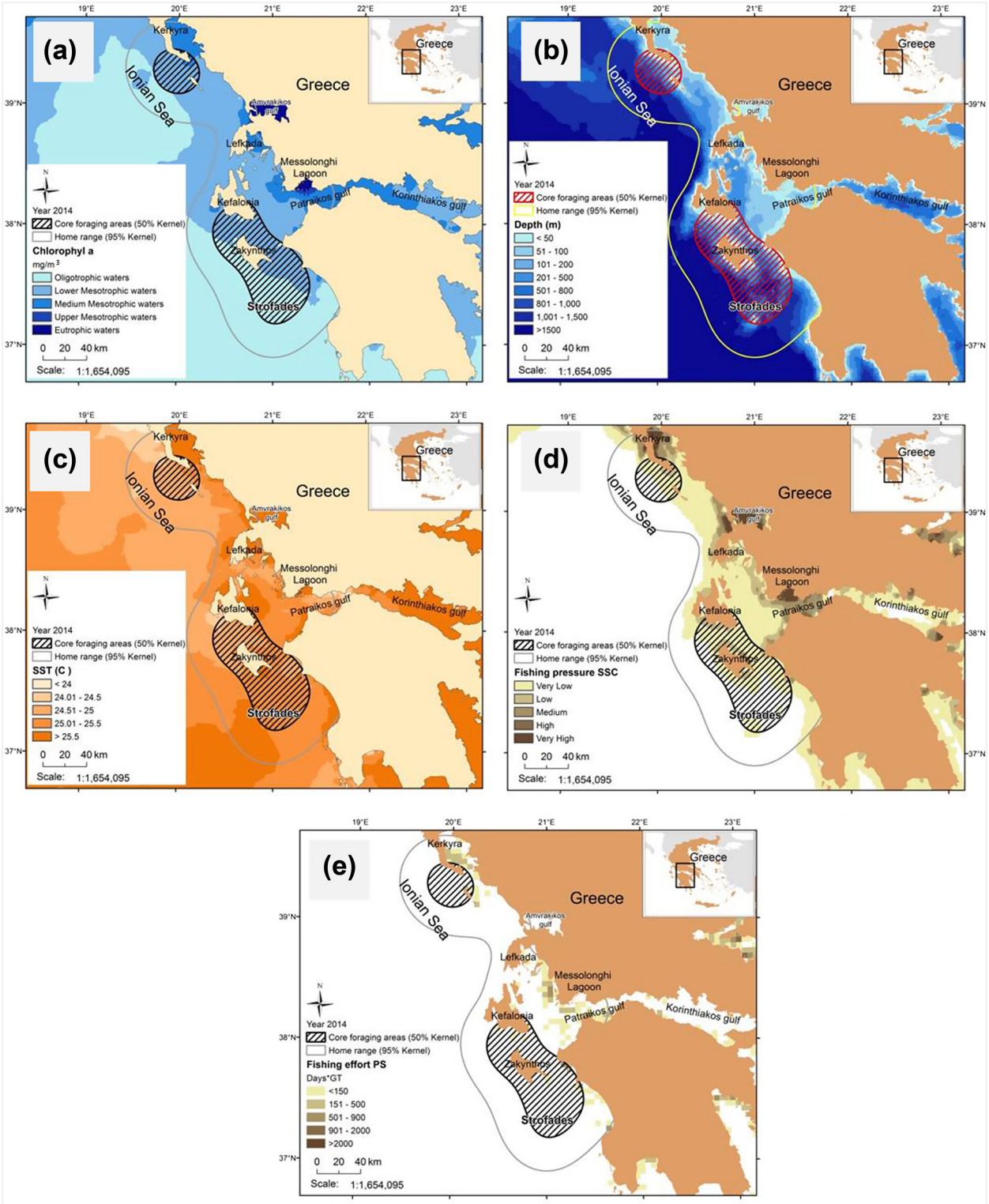

Figure 5. Home range and foraging areas of tracked Scopoli's shearwater breeders compared to (a) sea surface chlorophyll (CHL), (b) bathymetry, (c) sea surface temperature (SST), (d) annual fishing pressure index from small scale fisheries (SSC) in the study area and (e) fishing effort from purse seiners (PS) during July.

