

# Productivity changes in the Mediterranean Sea drive foraging movements of yelkouan shearwater *Puffinus yelkouan* from the core of its global breeding range

Francesco Pezzo<sup>1</sup>  | Marco Zenatello<sup>1</sup>  | Giulia Cerritelli<sup>2</sup> | Augusto Navone<sup>3</sup> | Dimitri Giunchi<sup>2</sup>  | Giovanna Spano<sup>3</sup> | Enrica Pollonara<sup>2</sup> | Alessandro Massolo<sup>2</sup> | Anna Gagliardo<sup>2</sup> | Nicola Baccetti<sup>1</sup>

<sup>1</sup>Istituto Superiore per la Protezione e Ricerca Ambientale (ISPRA), Ozzano Emilia, Italy

<sup>2</sup>Ethology Unit, Department of Biology, University of Pisa, Pisa, Italy

<sup>3</sup>Area Marina Protetta "Tavolara-Punta Coda Cavallo", Olbia, Italy

## Correspondence

Francesco Pezzo, Istituto Superiore per la Protezione e Ricerca Ambientale (ISPRA), Via Ca' Fornacetta 9, 40064, Ozzano Emilia (BO), Italy.

Email: francesco.pezzo@isprambiente.it

## Abstract

Pelagic seabirds are tied to their breeding colonies throughout their long-lasting breeding season, but at the same time, they have to feed in a highly dynamic marine environment where prey abundance and availability rapidly change across space and seasons. Here, we describe the foraging movements of yelkouan shearwater *Puffinus yelkouan*, a seabird endemic to the Mediterranean Sea that spends its entire life cycle within this enclosed basin and whose future conservation is intimately linked to human-driven and climatic changes affecting the sea. The aim was to understand the main factors underlying the choice of foraging locations during the reproductive phases. A total of 34 foraging trips were obtained from 21 breeding adults tagged and tracked on Tavolara Archipelago (N Sardinia, Italy). This is the largest and most important breeding area for the species, accounting for more than 50% of the world population. The relationships between foraging movements during two different breeding stages and the seasonal changes of primary productivity at sea were modeled. Movements appeared to be addressed toward inshore (<20 km), highly productive, and relatively shallow (<200 m) foraging areas, often in front of river mouths and at great distances from the colony. During incubation, the Bonifacio Strait and other coastal areas close to North and West Sardinia were the most preferred locations (up to 247 km from the colony). During the chick-rearing phase, some individuals reached areas placed at greater distances from the colony (up to 579 km), aiming at food-rich hotspots placed as far north as the Gulf of Lion (France). The need for such long distance and long-lasting foraging trips is hypothesized to be related to unfavorable conditions on the less productive (and already depleted) Sardinian waters.

## KEYWORDS

foraging ecology, GPS logger, marine primary productivity, Mediterranean Sea, *Puffinus yelkouan*, yelkouan shearwater

## 1 | INTRODUCTION

The Mediterranean Sea is an almost completely enclosed basin characterized by a low concentration of nutrients especially in its Eastern part (Bosc et al., 2004; Kress et al., 2003) and can be classified as an oligotrophic or even ultra-oligotrophic basin (Pujo-Pay et al., 2011). Its biological productivity is typically dominated by a winter–spring bloom occurring in some restricted areas mostly concentrated in its NW portion (D’Ortenzio & Ribera d’Alcala, 2009; Tanhua et al., 2013). As a consequence, if compared to the Atlantic Ocean, it hosts a simplified community of strictly marine seabirds (*sensu* Gaston, 2004), both in terms of species diversity and populations abundance, and characterized by a high proportion of endemic *taxa* of major conservation concern (Blondel et al., 2010; Coll et al. 2010; Zotier et al., 2003). Among them, the yelkouan shearwater *Puffinus yelkouan* shows a decreasing population trend: It is currently considered as a threatened species and has been categorized as Vulnerable on the IUCN Red List (BirdLife International, 2018). Despite this, it is still a poorly monitored species and large undiscovered colonies may exist in the Eastern Mediterranean or even in the Black Sea (BirdLife International, 2018; Derhé, 2012). Known breeding sites are mainly distributed in the central Mediterranean basin, from Menorca island and the Southern French coasts (Bourgeois & Vidal, 2008; Derhé, 2012) to the Sicilian Channel and the Aegean Sea, with a global population size recently re-assessed at 21,000–36,000 pairs (Gaudard, 2018). However, as for most other burrowing petrels breeding at hardly accessible locations such as cliffs and caves, reliable long-term trends and population estimates are scarce (Buxton et al., 2016). Hence, most population estimates have been achieved by imprecise methods such as counting birds while rafting on the water surface in the proximity of colonies (Bourgeois & Vidal, 2008; Raine et al., 2010). Not surprisingly, available data are subject to substantial reassessments following steady improvements in knowledge. It has been reliably ascertained that the range of this species, contrary to other procellariids, is confined to the Mediterranean and Black Sea both during the breeding and non-breeding seasons (Gaudard, 2018; Pérez-Ortega & İsfendiyaroğlu, 2017). As a consequence, the whole population appears to be strongly exposed to the overall condition of this area which is currently affected by major transformations (e.g., Lejeusne et al., 2010; Macias et al., 2015) and which is considered a climate-change hot spot (Giorgi, 2006). The human pressure is constantly increasing with a number of impacts on ecosystems of the Mediterranean Sea (Micheli et al., 2013) and on seabirds as a direct consequence. Concerning the yelkouan shearwater, main threats have been identified such as fisheries by-catch within foraging areas, mortality by alien predators such as rats and cats at breeding sites, fish stock depletion and chronic sea pollution (Bourgeois & Vidal, 2008; Capizzi et al., 2010; Gaudard, 2018; Ruffino et al., 2009). Information on the spatial ecology of the species is scarce, and the knowledge on feeding movements and feeding areas is based on observations carried out at diurnal concentration sites or near bottleneck areas such as the Bosphorous or the Bonifacio Strait (Şahin et al., 2012; Zenatello et al., 2006). Tracking

studies on yelkouan shearwaters breeding in the Mediterranean Sea indicated that birds from French colonies in the Hyères Archipelago mainly move westward along the coast to the adjacent Gulf of Lion (Péron et al., 2013), whereas those from the Maltese colonies show a high individual variability moving both toward the coast of Tunisia/western Libya and to the Aegean Sea (Gatt et al., 2019; Raine et al., 2013). The Sardinian key-site of Tavolara-Punta Coda Cavallo Marine Protected Area hosts the largest known breeding population of the species, estimated at 9,991–13,424 pairs (Zenatello et al., 2006) which, considering the most recent population estimates (Gaudard, 2018), could represent up to 55% of the global breeding population. Conservation actions in this area in the last decades consisted of rat eradication attempts on Molara island (Ragionieri et al., 2013; Sposimo et al., 2012a, 2012b) and in the successful deratization of Tavolara island (<http://www.lifepuffinustavolara.it>) in 2008 and 2017, respectively. However, no protection on foraging areas has been specifically enforced so far, and information on foraging strategies of this breeding population was totally lacking, despite its relevance for the conservation of this and other populations.

Here, we provide the first study describing the foraging movements of the yelkouan shearwaters from the world-largest colony of Tavolara, with the aims of: (i) identifying main foraging and rafting areas by means of GPS loggers; (ii) describing how key ecological factors affect the selection of foraging and resting areas and, as a consequence, the foraging trips length and duration in the course of incubation and chick rearing; (iii) hypothesizing how changes in the Mediterranean habitat could possibly affect spatial ecology; (iv) providing information for conservation scenarios to come.

## 2 | MATERIALS AND METHODS

### 2.1 | Study site and model species

The study was carried out from 2011 to 2015 on Tavolara Island (40°54’N, 09°42’E; Sardinia), in the largest known breeding site of the yelkouan shearwater (Gaudard, 2018; Zenatello et al., 2012). All activities were performed in a single cavern hosting up to 15 accessible nests that were usually in a rat-free condition. Birds were captured by hand on the nest and equipped with GPS loggers (Gypsy-2 and Gypsy-4 by Technosmart and I-gotU GT120 by Mobile Action Technology). GPS loggers were attached to the mantle feathers of breeding adults by adhesive TESA tape (total weight: 13–20 g according to battery size). The weight of GPS loggers was 3.1%–4.7% of the average mass of adults (424.5 g  $\pm$  28.6 g *SD*,  $n = 29$ ). Birds were handled for 15–30 min and then released where trapped (i.e., at their nest). Loggers were retrieved by recapturing breeders on their nests or at the entrance of the cave when returning from their foraging trips. Nests were regularly monitored during the whole study period to assess their breeding success (Table 1). Capture, handling, and tagging procedures were conducted by the Italian Institute for Environmental Protection and Research (ISPRA), under the authorization of Law 157/1992 (Art.4.1 and Art 7.5), which

**TABLE 1** Characteristics of the tracks obtained from GPS data loggers mounted on yellow shearwaters at Tavolara Island (Sardinia, IT) from 2011 to 2015. For each bird, Bird ID, Track ID (\*not included in the analysis), Breeding stage (I: incubation; CR, chick rearing), date and time of First and Last location recorded, GPS sampling rates, and number of fixes per track are reported. In the Track, column is specified if the tracking was complete (c) or if interrupted abruptly before the bird returned to the colony (i). The baseline between the maximum distant point reached and the colony is reported as Distance from Tavolara, while the Total Traveled Distance was measured as the sum of all the distances between successive locations

