



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

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3 294 Productivity changes in the Mediterranean Sea drive foraging movements of yelkouan shearwater

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5 295 *Puffinus yelkouan* from the core of its global breeding range

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55 317 marine primary productivity

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319 Abstract

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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 changes 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 **en**closed 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, as well as 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, **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 are hypothesized to be related to unfavorable conditions on the less productive (and already depleted) Sardinian waters.

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343 Introduction

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The Mediterranean Sea is an almost completely enclosed basin characterized by a low concentration of nutrients especially in its Eastern part (Kress et al. 2003; Bosc et al. 2004) 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 and 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. 2013). **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 (Derhé 2012; BirdLife International 2018). Known breeding sites are mainly distributed in the central Mediterranean basin, from Menorca island and the Southern French coasts (Bourgeois and 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 and 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 (Pérez-Ortega and İsfendiyaroğlu 2017; Gaudard 2018). **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 bycatch within foraging areas, mortality by alien predators such as rats and cats at breeding sites, fish stock depletion and

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3 376 chronic sea pollution (Bourgeois and Vidal 2008; Ruffino et al. 2009; Capizzi et al. 2010; Gaudard
4 377 2018). Information on the spatial ecology of the species is scarce and the knowledge on feeding
5 378 movements and feeding areas is based on observations carried out at diurnal concentration sites or
6 379 near bottleneck areas such as the Bosphorous or the Bonifacio Strait (Şahin et al. 2012, Zenatello et
7 380 al. 2006). **Tracking studies on yelkouan shearwaters breeding in the Mediterranean Sea**
8 381 **indicated that birds from French colonies in the Hyères Archipelago mainly move westward**
9 382 **along the coast to the adjacent Gulf of Lion (Péron et al. 2013), whereas those from the**
10 383 **Maltese colonies show a high individual variability moving both toward the coast of**
11 384 **Tunisia/western Libya and to the Aegean Sea (Raine et al. 2013; Gatt et al. 2019).** The
12 385 Sardinian key-site of Tavolara-Punta Coda Cavallo Marine Protected Area hosts the largest known
13 386 breeding population of the species, estimated at 9,991-13,424 pairs (Zenatello et al. 2012) which,
14 387 considering the most recent population estimates (Gaudard 2018), could represent up to 55% of the
15 388 global breeding population. Conservation actions in the last decades consisted of rat eradication
16 389 attempts on Molaria (Sposimo et al. 2012a, 2012b; Ragionieri et al. 2013) **and Tavolara**
17 390 **(<http://www.lifepuffinustavolara.it>) islands in 2008 and 2017, respectively.** However, no
18 391 protection on foraging areas has been **specifically** enforced so far, and information on foraging
19 392 strategies of this breeding population **was totally** lacking, despite its relevance for the conservation
20 393 of this and other populations.
21 394 Here we provide the first study describing the foraging movements of the yelkouan shearwaters
22 395 from the world-largest colony of Tavolara, with the aims of: a) identifying main foraging and
23 396 rafting areas by means of GPS loggers; b) describing how key ecological factors affect the selection
24 397 of foraging and resting areas and, as a consequence, the foraging trips length and duration **in the**
25 398 **course** of incubation and chick rearing; c) hypothesizing how changes in the Mediterranean habitat
26 399 could **possibly** affect spatial ecology; d) providing information for conservation scenarios to come.
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38 407 Materials and methods
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3 409 Study Site and Model Species

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5 410 The study was carried out from 2011 to 2015 on Tavolara Island (40°54'N, 09°42'E; Sardinia), in
6 411 the largest known breeding site of the yelkouan shearwater (Zenatello et al. 2012; Gaudard 2018).