waters of the study area during the summer months and could contribute to the provision of discards. For example, Karris et al. (2018) have shown that scavenging shearwaters extensively exploit Ionian trawler fishery discards during their pre-laying period in spring, and consume 70–80% of total fishery waste biomass, while they appear to avoid poisonous species and/or large-sized fish. Concerning the activity of purse seiners, the highest fishing effort is observed in July (Kavadas and Maina 2012) and coincides with egg hatching and the early chick-rearing phase of Scopoli's

shearwater. Nevertheless, this nocturnal fishery activity did not reveal a significant overlap with the foraging areas of shearwaters, contrary to Arcos and Oro (2002) who showed that purse seiners may provide feeding opportunities for seabirds (Fig. 5e). This outcome could be explained by the fact that purse seine vessels operate during moonless nights when shearwaters don't forage and usually visit their nests which is thought to be an adaptation strategy of nocturnal Procellariids to avoid terrestrial predators (Mougeot and Bretagnolle 2000, Keitt et al. 2004, Rubolini et al. 2015).

The current study provides a robust habitat preference analysis of Scopoli's shearwater breeders using a predictive model in which the residual autocorrelation aspects were taken into account to avoid biased outcomes. However, this study was based on a sample of 11 shearwaters tracked for four days during the early chick-rearing phase. We acknowledge that even though the results are reasonably robust since all factors in the final model of habitat preference are highly significant, further work is needed to supplement the model with additional data and explanatory variables such as the bird identity and temporal aspects.

Nevertheless, studies on the spatial ecology of marine top predators could contribute to the designation of conservation hotspot areas in the overexploited eastern Mediterranean Sea. For example, Soanes et al. (2013) pointed out the need for sufficient knowledge arising from telemetric methods when determining the distribution range of seabirds at the various stages of their annual cycle, so as to avoid major errors in designating important marine areas for each species. In the light of this, the current results should be viewed as preliminary, focused on a narrow time-frame, i.e. during the breeding cycle of the Strofades Islands shearwater colony. Ultimately, we believe that this baseline information about the at-sea distribution of shearwaters will contribute to an understanding of the highly dynamic marine ecosystem in the Ionian Sea as well as to ecosystem-based marine spatial management, as mentioned in recent studies (Katsanevakis et al. 2011, Issaris et al. 2012).

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References

Agostini, V. and Bakun, A. 2002. 'Ocean triads' in the Mediterranean Sea: physical mechanisms potentially structuring reproductive habitat suitability (with example application to European anchovy, *Engraulis encrasicolus*). – Fish. Oceanogr. 11: 129–142.

Allen, J. I. et al. 2002. Primary and bacterial production in the Mediterranean Sea: a modelling study. – J. Mar. Syst. 33–34: 473– 495.

Arcos, J. M. and Oro, D. 2002. Significance of nocturnal purse seine fisheries for seabirds: a case study off the Ebro Delta (NW Mediterranean). – Mar. Biol. 141: 277–286.

Arcos, J. M. et al. 2012. Assessing the location and stability of foraging hotspots for pelagic seabirds: an approach to identify marine Important Bird Areas (IBAs) in Spain. – Biol. Conserv. 156: 30–42.

Ben Rais Lasram, F. et al. 2009. Fish diversity patterns in the Mediterranean Sea: deviations from a mid-domain model. – Mar. Ecol. Prog. Ser. 376: 253–267.

Bodey, T. W. et al. 2017. A phylogenetically controlled meta-analysis of biologging device effects on birds: deleterious effects and a call for more standardized reporting of study data. – Methods Ecol. Evol. 9: 946–955.

Bosc, E. et al. 2004. Seasonal and interannual variability in algal biomass and primary production in the Mediterranean Sea, as derived from 4 years of SeaWiFS observations. – Global Biogeochem. Cycles 18: GB1005.

Bost, C. A. et al. 2009. The importance of oceanographic fronts to marine birds and mammals of the southern oceans. – J. Mar. Syst. 78: 363–376.

Cecere, J. G. et al. 2013. 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.

Cecere, J. G. et al. 2014. Effects of environmental variability and offspring growth on the movement ecology of breeding Scopoli's shearwaters *Calonectris diomedea*. – Curr. Zool. 60: 622–630.

Cecere, J. G. et al. 2015. Commercial fisheries, inter-colony competition and sea depth affect foraging location of breeding Scopoli's shearwaters *Calonectris diomedea*. – Ibis 157: 284–298.