Bird ID	Track ID	Breeding stage	First location	Last location	Total duration (days)	Year	Track	Sampling interval (min)	Fix	Distance from Tavolara (km)	Total traveled distance (km)
TA2226	T24*	I	03/04/2011 06:06:00	03/04/2011 13:16:00	1	2011	i	10	21	63	84
TJ3259	T23	I	05/04/2011 04:08:00	09/04/2011 10:38:00	4	2011	i	10	464	190	538
TA2229	T25	I	04/04/2011 05:35:00	08/04/2011 11:55:00	4	2011	i	10	87	165	361
T18	T18	CR	11/06/2012 03:37:00	17/06/2012 23:41:00	7	2012	c	60	162	141	941
T19*	T19*	CR	18/06/2012 03:43:00	18/06/2012 23:42:00	1	2012	c	60	21	69	
T06	T06	I	27/03/2013 07:23:00	03/04/2013 22:19:00	8	2013	c	20	511	225	1,266
TJ3270	T10*	I	16/04/2012 04:20:00	17/04/2012 23:35:00	2	2012	c	60	42	18	
TJ3267	T13*	I	16/04/2012 06:25:00	17/04/2012 00:19:00	1	2012	c	60	19	27	
T14*	T14*	I	17/04/2012 07:18:00	18/04/2012 23:38:00	2	2012	c	60	42	33	
TJ3263	T17	CR	11/06/2012 03:10:00	15/06/2012 00:58:00	4	2012	c	60	94	118	586
TA2223	T22	I	17/04/2012 05:30:07	18/04/2012 05:50:08	1	2012	i	20	58	53	286
T15	T15	CR	11/06/2012 03:03:00	13/06/2012 00:56:00	2	2012	c	60	47	107	406
T16	T16	CR	13/06/2012 05:54:00	16/06/2012 02:56:00	3	2012	c	60	70	128	553
TA2225	T11*	CR	17/04/2012 07:27:00	17/04/2012 22:17:00	1	2012	c	60	16	21	
T12*	T12*	CR	19/04/2012 07:21:00	19/04/2012 22:56:00	1	2012	c	60	17	26	
T08	T08	I	26/03/2013 06:41:00	30/03/2013 21:41:16	5	2013	c	20	309	120	189

(Continues)

TABLE 1 (Continued)

Bird ID	Track ID	Breeding stage	First location	Last location	Total duration (days)	Year	Track	Sampling interval (min)	Fix	Distance from Tavolara (km)	Total traveled distance (km)
TA2236	T20	CR	11/06/2012 03:57:00	13/06/2012 23:41:00	3	2012	c	60	67	134	389
	T21	CR	14/06/2012 05:37:00	16/06/2012 01:42:00	2	2012	c	60	45	137	357
	T03	I	26/03/2013 04:33:00	01/04/2013 22:58:00	7	2013	c	20	465	184	1,041
TJ3290	T04	I	23/03/2013 07:29:00	30/03/2013 22:49:00	8	2013	c	20	506	144	1,249
TA2228	T09	I	25/03/2013 03:35:00	31/03/2013 23:38:00	7	2013	c	20	468	120	1,073
TJ3258	T07	I	25/03/2013 04:09:00	30/03/2013 22:37:00	6	2013	c	20	399	189	887
TJ3300	T28	I	26/03/2013 18:42:00	31/03/2013 03:20:06	4	2013	i	20	303	247	636
TA2235	T02	I	27/03/2013 04:42:00	05/04/2013 00:48:00	9	2013	c	20	609	374	1808
TH1332	T05	I	27/03/2013 05:51:00	03/04/2013 23:13:00	8	2013	c	20	524	177	1,097
TJ3288	T29	I	29/03/2013 01:09:00	02/04/2013 01:18:00	4	2013	i	20	279	217	785
TJ3262	T26	I	30/03/2013 05:44:00	31/03/2013 04:20:04	1	2013	i	20	69	70	106
T86753	T01	I	31/03/2013 07:06:00	07/04/2013 13:16:00	7	2013	i	20	468	184	897
TJ3261	T27	I	26/03/2013 00:45:25	30/03/2013 17:44:00	5	2013	i	20	341	238	892
	T31	CR	14/06/2013 03:47:00	23/06/2013 22:16:00	10	2013	c	10	1,387	579	2,341
	T32	CR	24/06/2013 03:49:00	24/06/2013 22:29:00	1	2013	c	10	107	100	291
	T33	CR	25/06/2013 03:53:00	28/06/2013 19:43:00	4	2013	i	10	516	315	550
TA2231	T30	CR	15/06/2013 03:42:00	28/06/2013 04:44:00	13	2013	i	10	1846	570	2,601
TJ3271	T34	I	17/04/2015 04:47:00	21/04/2015 00:00:00	4	2015	c	20	270	206	658

regulates research on wild bird species. Three birds were tracked in subsequent years (Table 1). The datasets generated during and/or analyzed during the current study are available in the Movebank Data Repository, <https://doi.org/10.5441/001/1.k49p9t60> (Pezzo et al., 2021).

## 2.2 | Data analysis

The sampling rate of the loggers changed during the study period (10, 20 or 60 min) depending on GPS receiver, battery size, and breeding stage (see Table 1 for details). For each fix, the GPS loggers recorded date, time, speed, and positional data (Longitude and Latitude). Tracks were plotted on Qgis (<http://www.qgis.org/>), and individual foraging trips were identified as round-trips flights from the colony to feeding areas. One to four trips per individual was recorded. For each fix, the distance from the preceding fix and the distance from the colony (i.e., the minimal distance a bird can fly to reach the current point, assuming shearwaters did not fly over land) were calculated. In order to identify the foraging areas and the activity of the birds, each fix was classified into one of the following three categories: travelling (T), resting (R), foraging (F) corresponding to three distinct movement patterns. While travelling, the bird moves with a consistently high speed between two distant sites. The resting behavior is characterized by low speed movements within a short range attributable to the sea currents and waves. In the foraging areas, shearwaters perform short range movements either at low or medium speed (see below).

In detail, the classification was based on the following criteria:

1. Fixes with a speed greater than 10 km/h have been classified as T (Guilford et al., 2008), provided that their distance from the preceding fix was greater than 5, 10, and 30 km for the sampling rate of one fix every 10, 20, and 60 min, respectively. In addition, each fix with a speed greater than 10 km/h not meeting the previous conditions was anyhow classified as T, provided that the absolute difference between its distance from the colony and the preceding fix distance from the colony was greater than 2.5, 5, and 15 km, for the sampling rate of one fix every 10, 20, and 60 min, respectively. The latter criterion was adopted to discriminate patterns of birds travelling along a curved path (e.g., as needed to circumnavigate islands) from those displayed by birds moving rapidly within a restricted foraging area. All the distance categories for the classification of the T fixes have been arbitrarily chosen on the basis of the direct observation of the tracks of birds that were traveling between two distant areas.
2. R fixes included all the fixes with a speed lower than 5 km/h, provided that the distance from the preceding fix was shorter than 0.5 km when the sampling rate was every 10 and 20 min, and 1.5 km when the sampling rate was of 1 fix every 60 min. The criterion based on the distance from the preceding fix was actually

unreliable in case of either strong drift or short range movements within the foraging area (see below for the detection of foraging areas).

3. All the remaining fixes have been assigned to the F category.

Each individual track was subsequently plotted in Qgis for visual inspection. When a bird was resting for several hours sitting on the sea surface, a characteristic pattern of fixes resulted, due to the sea current and/or wind drifting the bird in a constant direction (Fayet et al. 2015). In these cases, the mean vector length (Batschelet, 1981) for a set of R fixes, computed averaging the direction of movement between two subsequent fixes, was greater than 0.90. Therefore, the mean vector length was used as a criterion when a visual inspection revealed possible inconsistencies in the fix class assignment. If the mean vector length of consecutive F fixes was greater than 0.90, the fixes were re-assigned to the R category. Conversely, if the mean vector length of consecutive R fixes was smaller than 0.75, the fixes were re-assigned to the F category. For each track, the first fixes (1–3) were not classifiable with the above criteria, and therefore, they have been excluded from the analysis.

The tracks sampled at one fix every 10 min were resampled at one fix every 20 min and used, together with the other 20 min sampling rate tracks, to perform a density kernel analysis with those locations ( $n = 27$  tracks). The core foraging distributions were calculated on the basis of the distribution of F fixes. The density of the distribution of F fixes was modeled using the fixed kernel technique (Worton, 1989) available in R-package *adehabitatHR* 4.15 (Calenge, 2006). The ad-hoc bandwidth for the smoothing parameter ( $h_{ad-hoc}$ ) was selected by sequentially reducing the reference bandwidth of the smoothing factor ( $h_{ref}$ , i.e., the optimal bandwidth under the assumption of bivariate normality) in 0.10 increments and choosing the smallest increment of  $h_{ref}$  that: (i) resulted in a contiguous K95% isopleth, and (ii) contained no lacuna within K95% (Kie, 2013). Core areas were identified by applying the Area Independent Method developed by Seaman and Powell (1990). The method divides the range in areas of high and low fix density using an objective criterion which is based on a graphical representation of the range area in relation to the density of the considered fixes. In this way, it is possible to identify the dividing point between high- and low-density areas, as the point where the plot is maximally distant from a straight line of slope +1 that represents a distribution of random use. We performed the analysis considering steps = 5% calculating subsequent range area sizes using *adehabitatHR*. On the basis of the point of maximum distance, we defined the core areas with a different percentage of volume contour per individual (median: 55%; IQR: 50%–55% volume contours).