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9 412 All activities were performed in a single cavern hosting up to 15 accessible nests, that were usually
10 413 in a rat-free condition. Birds were captured by hand on the nest and equipped with GPS loggers
11 (Gypsy-2 and Gypsy-4 by Technosmart and I-gotU GT120 by Mobile Action Technology). **The
12 414 weight of GPS-loggers was 3.1%-4.7% of the average mass of adults (424.5 g ± 28.6 g SD,
13 415 n=29). GPS-loggers were attached to the mantle feathers of breeding adults by adhesive TESA
14 416 tape (total weight: 13-20 g according to battery size). Birds were handled for 15-30 minutes
15 417 and then released where trapped (i.e. at their nest). Loggers were retrieved by recapturing
16 418 breeders on their nests or at the entrance of the cave when returning from their foraging
17 419 trips.** Nests were regularly monitored during the whole study period to assess their breeding
18 420 success (Table 1). **Capture, handling and tagging procedures were conducted by the Italian
19 421 Institute for Environmental Protection and Research (ISPRA), under the authorization of
20 422 Law 157/1992 (Art.4.1 and Art 7.5), which regulates research on wild bird species. Three
21 423 birds** were tracked in subsequent years (Table 1). All tracks are deposited in Movebank
22 424 (www.movebank.org) (DOI provided at publication).

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34 427 Data Analysis

35 428 The sampling rate of the loggers changed during the study period (10, 20 or 60 min) depending on
36 429 GPS receiver, battery size and breeding stage (see Table 1 for details). For each fix, the GPS
37 430 loggers recorded date, time, speed and positional data (Longitude and Latitude). Tracks were
38 431 plotted on Qgis (<http://www.qgis.org/>) and individual foraging trips were identified as round-trips
39 432 flights from the colony to feeding areas. One to four trips per individual were recorded. For each fix
40 433 the distance from the preceding fix and the distance from the colony (i.e., the minimal distance a
41 434 bird can fly to reach the current point, assuming shearwaters did not fly over land) was calculated.
42 435 In order to identify the foraging areas and the activity of the birds, each fix was classified into one
43 436 of the following three categories: travelling (T), resting (R), foraging (F) **corresponding to three
44 437 distinct movement patterns. While travelling, the bird moves with a consistent high speed
45 438 between two distant sites. The resting behaviour is characterized by low speed movements
46 439 within a short range attributable to the sea currents and waves. In the foraging areas
47 440 shearwaters perform short range movements either at low or medium speed (see below).
48 441 In detail, the classification was based on the following criteria:**

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3 442 a) **Fixes** with a speed greater than 10 km/h have been classified as T (Guilford et al. 2008),
4 443 provided that their distance from the preceding fix was greater than 5, 10 and 30 km for the
5 444 sampling rate of one fix every 10, 20 and 60 mins, respectively. **In addition, each fix with a speed**
6 445 **greater than 10 km/h not meeting the previous conditions was anyhow classified as T,**
7 446 **provided that the absolute difference between its distance from the colony and the preceding**
8 447 **fix distance from the colony was greater than 2.5, 5 and 15 km, for the sampling rate of one**
9 448 **fix every 10, 20 and 60 mins, respectively.** The latter criterion was adopted to discriminate
10 449 **patterns** of birds travelling along a curved path (e.g. as the one needed to circumnavigate islands)
11 450 from those displayed by birds moving rapidly within a restricted foraging area. **All the distances**
12 451 **categories for the classification of the T fixes have been arbitrarily chosen on the basis of the**
13 452 **direct observation of the tracks of birds that were travelling between two distant areas.**

14 453 b) R fixes included all the fixes with a speed lower than 5 km/h, provided that the distance from the
15 454 preceding fix was shorter than 0.5 km when the sampling rate was every 10 and 20 min, and 1.5 km
16 455 when the sampling rate was of 1 fix every 60 min. The criterion based on the distance from the
17 456 preceding fix was actually unreliable in case of either strong **drift** or short range movements within
18 457 the foraging area (see below for the detection of foraging areas).

19 458 c) All the remaining fixes have been assigned to the F category.

20 459 Each individual track was subsequently plotted in Qgis for visual inspection. When a bird was
21 460 resting for several hours sitting on the sea surface, a characteristic pattern of fixes **resulted**, due to
22 461 the sea current and/or wind drifting the bird in a constant direction (Fayet et al 2015). In these cases,
23 462 the mean vector length (Batschelet 1981) for a set of R fixes, computed averaging the direction of
24 463 movement between two subsequent fixes, was greater than 0.90. Therefore, the mean vector length
25 464 was used as a criterion when a visual inspection revealed possible inconsistencies in the fix class
26 465 assignment. If the mean vector length of consecutive F fixes was greater than 0.90, the fixes were
27 466 re-assigned to the R category. **Conversely**, if the mean vector length of consecutive R fixes was
28 467 smaller than 0.75, the fixes were re-assigned to the F category. For each track the first fixes (1-3)
29 468 were not classifiable with the above criteria and therefore they have been excluded from the
30 469 analysis.