Coll, M. et al. 2010. The biodiversity of the Mediterranean Sea: estimates, patterns and threats. – PLoS One 5: e11842.

Davoren, G. K. 2013. Distribution of marine predator hotspots explained by persistent areas of prey. – Mar. Biol. 160: 3043–3058.

Dell' Ariccia, G. et al. 2010. First GPS-tracking of Cory's shearwater in the Mediterranean Sea. – Ital. J. Zool. 77: 339–346.

EC 2003. Council Regulation (EC) 2244/2003 of 18 December 2003 laying down detailed provisions regarding satellite based Vessel Monitoring Systems. – European Commission.

Erikstad, K. E. et al. 1990. Correlations between pelagic distribution of common and Brünnich's guillemots and their prey in the Barents Sea. – Polar Res. 8: 77–87.

Erwin, C. A. and Congdon, B. C. 2007. Day-to-day in sea surface temperature reduces sooty tern *Sterna fuscata* foraging success on the Great Barrier Reef, Australia. – Mar. Ecol. Prog. Ser. 331: 255–266.

ESRI 2007. ArcGIS Desktop: Release 9.2. – Environmental Systems Res. Inst.

FAO 2016. The State of Mediterranean and Black Sea Fisheries. – General Fisheries Commission for the Mediterranean. Rome, Italy.

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

Fric, J. et al. 2012. Conservation actions for the Mediterranean shag *Phalacrocorax aristotelis desmarestii* and Audouin's gull *Larus audouinii* in Greece, including the inventory of relevant marine IBA's. – In: Yésou, P. et al. (eds), Ecology and conservation of Mediterranean seabirds and other bird species under the Barcelona Convention. Proc. 13th Medmaravis Pan-Mediterranean Symposium, Alghero, Sardinia, pp. 223–228.

Giannoulaki, M. et al. 2011. Habitat suitability modelling for sardine (*Sardina pilchardus*) juveniles in the Mediterranean Sea. – Fish. Oceanogr. 20: 367–382.