We used the R fixes distribution to assess whether and which of the tracked birds rested in areas proximal (within 5 km radius; the distance range from the colony within which rafts are usually observed) to yelkouan shearwaters colonies other than those of Tavolara archipelago and adjacent Cape Figari area that are all located one next to another. A 5 km radius buffer was created with

Qgis around each yelkouan shearwater colony known in Italy and France (Baccetti et al., 2009; Cadiou et al., 2004). We intersected the 5 km radius buffer with the R fixes distribution, in order to count which colonies were approached by the tracked birds. In addition, we identified the areas mostly used for resting by the tracked birds. To do so, a 10 km hexagonal grid was created in Qgis; for each individual, we computed the percentage of R fixes falling in each hexagon. For each track, the number of R fixes in each cell was computed and categorized in three categories depending on the proportion of R fixes contained in a cell: (i) number of fixes below the median value; (ii) number of fixes ranging between the median value and the third percentile; (iii) values higher than the third percentile. For each cell, we summed the scores obtained from all the tracks in order to identify areas with the highest score, that is, those most likely frequented by resting birds.

For each fix of the tracks, the distance from the nearest coast was computed. In order to assess whether the birds had a preference for staying near to or far from the coast, for each bird the percentage of fixes of each considered category (T, R, F) located within 20 km and further than 20 km was compared by Wilcoxon test for paired data. When more than one tracks per bird were available, the individual mean values were considered.

Each location was classified as “day” or “night” according to their corresponding time of nautical dawn and dusk obtained using the “R-package” *suncalc 0.5.0* (Thieurmel & Elmarhraoui, 2019). Differences in the activity between day and night were tested by applying the Wilcoxon test for paired data to the individual percentage of each behavioral category. As before, when more than one track per bird were available, the individual mean values were considered.

To analyze foraging habitat selection (sensu Manly et al., 2002) by yelkouan shearwaters, we used remote sensing data to quantify Bathymetry (ETOPO Global Relief Model, NOAA) and Ocean Productivity (MODIS) at a resolution of 1.6 and 9 km, respectively. Productivity data ( $\text{g C}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ ) used were averaged over eight days (octads) and were as much as possible contemporary to each foraging trip. Given the resolution of the remote sensing data, use and availability were estimated at the individual and population level, respectively (first order resource selection; Meyer & Thuiller, 2006). On the basis of the productivity raster data, a grid with 9 km squared cell was created. For each cell with at least one F fix, five cells were randomly sampled within the population 95% range (calculated with the same kernel approach described above) by considering the F fixes of all tracks. This process was repeated for all available foraging trips. For all used and random locations, we extracted the values of bathymetry, distance from the colony site to the center of the cell, and productivity. Due to the low sample size, the year of tagging was not included in the analysis. Data exploration was carried out following the protocol described in Zuur and Ieno (2016).

The resource selection function (Manly et al., 2002) was calculated with a Generalized Linear Mixed Model with a binomial error distribution, and bird ID and track ID (nested within bird ID) as random intercepts by means of the R-package *glmmTMP 1.0.2.1* (Brooks et al., 2017). The variables considered in the full model were

as follows: sea productivity (PROD, inverse transformed), bathymetry (BATHY), distance from the colony (DCOL), and the reproductive stage (STAGE, two-levels factor: incubation and chick rearing). We hypothesized that the probability of selection use was higher for cells with higher PROD, and lower BATHY and DCOL. We tested whether the incubation period modified the way the birds used the resources by including the second-order interactions STAGE:DCOL, STAGE:BATHY, STAGE:PROD. The fixed part of the model was simplified by means of the Akaike Information Criterion corrected for small sample size (AICc, Burnham & Anderson, 2002), considering all the models between the full model and the model which included all main effects. Significance was tested by means of the type II Wald  $\chi^2$  test using the R-package *car 3.0-10* (Fox & Weisberg, 2019). Model fit, overdispersion, collinearity, and spatial autocorrelation of the residuals were checked before using the final model for inference by means of the R-packages *DHARMA 0.3.3.0* (Hartig, 2020) and *performance 0.7.0* (Lüdtke et al., 2020). The marginal  $R^2$  ( $\text{mR}^2$ ), which represents the variance explained by fixed factors only (Nakagawa & Schielzeth, 2013), was calculated using the R-package *MuMIn 1.43.17* (Bartoń, 2020). The performance of the final models was also evaluated using the Area Under the Curve (AUC) generated by the Receiver Operating Characteristic (ROC; Fielding & Bell, 1997; Pearce & Ferrier, 2000) by means of the R-package *ROCR 1.0-7* (Sing et al., 2005). All calculations were performed using R 4.0.4 (R Core Team, 2021).

To further investigate bird foraging strategies in the two phases of the nesting period, we analyzed how sea productivity varied in cells located at different distance from the colony over the study period. In this analysis, we considered only the cells with at least one F fix during the whole study period, that is, the cells used at least once by tracked birds for foraging, and with no missing data on productivity ( $n = 333$ ). To reduce sampling bias, we excluded the years where birds were tracked during incubation or chick rearing only (i.e., 2011 and 2015). The available cells were then resampled to avoid including adjacent cells in the analysis, in order to reduce spatial autocorrelation, by means of the R-package *spThin 0.2.0* (Aiello-Lammens et al., 2015). The number of cells considered in the analysis was 91. Data were modeled by means of Linear Mixed Models considering productivity (inverse transformed) as dependent variable and cell ID as random intercept. The independent variables considered in the model were as follows: octad (OCTAD, 5-level factor coded using the first Julian day of the octad: 81, 89, 105, 161, 169), distance from the colony (DCOL), bathymetry (BATHY) and the second-order interactions OCTAD:DCOL and OCTAD:BATHY. Based on observed productivity variations, we hypothesized that the productivity of cells nearest to the colony decreases over time much more strongly than that of cells more distant from the colony site, thus inducing birds to increase the frequency of long foraging trips. The packages and the procedures used to check model assumptions, to test significance, and to evaluate model fit were the same as described above. Throughout the text, means are reported along with their standard deviation (mean  $\pm$  SD) unless otherwise specified.

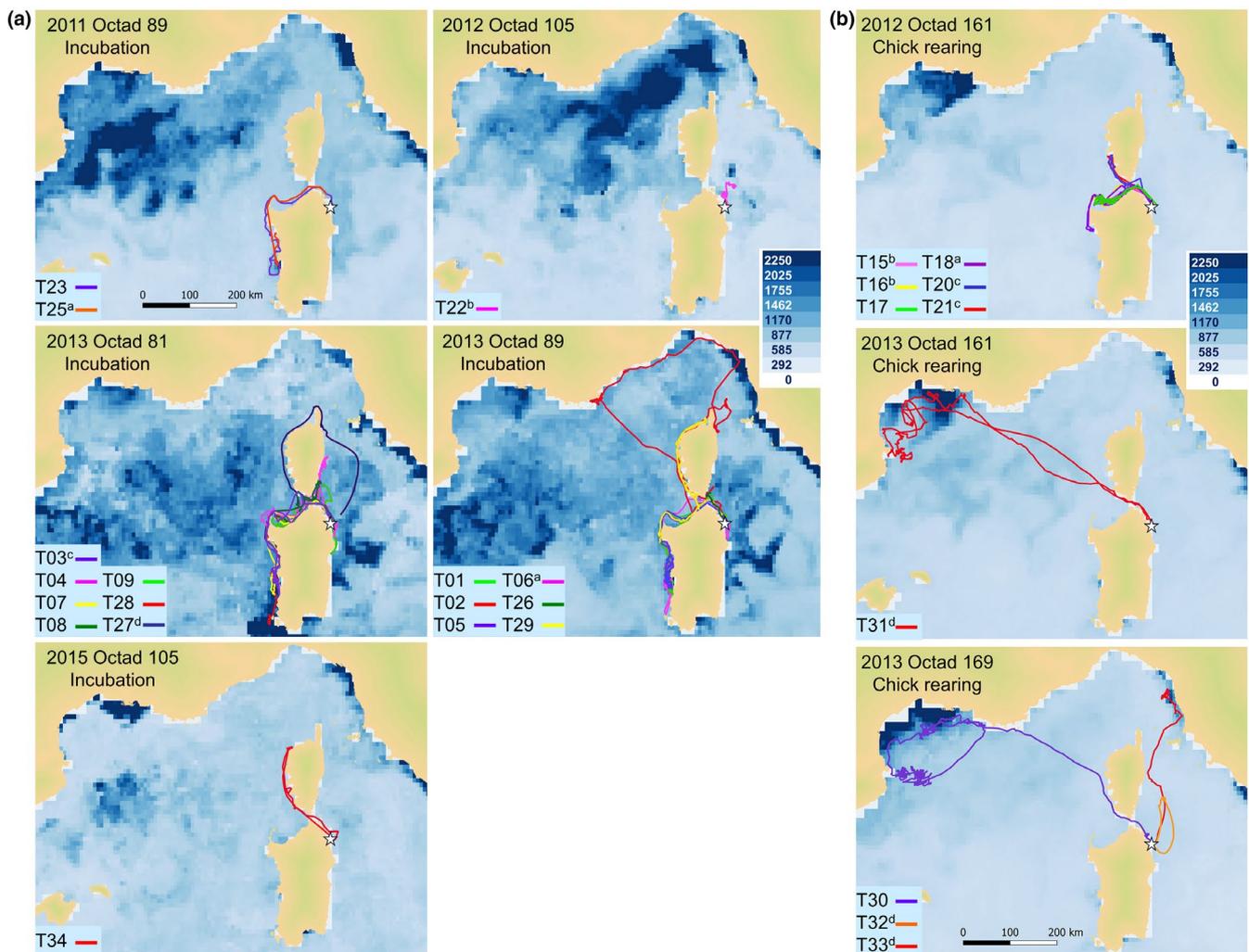
### 3 | RESULTS

Out of a total of 43 capture events in subsequent years and 60 GPS deployed, net of the birds not recaptured ( $n = 7$ ), recaptured without logger ( $n = 14$ ), or recaptured with improperly functioning loggers ( $n = 5$ ), we obtained 34 foraging trips from 21 birds tracked during incubation (March–April;  $n = 21$  trips) and chick-rearing period (May–June;  $n = 13$  trips). No breeding failures were recorded between capture and recapture. Table 1 reports the details of the tracks recorded, such as whether they were complete (the entire journey from the colony to the foraging area and back was recorded), or interrupted (the power ran out before the bird homed after the foraging trip), and tracks excluded from the analysis due to both the low sampling rate (1 fix every 60 min) and low number of fixes ( $<45$ ).