31 470 The tracks sampled at one fix every 10 min were re-sampled at one fix every 20 minutes and used,
32 471 together with the other 20 min sampling rate tracks, to perform a density kernel analysis with those
33 472 locations (n=27 tracks). The core foraging distributions were calculated on the basis of the
34 473 distribution of F fixes. The density of the distribution of F **fixes** was modeled using the fixed kernel
35 474 technique (Worton 1989) **available in R-package *adehabitatHR 4.15* (Calenge 2006).** The ad-hoc
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3 475 bandwidth for the smoothing parameter ($h_{\text{ad-hoc}}$) was selected by sequentially reducing the reference
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5 476 bandwidth of the smoothing factor (h_{ref} , i.e. the optimal bandwidth under the assumption of
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7 477 bivariate normality) in 0.10 increments and choosing the smallest increment of h_{ref} that: 1) resulted
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9 478 in a contiguous K95% isopleth, and 2) contained no lacuna within K95% (Kie 2013). Core areas
10 479 were identified by applying the Area Independent Method developed by Seaman and Powell (1990).
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12 480 The method divides the range in areas of high and low fix density using an objective criterion
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14 481 **which** is based on a graphical representation of the range area in relation to the density of the
15 482 considered fixes. In this way it is possible to identify the dividing point between high- and low-
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17 483 density areas, as the point where the plot is maximally distant from a straight line of slope +1, that
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19 484 represents a distribution of random use. We performed the analysis considering steps = 5%
20 485 **calculating subsequent range area sizes using *adehabitatHR***. On the basis of the point of
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22 486 maximum distance we defined the core areas with a different percentage of volume contour per
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24 487 individual (median: 55%; IQR: 50%-55% volume contours).
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26 488 We used the R fixes distribution to assess whether and which of the tracked birds rested in areas
27 489 proximal (within 5 km radius; **the distance range from the colony within which rafts are usually**
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29 490 **observed**) to yelkouan shearwaters colonies other than those of Tavolara archipelago and adjacent
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31 491 Cape Figari area, that are all located one next to another. A 5 km radius buffer was created with
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33 492 Qgis around each yelkouan shearwater colony known in Italy and France (Baccetti et al. 2009;
34 493 **Cadiou et al. 2004**). We intersected the 5 km radius buffer with the R fixes distribution, in order to
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36 494 count which colonies were approached by the tracked birds. **In addition, we identified the areas**
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38 495 **mostly used for resting by the tracked birds**. To do so, a 10 km hexagonal grid was created in
39 496 Qgis; for each individual we computed the percentage of R fixes falling in each hexagon. For each
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41 497 track the number of R fixes in each cell was computed and categorized in 3 categories depending on
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43 498 the proportion of R fixes contained in a cell: 1, number of fixes below the median value; 2, number
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45 499 of fixes ranging between the median value and the third percentile; 3, values higher than the third
46 500 percentile. For each cell we summed the scores obtained from all the tracks in order to identify
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48 501 areas with the highest score, i.e. those most likely frequented by resting birds.
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50 502 **For each fix of the tracks the distance from the nearest coast was computed. In order to assess**
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52 503 **whether the birds had a preference for staying near to or far from the coast, for each bird the**
53 504 **percentage of fixes of each considered category (T, R, F) located within 20 km and further**
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55 505 **than 20 km was compared by Wilcoxon test for paired data. When more than one tracks per**
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57 506 **bird were available, the individual mean values were considered.**
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3 507 Each location was classified as “day” or “night” according to their corresponding time of nautical
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5 508 dawn and dusk obtained using the "R-package" *suncalc 0.5.0* (Thieurmel and Elmarhraoui 2019).
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7 509 Differences in the activity between day and night were tested by applying the Wilcoxon test **for**
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9 510 **paired data** to the individual percentage of each behavioural category. **As before, when more than**
10 511 **one track per bird were available, the individual mean values were considered.**
11
12 512 To analyse **foraging** habitat selection (sensu Manly et al. 2002) by yelkouan shearwaters, we used
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14 513 remote sensing data to quantify Bathymetry (ETOPO Global Relief Model, NOAA) and Ocean
15 514 Productivity (MODIS) at a resolution of 1.6 and 9 km respectively. Productivity data (**$g C \cdot m^{-2} \cdot$**
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17 515 **day⁻¹**) used were averaged over eight days (octads) and were as much as possible contemporary to
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19 516 each foraging trip. Given the resolution of the remote sensing data, use and availability were
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21 517 estimated at the individual and population level, respectively (first order resource selection; Meyer