Granadeiro, J. P. et al. 1998. Flexible foraging strategy of Cory's shearwater, *Calonectris diomedea*, during the chick-rearing period. – Anim. Behav. 56: 1169–1176.
Gotsis-Skretas, O. et al. 1999. Seasonal horizontal and vertical variability in primary production and standing stocks in phytoplankton and zooplankton in the Cretan Sea and Straits of the Cretan Arc (March 1994–January 1995). – Prog. Oceanogr. 44: 625–649.
Grémillet, D. et al. 2014. Irreplaceable area extends marine conservation hotspot off Tunisia: insights from GPS-tracking Scopoli's shearwaters from the largest seabird colony in the Mediterranean. – Mar. Biol. 161: 2669–2680.
Hastie, T. J. and Tibshirani, R. J. 1990. Generalized additive models. – Chapman & Hall/CRC.
Issaris, Y. et al. 2012. Greek Ionian Sea and the adjacent gulfs: ecological mapping considering uncertainty for the needs of ecosystem-based marine spatial management. – Mediterr. Mar. Sci. 13: 297–311.
Kalaroni, S. et al. 2016. Data assimilation of depth-distributed satellite chlorophyll-a in two Mediterranean contrasting sites. – J. Mar. Syst. 160: 40–53.
Karris, G. 2014. The breeding ecology of Scopoli's shearwater (*Calonectris diomedea*) on Strofades Islands. – PhD thesis, Univ. of Patras. Greece (in Greek with English summary).
Karris, G. et al. 2013. Does by-catch pose a threat for the conservation of seabird populations in the southern Ionian Sea (eastern Mediterranean)? A questionnaire-based survey of local fisheries. – Mediterr. Mar. Sci. 14: 19–25.
Karris, G. et al. 2017. Estimating the population size of Scopoli's shearwaters (*Calonectris diomedea*) frequenting the Strofades islands (Ionian Sea, western Greece) by raft counts and surveys of breeding pairs. – North-West. J. Zool. 13: 101–108.
Karris, G. et al. 2018. The use of demersal trawling discards as a food source for two scavenging seabird species: a case study of an eastern Mediterranean oligotrophic marine ecosystem. – Avian Res. 9: 26.
Katsanevakis, S. et al. 2011. Ecosystem-based marine spatial management: review of concepts, policies, tools and critical issues. – Ocean Coast. Manage. 54: 807–820.
Kavadas, S. and Maina, I. 2012. Methodology of analysis of vessel monitoring system data: estimation of fishing effort for the fleet of open sea fishery. – In: 10th Panhellenic Symp. Oceanogr. Fish., May, 2012, Athens, Greece. Book of abstracts, Vol. 1, pp. 164.
Kavadas, S. et al. 2013. IMAS-Fish: integrated management system to support the sustainability of Greek fisheries resources. A multidisciplinary web-based database management system: implementation, capabilities, utilization and future prospects for fisheries stakeholder. – Mediterr. Mar. Sci. 14: 109–118.
Kavadas, S. et al. 2015. Multi-criteria decision analysis as a tool to extract fishing footprints: application to small scale fisheries and implications for management in the context of the Maritime Spatial Planning Directive. – Mediterr. Mar. Sci. 16: 294–304.
Keitt, B. S. et al. 2004. Nocturnal behavior reduces predation pressure on Black-vented Shearwaters *Puffinus opisthomelas*. – Mar. Ornithol. 32: 173–178.
Keller, S. et al. 2016. Large-scale spatio-temporal patterns of Mediterranean cephalopod diversity. – PLoS One 11: e0146469.
Larnicol, G. et al. 2002. Major changes in Mediterranean Sea level variability from seven years of TOPEX/Poseidon and ERS-1/2 data. – J. Mar. Syst. 33–34:63–89.
Lazzari, P. et al. 2012. Seasonal and inter-annual variability of plankton chlorophyll and primary production in the Mediterranean Sea: a modelling approach. – Biogeosciences 9: 217–233.
Louzao, M. et al. 2009. Combining vessel-based surveys and tracking data to identify key marine areas for seabirds. – Mar. Ecol. Prog. Ser. 391: 183–197.
Machias, A. et al. 2001. Bottom trawl discards in the N.E. Mediterranean Sea. – Fish. Res. 53: 181–195.
Magalhães, M. C. et al. 2008. Dual-foraging of Cory's shearwaters in the Azores: feeding locations, behaviour at sea and implications for food provisioning of chicks. – Mar. Ecol. Prog. Ser. 359: 283–293.
Maina, I. et al. 2016. A methodological approach to identify fishing grounds: a case study on Greek trawlers. – Fish. Res. 183: 326–339.
Massa, B. and Lo Valvo, M. 1986. Biometrical and biological considerations on the Cory's shearwater *Calonectris diomedea*. – In: Medmaravis and Monbailliu, X. (eds), Mediterranean marine avifauna: population studies and conservation. Springer, pp. 293–313.
Mazaris, A. D. et al. 2009. Sea surface temperature variations in core foraging grounds drive nesting trends and phenology of loggerhead turtles in the Mediterranean Sea. – J. Exp. Mar. Biol. Ecol. 379: 23–27.
Mehlum, F. et al. 1996. The importance of prey aggregations to the distribution of Brünnich's guillemots in Storfjorden, Svalbard. – Polar Biol. 16: 537–547.
Mougeot, F. and Bretagnolle, V. 2000. Predation risk and moonlight avoidance in nocturnal seabirds. – J. Avian Biol. 31: 376–386.
Moutin, T. and Raimbault, P. 2002. Primary production, carbon export and nutrients availability in western and eastern Mediterranean Sea in early summer 1996 (MINOS cruise). – J. Mar. Syst. 33–34:273–288.
Navarro, J. and González-Solís, J. 2009. Environmental determinants of foraging strategies in Cory's shearwaters *Calonectris diomedea*. – Mar. Ecol. Prog. Ser. 378: 259–267.
Navarro, J. et al. 2009. Foraging segregation between two closely related shearwaters breeding in sympatry. – Biol. Lett. 5: 545–548.
Olivar, M. P. et al. 2010. The role of oceanographic conditions and plankton availability in larval fish assemblages off the Catalan coast (NW Maditerranean). – Fish. Oceanogr. 19: 209–229.
Paiva, V. H. et al. 2010a. How area restricted search of a pelagic seabird changes while performing a dual foraging strategy. – Oikos 119: 1423–1434.
Paiva, V. H. et al. 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.
Passos, C. et al. 2010. Effects of extra mass on the pelagic behavior of a seabird. – Auk 127: 100–107.
Peck, D. R. et al. 2004. Sea surface temperature constrains wedge-tailed shearwater foraging success within breeding seasons. – Mar. Ecol. Prog. Ser. 281: 259–266.
Phillips, R. A. et al. 2003. Effects of satellite transmitters on albatrosses and petrels. – Auk 120: 1082–1090.
Piroddi, C. et al. 2017. Historical changes of the Mediterranean Sea ecosystem: modelling the role and impact of primary productivity and fisheries changes over time. – Sci. Rep. 7: 44491.
Ramos, R. et al. 2013. Meta-population feeding grounds of Cory's shearwater in the subtropical Atlantic Ocean: implications for the definition of Marine Protected Areas based on tracking studies. – Divers. Distrib. 19: 1284–1298.
Rayner, M. J. et al. 2010. Central place foraging by breeding Cook's petrel *Pterodroma cookii*: foraging duration reflects range, diet and chick meal mass. – Mar. Biol. 157: 2187–2194.
Rodgers, A. R. et al. 2007. HRT: home range tools for ArcGIS. Ver. 1.1. – Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada.
Rubolini, D. et al. 2015. The effect of moonlight on Scopoli's shearwater *Calonectris diomedea* colony attendance patterns and nocturnal foraging: a test of the foraging efficiency hypothesis. – Ethology 121: 284–299.