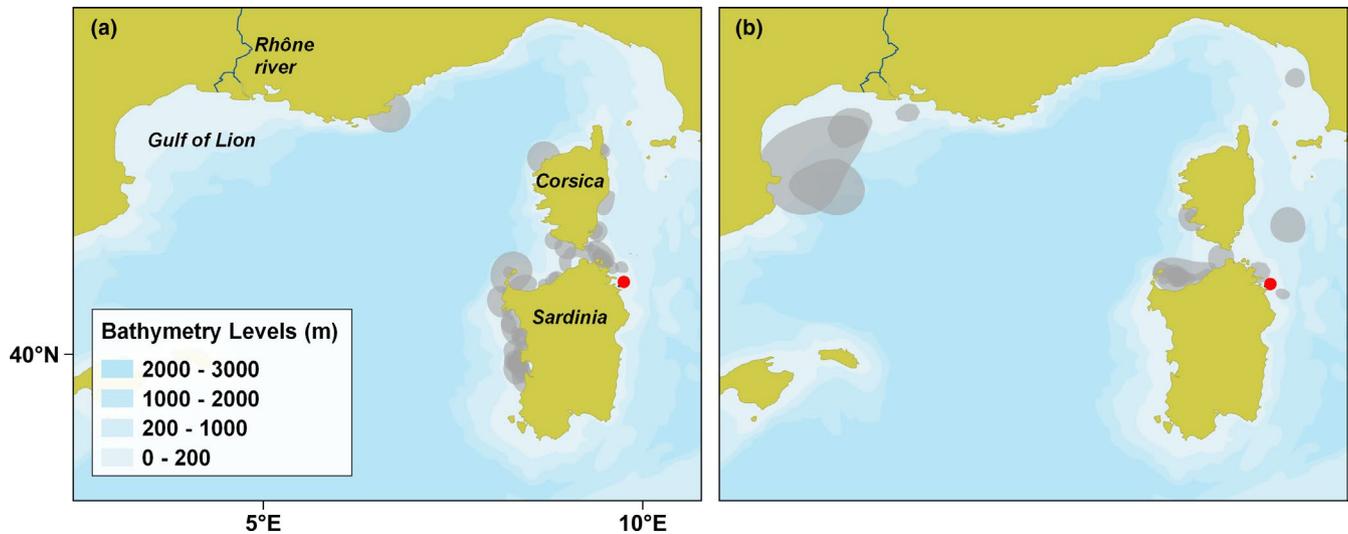
Birds returned to the colony after 6.5 days (median; range 1–8 days) during the incubation period ( $n = 12$  complete tracks from 11 birds) and after 2.0 days (median; range 1–10 days) during

the chick-rearing period ( $n = 11$  complete tracks from 6 birds). Considering only the complete tracks included in the analysis (9 tracks from 9 birds in the incubation period, and 8 tracks from 5 birds during the chick-rearing period; see Table 1), it appeared that during the incubation and chick-rearing periods, the mean track length was  $1,030 \pm 140$  km and  $733 \pm 225$  km, respectively, reaching a mean distance from the colony of  $193 \pm 24$  km and  $181 \pm 53$  km, respectively.

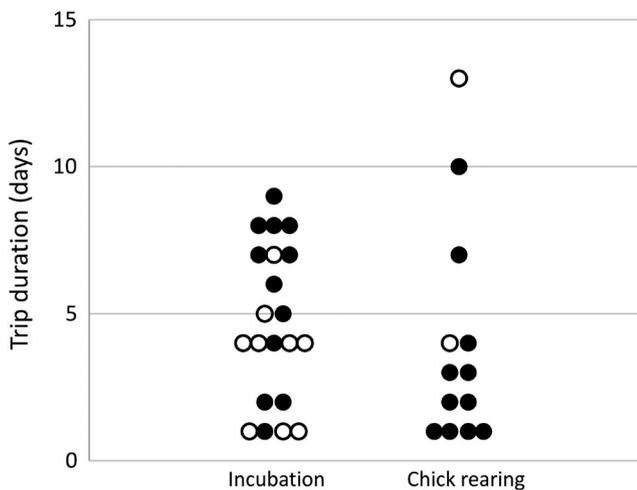
During the incubation period, foraging trips were mostly concentrated in proximity of the Western and Northern coasts of Sardinia and South Corsica (Figure 1a). During the chick-rearing period, Western Sardinia was almost entirely deserted, and new core feeding areas were used in the French/Spanish waters of the Gulf of Lion (max distance 579 Km). A number of birds continued to feed along North Sardinia and South Corsica (Figures 1b and 2). Considering all tracks, during the incubation foraging trips ranged from 1 to 9 days, while during chick-rearing period, most foraging trips lasted less than



**FIGURE 1** Tracks of yelkouan shearwaters GPS tagged from 2011 to 2015 at Tavolaria Island, Sardinia, IT (white star). The blue shades show sea net primary productivity (expressed as  $\text{mg C}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ ) grouped according to Octads (8 days periods) in 2011–2015. Each panel contains the tracks obtained in the octad for which sea productivity was calculated and included in the analysis (see Table 1). T indicates the track ID; the apical letters (a to d) denote tracks from the same individual. The reproductive stage (a, incubation; b, chick rearing) of birds at the time of recording is written in each panel



**FIGURE 2** Foraging core areas with a different percentage of volume contour per individual (median: 55%; IQR: 50%–55% volume contours) obtained from the distribution of the fixes categorized as F (feeding activity) of yelkouan shearwaters GPS tagged from 2011 to 2015 at Tavolara Island (red dot; Sardinia, IT). (a) Incubation period ( $n$  tracks = 17,  $n$  individuals = 16); (b) Chick-rearing period ( $n$  tracks = 10,  $n$  individuals = 6)



**FIGURE 3** Trip duration in days estimated from yelkouan shearwaters tracks ( $N = 34$ ) recorded during incubation and chick rearing stages from 2011 to 2015 at Tavolara Island (Sardinia, IT). Open dots represent incomplete tracks

4 days (Figure 3), although some individuals ( $n = 3$ ) returned to the colony after much longer trips. Yelkouan shearwaters were mainly detected within coastal marine areas (Figure and tracks deposited in Movebank). In particular, most of the fixes of all three behavioral categories were collected within 20 km from the coast (Figure 4). Proportions of fixes obtained within 20 km from the coast were significantly higher than those located further (Wilcoxon test, Resting  $N = 18$ ,  $T = 2$ ,  $p < .001$ ; Feeding,  $N = 18$ ,  $T = 3$ ,  $p < .001$ ; Traveling  $N = 18$ ,  $T = 3$ ,  $p < .001$ ) and core foraging areas were located in coastal marine areas.

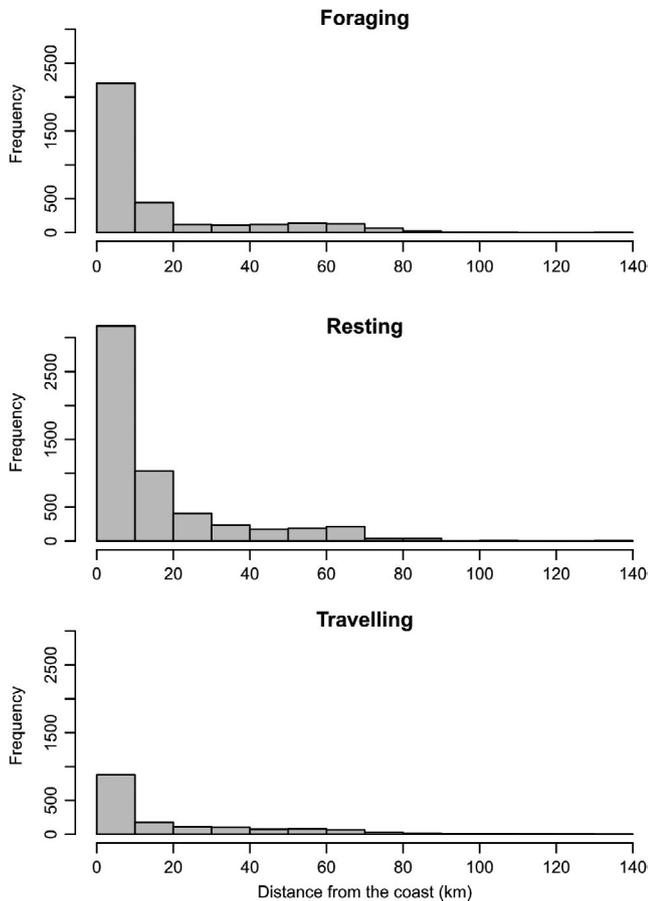
Considering both the tracks collected during the incubation and the chick-rearing periods, it emerged that birds spent half of their time resting on the water ( $R$ ,  $50.8 \pm 8.2\%$ ), while the remaining time

was spent mostly foraging ( $F$ ,  $35.6 \pm 6.6\%$ ) and, to a lesser extent, travelling ( $T$ ,  $13.6 \pm 4.0\%$ ). The 24 hr pattern of activity (Figure 5) showed that foraging ( $F$ ) and travelling ( $T$ ) fixes turned out to mostly occur, for all birds, during the day (Wilcoxon test,  $N = 18$ ,  $T = 0$ ,  $p < .001$ ). Foraging fixes ( $F$  class) occurred during the whole daytime and immediately after sunset. Traveling started one hour after sunrise. In June, the travelling activity was not performed throughout the day, showing a decrease during the central part of the day (Figure 5). The time spent by the birds resting on the water during day and night was comparable (Wilcoxon test,  $N = 18$ ,  $T = 56$ ,  $p > .05$ ).