22 518 and Thuiller 2006). On the basis of the productivity raster data, a grid with 9 km squared cell was
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24 519 created. For each cell with at least one F fix, five cells were randomly sampled within the
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26 520 population 95% range (calculated with the same kernel approach described above) by considering
27 521 the F fixes of all tracks. This process was repeated for all available foraging trips. For all used and
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29 522 random locations, we extracted the values of bathymetry, distance from the colony site to the centre
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31 523 of the cell, and productivity. Due to the low sample size, the year of tagging was not included in the
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33 524 analysis. Data exploration was carried out following the protocol described in Zuur and Ieno (2016).
34 525 The resource selection function (Manly et al. 2002) was calculated with a Generalized Linear
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36 526 Mixed Model with a binomial error distribution, and bird ID **and track ID (nested within bird ID)**
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38 527 as random intercepts by means of the R-package *glmmTMP 1.0.2.1* (Brooks et al. 2017). The
39 528 variables considered in the full model were: **sea productivity (PROD, inverse transformed),**
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41 529 **bathymetry (BATHY), distance from the colony (DCOL), and the reproductive stage**
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43 530 **(STAGE, two-levels factor: incubation and chick rearing).** We hypothesized that the probability
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45 531 of selection use was higher for cells with higher PROD, and lower BATHY and DCOL. We tested
46 532 whether the incubation period modified the way the birds used the resources by including the
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48 533 second order interactions STAGE:DCOL, STAGE:BATHY, STAGE:PROD. The fixed part of the
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50 534 model was simplified by means of the Akaike Information Criterion corrected for small sample size
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52 535 (AICc, Burnham and Anderson 2002), considering all the models between the full model and the
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54 536 model which included all main effects. Significance was tested by means **of the type II Wald χ^2**
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56 537 **test using the R-package *car 3.0-10* (Fox 2019). Model fit, overdispersion, collinearity and**
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58 538 **spatial autocorrelation of the residuals were checked before using the final model for**
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3 539 **inference by means of the R-packages *DHARMa* 0.3.3.0 (Hartig 2020) and *performance* 0.7.0**
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5 540 **(Lüdecke et al. 2020).** The marginal R^2 (mR^2), which represents the variance explained by fixed
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7 541 factors only (Nakagawa and Schielzeth 2013), was calculated using the R-package ***MuMIn* 1.43.17**
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9 542 **(Bartoń 2020).** The performance of the final models was also evaluated using the Area Under the
10 543 Curve (AUC) generated by the Receiver Operating Characteristic (ROC; Fielding and Bell 1997;
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12 544 Pearce and Ferrier 2000) **by means of the R-package *ROCR* 1.0-7 (Sing et al. 2005).** All
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14 545 **calculations were performed using R 4.0.4 (R Core Team 2021).**
15 546 To further investigate bird foraging strategies in the two phases of the nesting period, **we analysed**
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17 547 **how sea productivity varied in cells located at different distance from the colony over the**
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19 548 **study period.** In this analysis we considered only the cells with at least one F fix during the whole
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21 549 study period, i.e. the cells used at least once by tracked birds for foraging, and with no missing data
22 550 on productivity (n = 333). To reduce sampling bias, we excluded the years where birds were tracked
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24 551 during incubation or chick rearing only (i.e. 2011 and 2015). **The available cells were then**
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26 552 **resampled in order to not include adjacent cells in the analysis, in order to reduce spatial**
27 553 **autocorrelation, by means of the R-package *spThin* 0.2.0 (Aiello-Lammens et al. 2015).** The
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29 554 **number of cells considered in the analysis was 91.** Data were modelled by means of Linear
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31 555 Mixed Models considering productivity (**inverse transformed**) as dependent variable and cell ID as
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33 556 random intercept. The independent variables considered in the model were: octad (OCTAD, 5-level
34 557 factor coded using the first Julian day of the octad: 81, 89, 105, 161, 169), distance from the colony
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36 558 **(DCOL), bathymetry (BATHY) and the second order interactions OCTAD:DCOL and**
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38 559 **OCTAD:BATHY. Based on observed productivity variations, we** hypothesised that the
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40 560 productivity of cells nearest to the colony decreases over time much more **strongly** than that of cells
41 561 more distant from the colonial site, thus inducing birds to increase the frequency of long foraging
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43 562 trips. **The packages and the procedures used to check model assumptions, to test significance**
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45 563 **and to evaluate model fit were the same as described above.** Throughout the text, means are
46 564 reported along with their standard deviation (mean \pm SD) **unless otherwise specified.**
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50 566 Results