Sarà, M. 1993. Feeding habits of Cory's shearwater (*Calonectris diomedea*) in the central Mediterranean Sea. – In: Aguilar, J. S. et al. (eds), Status and conservation of seabirds. SEO/BirdLife and Medmaravis, Madrid, pp. 213–220.
Shealer, D. A. 2002. Foraging behavior and food of seabirds. – In: Schreiber, E. A. and Burger, J. (eds), Biology of marine birds. CRC Press, pp. 137–178.
Soanes, L. M. et al. 2013. How many seabirds do we need to track to define home-range area? – J. Appl. Ecol. 50: 671–679.
Somarakis, S. et al. 2011. Larval fish assemblages in coastal waters of central Greece: reflections of topographic and oceanographic heterogeneity. – Sci. Mar. 75: 605–618.
Turley, C. M. et al. 2000. Relationship between primary producers and bacteria in an oligotrophic sea-the Mediterranean and biogeochemical implications. – Mar. Ecol. Prog. Ser. 193: 11–18.
Tweedie, M. C. K. 1984. An index which distinguishes between some important exponential families. – In: Ghosh, J. K. and Roy, J. (eds), Statistics: applications and new directions. Proc of the Indian Statistical Institute Golden Jubilee International Conference, Calcutta, pp. 579–604.
van Winkle, W. 1975. Comparison of several probabilistic home-range models. – J. Wildl. Manage. 39: 118–123.
Vaughan, R. 1980. Notes on Cory's shearwater (*Calonectris diomedea*) and some other birds on Linosa, Pelagic Isles. – Riv. Ital. Orn. 50: 143–154.
Weeks, S. J. et al. 2013. Oceanography and seabird foraging: within-season impacts of increasing sea surface temperature on the Great Barrier Reef. – Mar. Ecol. Prog. Ser. 490: 247–254.
Weimerskirch, H. 2007. Are seabirds foraging for unpredictable resources? – Deep-Sea Res. II 54: 211–223.
Wilson, L. J. et al. 2009. Radio-telemetry as a tool to define protected areas for seabirds in the marine environment. – Biol. Conserv. 142: 1808–1817.
Wood, S. N. 2006. Generalized additive models: an introduction with R. – Chapman & Hall/CRC.
Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. – J. R. Stat. Soc. B 73: 3–36.
Wood, S. N. 2017. Generalized additive models: an introduction with R, 2nd edn. –Chapman and Hall/CRC.
Wood, S. N. et al. 2008. Soap film smoothing. – J. R. Stat. Soc. B 70: 931–955.
Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. – Ecology 70: 164–168.
Zuur, A. F. et al. 2010. A protocol for data exploration to avoid common statistical problems. – Methods Ecol. Evol. 1: 3–14.

Supplementary material (available online as Appendix wlb-00388 at <www.wildlifebiology.org/appendix/wlb-00388>). Appendix 1.