The analysis of the spatial distribution of the Resting fixes (Figure 6) showed that the mean and median score computed on 273 cells containing at least one  $R$  fix was 3.18 and 2, respectively. Only 12 hexagonal cells of the grid obtained the highest scores ranging from 9 to 29 (see Materials and Methods for details) showing that birds were highly concentrated for resting near their breeding colony and along the Western Sardinian coast, near the Oristano Gulf. Lower concentration areas were also observed along the coast of Northern Sardinia (Figure 6).

According to AICc, the most supported model for foraging habitat selection among the considered set included all main effects and the interactions between nesting period and bathymetry or distance from the colony (Table 2 and 3). This model had a strong support, as the second best model was not truly competitive because its additional parameter did not significantly improve the fit. Indeed, the value of the maximized log-likelihood increased only slightly ( $-807.19$  vs.  $-806.95$ ; see Burnham & Anderson, 2002) and the two measures of performance ( $mR^2$  and AUC) did not change noticeably (Table 2).

As expected, sea productivity had a positive effect on the probability of use, irrespective of the reproductive stage (Table 3). During incubation, birds foraged preferentially in areas relatively near to the colony and at shallow sea depths, while during chick rearing, they



**FIGURE 4** Frequency distribution of the distances from the coast of fixes belonging to the three behavioral categories (Feeding, Resting, Travelling) obtained from GPS tagged yelkouan shearwaters at Tavolara Island (Sardinia, IT) from 2011 to 2015. The reported data refer to the tracks of all animals in both breeding stages (incubation and chick rearing)

preferred to use cells located at a greater distance from the colony and did not avoid areas with deeper sea (Figure 7).

The results of the model used to investigate the variability of sea productivity during the tracking period revealed a significant effect of the interactions between sampled octad and bathymetry or distance from the colony (OCTAD:BATHY and OCTAD:DCOL) (Table 4). As expected, cells located near the colony showed a marked productivity decrease late in the breeding season; the productivity of cells located far from the colony site was high and did not show any trend across octads (Figure 8).

## 4 | DISCUSSION

Yelkouan shearwaters showed a strong spatial preference for coastal waters (<20 km from the coast) that were located within the continental shelf (<200 m isobaths, neritic zone) and characterized by a high primary productivity. These findings are consistent with what has been described for yelkouan shearwaters breeding in France (Lambert et al., 2017; Péron et al., 2013) as well as for the closely

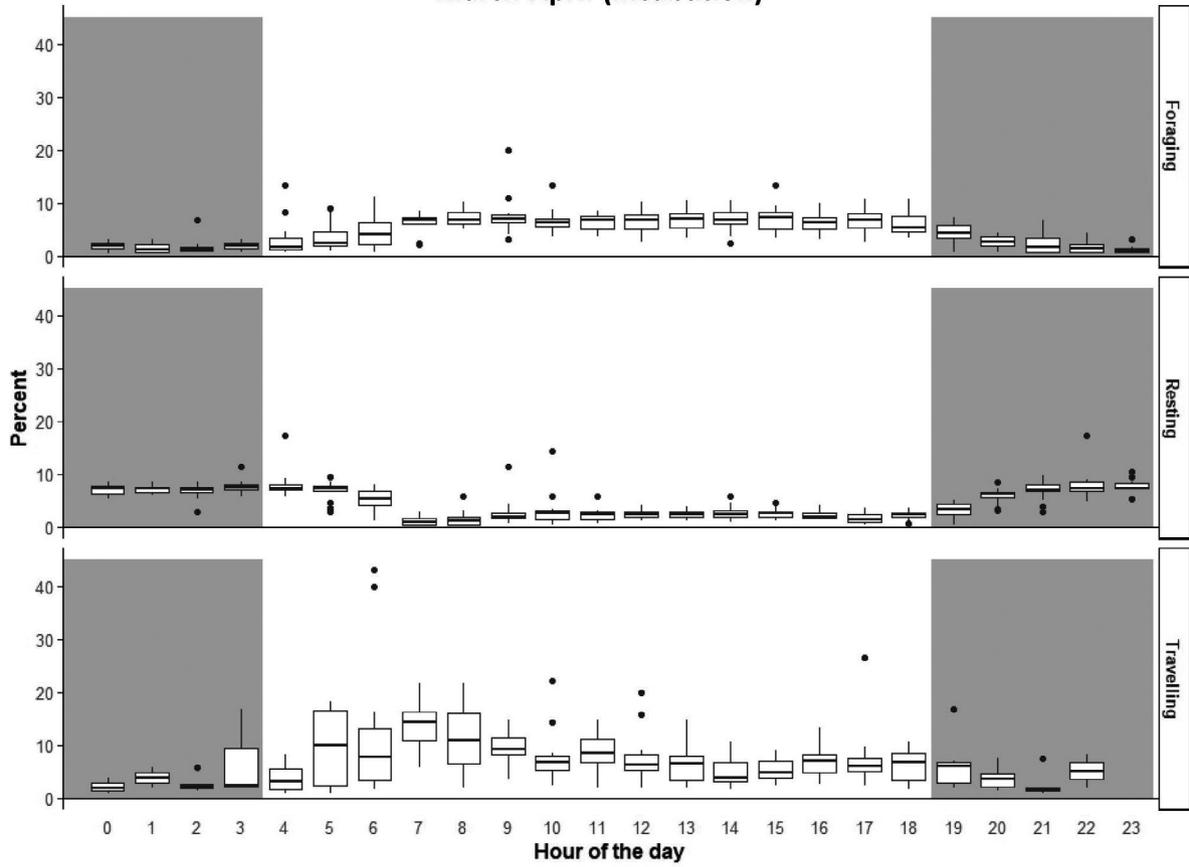
related Balearic shearwater *Puffinus mauretanicus* within the NW Mediterranean and along the Portuguese coasts during the post-breeding period (Araújo et al., 2017; Meier et al., 2015). The positive selection of coastal and relatively shallow waters by the yelkouan shearwater has been documented also during the non-breeding period, both in the Northern African coastal waters (Raine et al., 2013) and in the Black Sea (Pérez-Ortega & İsfendiyaroğlu, 2017).

Tagged birds mostly used the North and Western coast of Sardinia and the Southern coast of Corsica during their foraging activities through the incubation. The importance of the Bonifacio Strait, as a bottleneck for birds that move between the breeding and the feeding areas, has since long been known from land-based observations (Cesaraccio, 1989; Thibault & Bonaccorsi, 1999) and from counts aimed at assessing the size and distribution of yelkouan shearwater stocks around Sardinia (Zenatello et al., 2012). It is noteworthy that all birds seemed to prefer to circumnavigate Sardinia anticlockwise from the North side to reach the Western side of Sardinia, instead of moving southward from their home colony along a route of comparable length. As a consequence, the coastal marine area south of Tavolara appeared to be unexpectedly underexploited by the tagged birds. Our data do not exclude important feeding areas in East Sardinia under different conditions from those prevailing during our study periods, but the narrow continental shelf and the deep waters characterizing this stretch of coastline suggest that it could be less suitable as a feeding zone.

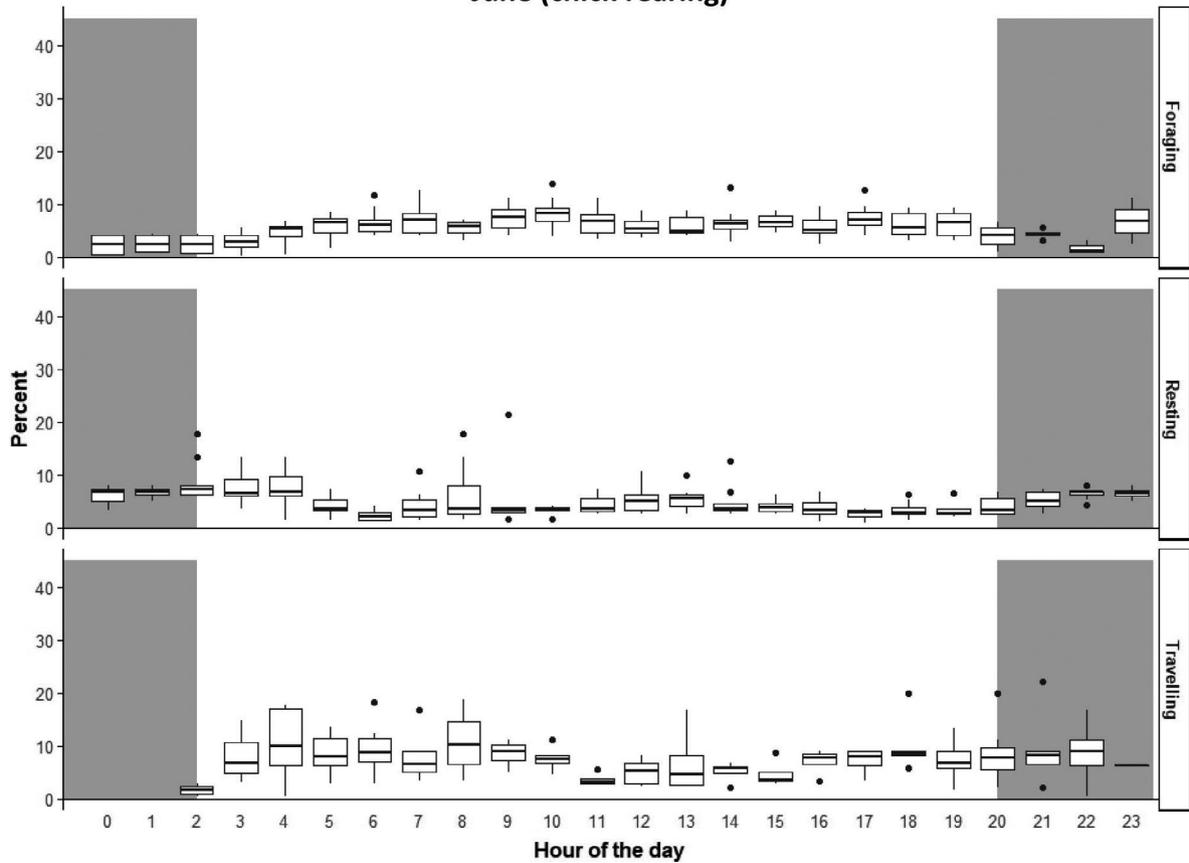
Key foraging areas changed during the course of the breeding season. Incubating birds mostly concentrated in the Bonifacio Strait, along the coast of North Sardinia (Asinara Gulf) and in West Sardinia (waters off the Oristano Gulf), whereas during chick-rearing foraging trips heading to North Sardinia and Southern Corsica decreased, and trips toward more distant (up to 579 Km) foraging areas (namely the Gulf of Lion and Northern Tuscany) were recorded. Notably, the West Sardinian waters, which represented the main foraging area during incubation, were not visited during the chick-rearing stage. Two birds traveled with a direct flight in a NW direction across the Mediterranean to the Gulf of Lion, which appeared to be an important foraging area for birds nesting at Tavolara during the late breeding stages. It is worth noticing that breeding yelkouan shearwaters from the French islands of Porquerolles and Port-Cros colonies also show regular movements to the Gulf of Lion (Péron et al., 2013), where their distribution largely overlaps the core foraging areas locally identified by the present study. The Gulf of Lion hosts up to 10,000 yelkouan shearwaters, with peaks in February-June (Bourgeois & Vidal, 2008). Since the French breeding population is relatively small (500–1,000 breeding pairs) (Gaudard, 2018), this area likely acts as foraging ground also for birds coming from more distant colonies (Carboneras, 2013). Our study confirms this observation and the role of this gulf as a feeding hotspot for yelkouan shearwaters coming from the core of the breeding range.

As a general pattern, the main foraging areas were largely located in shallow (<200 m depth) areas with high nutrient inflows brought to the sea by large rivers, which trigger complex food chains (Caddy, 2000; Darnaude, 2005; Ludwig et al., 2009) and increase

### March-April (incubation)

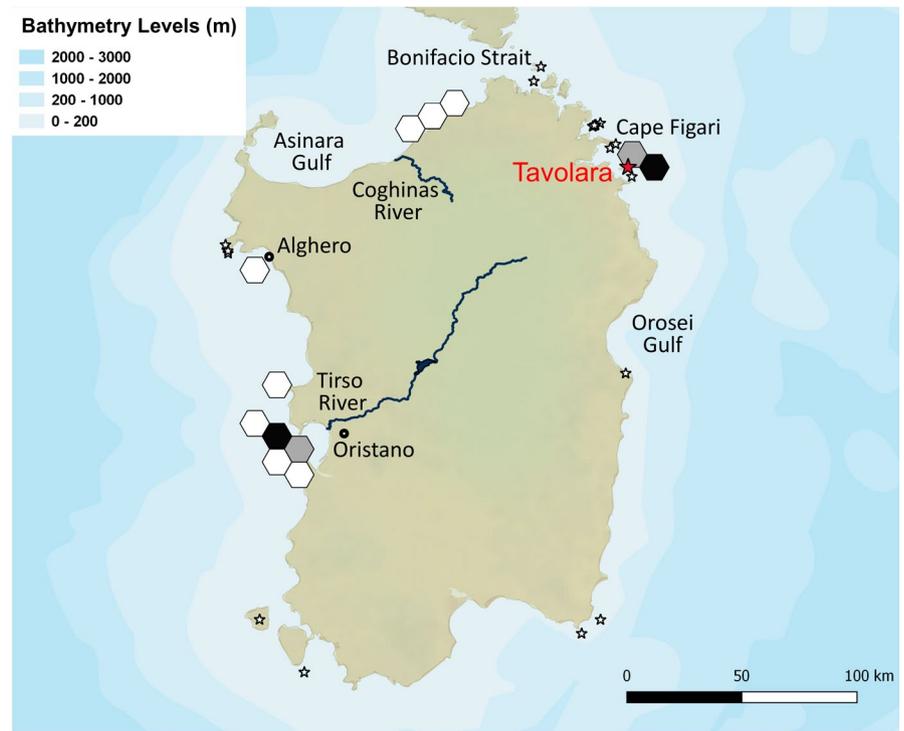


### June (chick rearing)



**FIGURE 5** Daily distribution (in %) of fixes classified as Foraging, Resting, and Travelling in the 24 hr. The mean nautical dawn and dusk were used to identify the night-hours (gray shadow in the graph) for the two periods considered: March–April (incubation): 18:30–3:30; June (chick rearing): 20:00–2:00. Boxplots represent: Box, 1st and 3rd quartiles; thick line, 2nd quartile (median); whiskers, extreme values; dots, outliers

**FIGURE 6** Resting sites of yelkouan shearwaters GPS tagged from 2011 to 2015 at the Tavolara Island (Sardinia, IT). Score of use in cells of a 10 km spaced hexagonal: white, gray, and black cells represent a score ranging from 9–15, 16–22, and 23–29, respectively. See Materials and Methods for details. Stars represent the locations of known colonies of yelkouan shearwaters in Sardinia



**TABLE 2** Comparison of Generalized Linear Mixed Models developed to describe foraging habitat selection of Yelkouan shearwaters tagged at the colony of Tavolara Island (Sardinia, IT) from 2011 to 2015 (error distribution: binomial; random intercepts: bird ID and track ID nested within bird ID). k, number of parameters; logLik, log-likelihood; AICc, corrected Akaike's information criterion value;  $\Delta$ AICc, difference in AICc between a given model and the model with the lowest AICc;  $w_i$ , Akaike weights;  $mR^2$  = marginal  $R^2$ ; AUC, area under the ROC curve. STAGE, reproductive stage (two-levels factor: incubation and chick rearing; BATHY, bathymetry (km); DCOL, distance from the colony site (100 km); PROD, inverse-transformed sea productivity ( $\text{mg C}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ ); STAGE:BATHY, STAGE:DCOL, and STAGE:PROD, interaction terms.  $mR^2$  and AUC were reported only for the models within 2 AICc units from the best model

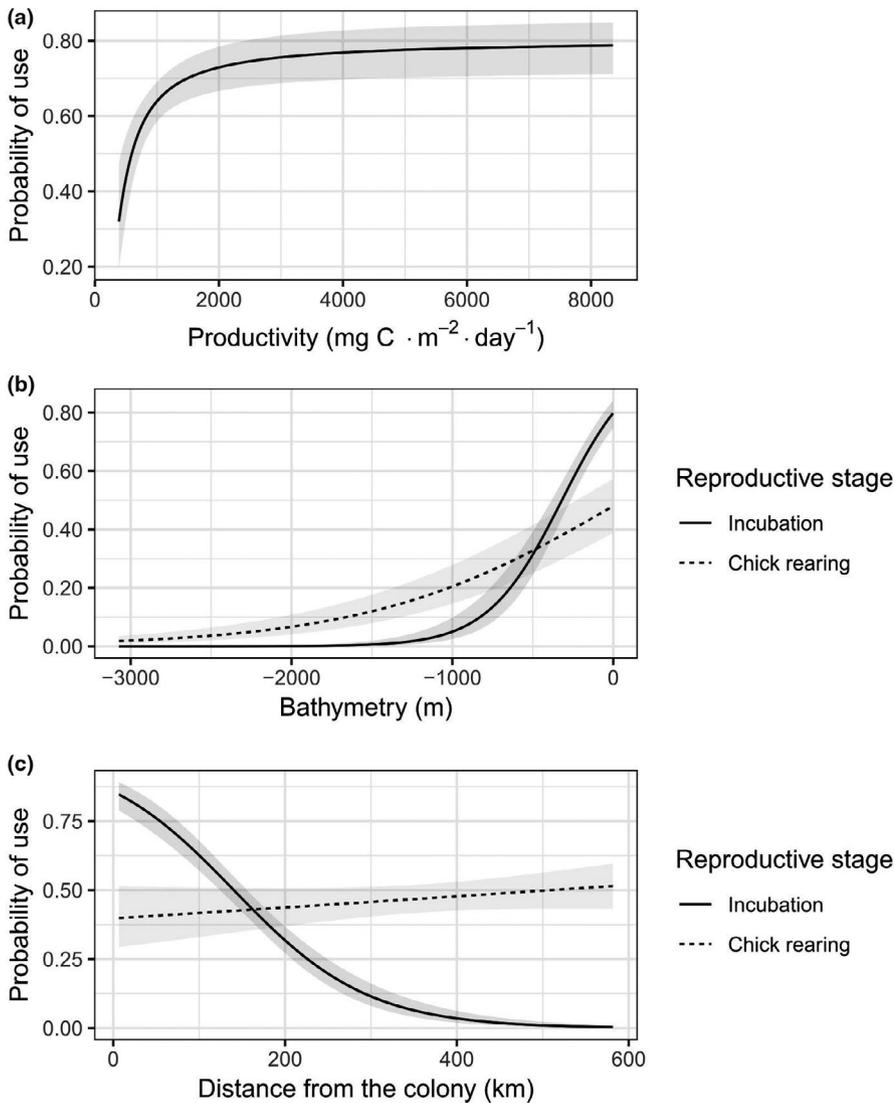
Model	k	logLik	$\Delta$ AICc	$w_i$	$mR^2$	AUC
STAGE+BATHY+DCOL+PROD+STAGE:BATHY+STAGE:DCOL	9	-807.19	0	0.68	0.88	0.93
STAGE+BATHY+DCOL+PROD+STAGE:BATHY+STAGE:DCOL+STAGE:PROD	10	-806.95	1.52	0.32	0.88	0.93
STAGE+BATHY+DCOL+PROD+STAGE:DCOL+STAGE:PROD	9	-841.75	69.11	0.00		
STAGE+BATHY+DCOL+PROD+STAGE:DCOL	8	-844.76	73.12	0.00		
STAGE+BATHY+DCOL+PROD+STAGE:BATHY+STAGE:PROD	9	-876.20	138.02	0.00		
STAGE+BATHY+DCOL+PROD+STAGE:BATHY	8	-889.96	163.53	0.00		
STAGE+BATHY+DCOL+PROD+STAGE:PROD	8	-923.01	229.63	0.00		
STAGE+BATHY+DCOL+PROD	7	-929.74	241.08	0.00		

local biodiversity (Harmelin-Vivien et al., 2009). In particular, the Gulf of Lion, owing to hydrographic features that include the Rhône river run-off and wind-driven coastal upwelling processes, is one of the most productive areas of the Mediterranean (Millot, 1990) where small epipelagic teleosts (European pilchard *Sardina pilchardus* and

European anchovy *Engraulus encrasicolus*) are the dominant species in term of fish biomass (Banaru et al. 2013). As a consequence, a large number of marine predators (whales, dolphins, seabirds) are attracted and congregate here, especially during summer (David & Di-Méglio, 2013; Lambert et al., 2017).

**TABLE 3** Estimated parameter (Coeff), with SE, Wald 95% confidence interval (95% CI), and variable testing (the type II Wald  $\chi^2$  test) results of the best Generalized Linear Mixed Model developed to describe foraging habitat selection of Yelkouan shearwaters tagged at the colony of Tavolara Island (Sardinia, IT) from 2011 to 2015 (error distribution: binomial; random intercepts: bird ID and track ID nested within bird ID). STAGE, reproductive stage (two-levels factor: incubation and chick rearing); BATHY, bathymetry (km); DCOL, distance from the colony site (100 km); PROD, inverse-transformed sea productivity ( $\text{g C}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ ); STAGE[chick rearing]:BATHY and STAGE[chick rearing]:DCOL, interaction terms. Number of considered cells: 3,288; Number of birds: 21; Number of tracks: 27. Variance for the random factors (bird ID and track ID nested within bird ID) = 0

Variable	Coeff	SE	95% CI	Wald $\chi^2$	df	p
(Intercept)	3.55	0.30	2.96 to 4.15			
STAGE[chick rearing]	-2.82	0.34	-3.5 to -2.15	5.34	1	.02
BATHY	4.32	0.44	3.45 to 5.19	192.88	1	<.0001
DCOL	-1.28	0.12	-1.51 to -1.05	11.15	1	.0008
PROD	-0.84	0.20	-1.22 to -0.45	17.94	1	<.0001
STAGE[chick rearing]:BATHY	-3.04	0.45	-3.93 to -2.16	45.07	1	<.0001
STAGE[chick rearing]:DCOL	1.36	0.13	1.10 to 1.62	107.09	1	<.0001



**FIGURE 7** Plots of the effects of sea productivity (a; bathymetry = -100 m, distance from the colony = 100 km), of the interaction between reproductive stage and bathymetry (b; distance from the colony = 100 km, sea productivity =  $2,000 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ ) and of the interaction between reproductive stage and distance from the colony (c; bathymetry = -100 m, sea productivity =  $2,000 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ ) on the probability of use of a given  $9 \times 9$  km cell. Shaded areas = 95% Confidence bands. Results from the best Generalized Linear Mixed Model developed to describe foraging habitat selection of yelkouan shearwaters tagged at the colony of Tavolara Island (Sardinia, IT) from 2011 to 2015 (error distribution: binomial; random intercepts: bird ID and track ID nested within bird ID). Number of considered cells: 3,288; Number of birds: 21; Number of tracks: 27. See Table 3 for numerical results

Most seabirds occurring in the Gulf of Lion are supposed to originate from colonies situated 150–500 km away, because the surrounding area offers few opportunities for rocky island-nesters to breed (Carboneras, 2013). Food richness and seasonal availability may well account for the long distance travels of Tavolara's yelkouan shearwaters late in the breeding season and fits with the general pattern of other predators migrating in this gulf at the same time. As shown by our analysis, the departure toward farthest feeding areas is also concurrent to, and could be explained by, the shortness of food resources closer to the natal colony during the highly demanding chick-rearing period. We should also remark that some of the Sardinian hotspots fall near river mouths, such as the Tirso in the Oristano Gulf and the Coghinas on the northern coast, and this may be explained by the high levels of productivity recorded in spring time during the incubation period that may have allowed individuals to find sufficient food resources relatively near to the colony.

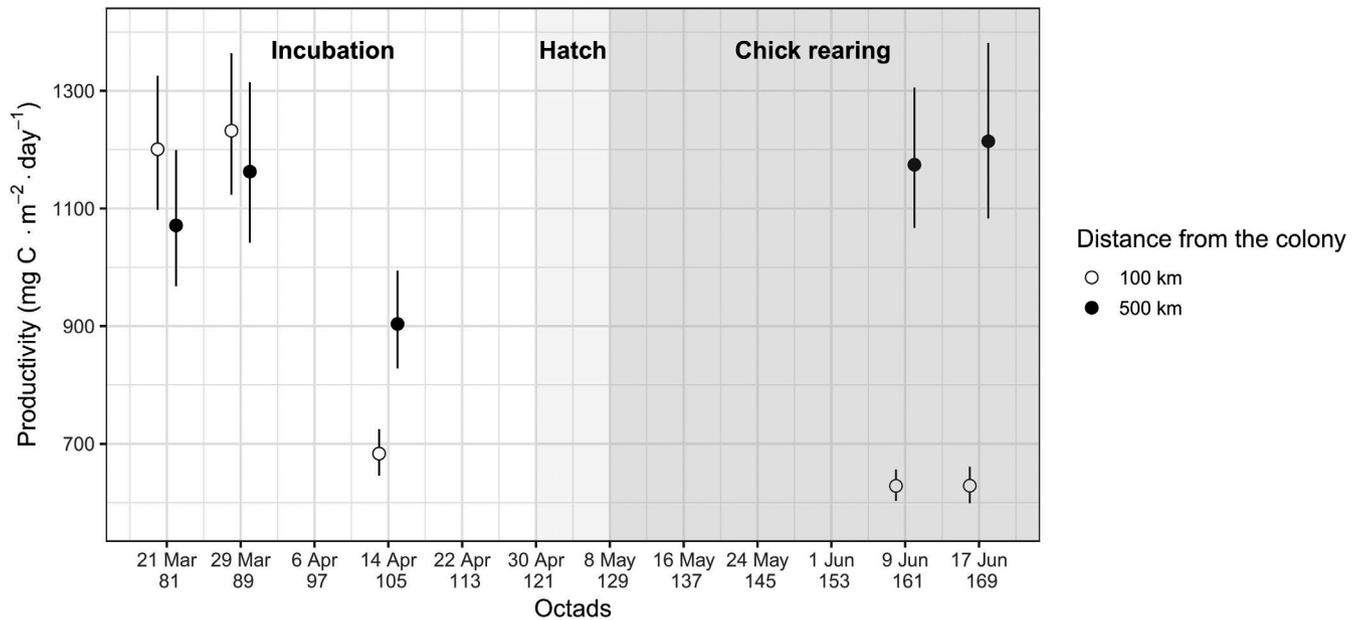
From a behavioral point of view, the decision of undertaking long distance foraging trips might entail the adoption of a dual-foraging strategy (Chaurand & Weimerskirch, 1994; Weimerskirch et al., 1994). The paucity of data from consecutive trips of a same individual (Table 1) and the absence of tracks simultaneously involving both members of a pair prevent us from confirming whether the bimodal pattern of trip duration, particularly obvious during the chick-rearing period, could be safely interpreted as a dual strategy. Among

seabirds, a dual-foraging strategy has been explained as the need to alternate short trips for searching food for the chick with long trips for self-provision (Stahl & Sagar, 2000; Terauds & Gales, 2006; Weimerskirch et al., 1994). Such a pattern has been associated to conditions of low/insufficient prey availability in the vicinity of the colonies for several species, such as the closely related Manx shearwater *Puffinus puffinus*, (Fayet et al., 2015; Riou et al., 2011; Tyson et al., 2017), Cory's shearwater *Calonectris borealis* (Granadeiro et al., 1998; Magalhães et al., 2008), Scopoli's shearwater *Calonectris diomedea* (Cecere et al., 2014). In the case of Tavolara's birds, the need to cope with increased food requirements and decreasing productivity in foraging areas used during incubation may force parents to perform longer trips to richer (albeit distant) feeding areas such as the Gulf of Lion. We believe that this is the main reason for the long trips rather than a dual-foraging strategy per se.

The location of seabird colonies has been positively associated to areas of high minimum food availability across years (Sandvik et al., 2016). Direct flights across the open sea to predictably rich and shallow feeding areas along the North Mediterranean coasts during the chick-rearing period show that adult yelkouan shearwaters from the Tavolara colony can efficiently adapt their foraging range to seasonal changes of marine productivity. Under increasingly frequent scenarios of food shortage, the ability to shape their foraging strategy according to productivity changes (as suggested

**TABLE 4** Estimated parameter, with corresponding SE, Wald 95% confidence interval (95% CI), and variable testing (the type II Wald  $\chi^2$  test) results of the linear mixed model (LMM) analyzing the inverse-transformed sea productivity ( $\text{g C}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ ) in the cells with at least one foraging fix during the study period as a function of the distance from the colony site (DCOL, 100 km), bathymetry (BATHY, km), the octads when the foraging trips of yelkouan shearwaters tagged at the Tavolara Island (Sardinia, IT) from 2011 to 2015 were recorded (OCTAD) and the interactions OCTAD:DCOL and OCTAD:BATHY. The years where birds were tracked during incubation or chick rearing only (i.e., 2011 and 2015) were excluded to reduce the sampling bias. Number of observations: 536; number of cells: 91. Variance for the random factor (cell ID) = 0.03. Marginal  $R^2 = 0.53$

Variable	Coeff	SE	95%CI	Wald $\chi^2$	df	p
(Intercept)	0.80	0.05	0.70 to 0.90			
OCTAD						
89 versus 81	0.00	0.05	-0.11 to 0.10	634.08	4	<.0001
105 versus 81	0.77	0.06	0.66 to 0.89			
161 versus 81	0.96	0.05	0.87 to 1.05			
169 versus 81	0.97	0.05	0.86 to 1.07			
BATHY	0.03	0.02	-0.01 to 0.06	75.91	1	<.0001
DCOL	-0.10	0.05	-0.20 to 0.00	6.33	1	.01
OCTAD:BATHY						
89:BATHY versus 81:BATHY	-0.01	0.02	-0.04 to 0.02	393.08	4	<.0001
105:BATHY versus 81:BATHY	-0.11	0.02	-0.15 to -0.08			
161:BATHY versus 81:BATHY	-0.21	0.01	-0.24 to -0.18			
169:BATHY versus 81:BATHY	-0.22	0.02	-0.25 to -0.19			
OCTAD:DCOL						
89:DCOL versus 81:DCOL	0.05	0.05	-0.05 to 0.16	81.39	4	<.0001
105:DCOL versus 81:DCOL	0.29	0.05	0.19 to 0.39			
161:DCOL versus 81:DCOL	-0.10	0.05	-0.19 to -0.01			
169:DCOL versus 81:DCOL	-0.09	0.05	-0.19 to 0.02			



**FIGURE 8** Plot of the effects of octads and distance from the colony on sea productivity estimated at bathymetry = -100 m. Error bars = 95% Confidence Intervals. Results from the linear mixed model (LMM) analyzing the inverse-transformed sea productivity in the cells with at least one foraging fix in the octads where foraging trips of yelkouan shearwaters tagged at the Tavolara Island (Sardinia, IT) were recorded as a function of the distance of the colony and bathymetry (see Table 4 for numerical results). Number of observations: 536; number of cells: 91

by the recent northerly shift in the foraging areas of manx and balearic shearwaters; Guilford et al., 2008; Wynn et al., 2007) may allow yelkouan shearwaters to maintain their breeding philopatry even when the colonies are misplaced with respect to the most profitable feeding locations (cf. Grémillet et al., 2008).

Concerning the daily time budget, fixes of yelkouan shearwaters breeding at Tavolara were classified as indicating "resting" activities in 50.1% of the cases and "foraging" activities in 35.7% of the cases. Péron et al., (2013) obtained similar findings at their study colonies on the French Mediterranean coast. Feeding turned out to be almost totally diurnal. The birds mostly traveled in the first hours of the day (soon after their morning rafts) and in the evening, before and after sunset. This overall activity pattern agrees with data collected on the closely related balearic shearwater (Meier et al., 2015) and on the manx shearwater (Dean et al., 2013; Fayet et al., 2015). Such findings could help to interpret and standardize the raft census methodology which is already in use for population size assessment.

During their excursions at sea, the tracked birds spent most of the time resting on the sea surface, particularly at night, in the early morning and during the central hours of the day. Early morning rafts, after leaving the colony, had been specifically described by Raine et al., (2010) and could allow information exchanges before heading to different diurnal feeding areas. The rather high proportion of time spent "resting" in water has been associated to other additional functions, such as prey digestion (Ropert-Coudert et al., 2004), resting during feeding trips (Shamoun-Baranes et al., 2011), waiting for a proper time to enter their nest (Shiomi et al., 2012), either in proximity of the colony or at more distant sites (Borg et al., 2016; Dean et al., 2013; Raine et al., 2010). A sit-and-wait feeding strategy

in areas rich of food (Freeman et al., 2013; Yoda et al., 2014) and the location of productive areas by odor transported by the ocean flow (Nevitt & Bonadonna, 2005) have been proposed as possible additional explanations, when this behavior takes place within the feeding areas.

Since most of population estimates of this species rely on counting birds rafting near or heading to colonies, we evaluated the spatial distribution of resting areas. The location of coastal patches selected for rafting suggests an important role of the waters surrounding Tavolara island as a resting area before and after visiting the colony. The other selected patches coincide with some of the most important feeding areas: mouth of Coghinas river (North Sardinia), Alghero (Northwest Sardinia) and Oristano (West Sardinia). The latter area is the main feeding destination of yelkouan shearwaters from Tavolara during the incubation stage. An attractive effect of non-home colonies (as suggested by e.g., Borg et al., 2016; Bourgeois & Vidal, 2008) did not emerge from our data, although one of the resting spots is close to known colonies (Alghero, Northwest Sardinia).

Traveling toward distant feeding localities could also be interpreted as an indirect consequence of bluefin tuna *Thunnus thynnus* overfishing in the Italian waters (Sardinia included). Since the traditional tuna trapping fisheries were almost completely replaced by industrial fishing, bluefin tuna started to be harvested at a rate exceeding the reproductive capabilities of the existing stock (Longo & Clark, 2012) and, in a few decades, the stocks have collapsed (ICCAT, 2010; MacKenzie et al., 2009). Tunas drive small fishes toward the surface and are considered as "facilitators" for seabirds to whom they are strongly associated both in tropical and temperate seas (Le Corre & Jaquemet, 2005; Veit & Harrison, 2017). In late

spring in the Mediterranean Sea, tunas, during their migration, get close to the coasts when yelkouan shearwaters are raising chicks. Then, the drop of tuna population may have reduced the feeding opportunities for shearwaters, forcing them to move further. Because the yelkouan shearwater is an endemism confined to the Mediterranean and Tavolara island hosts around half of its global population, our findings suggest that, beside direct threats (mortality due to bycatch and overfishing of prey species: Gaudard, 2018), conservation measures to be enforced at sea should address the full sustainability of all fisheries across an area encompassing the foraging hotspots identified (namely the Oristano and Alghero waters, the Bonifacio Strait and the Gulf of Lion).

In conclusion, despite the limitations associated with the relatively low number of marked individuals, some relevant patterns of the spatial ecology of the yelkouan shearwater could be described. Their main value seems that of referring to the globally most important colony known to date. Studies on different populations are strongly needed in order to assess and implement an effective pan-Mediterranean conservation strategy for this endemic and charismatic taxon.

#### ACKNOWLEDGEMENTS

Fabio Cherchi, Gian Mario Pitzianti, and Massimo Putzu gave an invaluable field support for GPS retrieval, challenging bad sea and inclement weather during long-lasting nights in the field. We warmly thank Francesco Angioni, Roberto Cogoni, Sergio Nissardi, Pier Panzalis, Tore Vitale for supporting us during deployment and retrieval, joining monitoring activities and helping organizing periodical field trips. FP was funded by the Italian Ministry for Environment, Land and Sea Protection of Italy (MATTM) which also provided funds for fieldwork and data loggers.

#### CONFLICT OF INTEREST

The authors have no conflicting interests.

#### AUTHOR CONTRIBUTIONS

NB and MZ conceived the project; NB, MZ, FP, AN, and GS coordinated the data collection; GC, DG, AM, AG, and EP performed data management/analyses and drafted part of the manuscript; FP and MZ drafted the manuscript and FP and EP guided the final writing with contributions from all authors. NB supervised all phases of the project since its beginning. All authors read and approved the final manuscript.

#### ETHICAL APPROVAL

All procedures performed in this study were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

#### ORCID

Francesco Pezzo  <https://orcid.org/0000-0003-4437-3805>

Marco Zenatello  <https://orcid.org/0000-0002-9225-6737>

Dimitri Giunchi  <https://orcid.org/0000-0003-2753-8997>

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**How to cite this article:** Pezzo, F., Zenatello M., Cerritelli G., Navone A., Giunchi D., Spano G., Pollonara E., Massolo A., Gagliardo A., & Baccetti N. (2021). Productivity changes in the Mediterranean Sea drive foraging movements of yelkouan shearwater *Puffinus yelkouan* from the core of its global breeding range. *Marine Ecology*, 00e1–18. <https://doi.org/10.1111/maec.12668>