51 567 Out of a total of 43 capture events in subsequent years and 60 GPS deployed, net of the birds not
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53 568 recaptured (n=7), recaptured without **logger** (n=14) or recaptured with improperly functioning
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55 569 loggers (**n=5**), we obtained 34 foraging trips from 21 birds tracked during incubation (March-April;
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57 570 n=21 trips) and chick rearing period (May-June; n=13 trips). **Table 1 reports the details of the**
58 571 **tracks recorded, such as whether they were complete (the entire journey from the colony to**
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3 572 **the foraging area and back was recorded), or interrupted (the power run out before the bird**
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5 573 **homed after the foraging trip), and which tracks were excluded from the analysis due to both**
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7 574 **the low sampling rate (1 fix every 60 minutes) and low number of fixes (less than 45).**

8 575 Birds returned to the colony after 6.5 days (median; range 1-8 days) during the incubation period
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10 576 (n=12 complete tracks from 11 birds) and **after** 2.0 days (median; range 1-10 days) during the chick
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12 577 rearing period (n=11 complete tracks from 6 birds). **Considering only the complete tracks**
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14 578 **included in the analysis (9 tracks from 9 birds in the incubation period, and 8 tracks from 5**
15 579 **birds during the chick rearing period; see Table 1), it appeared that during the incubation**
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17 580 **and chick rearing periods the mean track length was 1030±140 km and 733±225 km,**
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19 581 **respectively, reaching a distance from the colony of 193±24 km and 181±53 km, respectively.**
20 582 **No breeding failures were recorded between capture and recapture.**

21
22 583 **During the incubation period, foraging trips was mostly concentrated in proximity of the**
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24 584 **Western and Northern coasts of Sardinia and South Corsica (Figure 1a). During the chick**
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26 585 **rearing period, Western Sardinia was almost entirely deserted, and new core feeding areas**
27 586 **were used in the French waters of the Gulf of Lion. A number of birds continued to feed along**
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29 587 **North Sardinia and South Corsica (Figs. 1b and 4). During the incubation foraging trips ranged**
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31 588 **from 1 to 9 days, while during chick rearing period, most foraging trips lasted less than 4 days (Fig.**
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33 589 **2), although some individuals (n=3) returned to the colony after much longer trips. Yelkouan**
34 590 **shearwaters were mainly detected within coastal marine areas (Fig. 1 and tracks deposited in**
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36 591 **Movebank). In particular, most of the fixes of all three behavioural categories, were collected**
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38 592 **within 20 km from the coast (Fig. 3). Proportions of fixes obtained within 20 km from the**
39 593 **coast were significantly higher than those located further (Wilcoxon test, Resting N=18, T=2,**
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41 594 **p<0.001; Feeding, N= 18, T= 3, p<0.001; Travelling N=18, T=3, p<0.001) and core foraging**
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43 595 **areas were located in coastal marine areas.**

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45 596 **Considering both the tracks collected during the incubation and the chick rearing periods, it**
46 597 **emerged that** birds spent half of their time resting on the water (R, 50.8±8.2%), while the
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48 598 remaining time was spent mostly foraging (F, 35.6±6.6%) and, to a lesser extent, travelling (T,
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50 599 13.6±4.0%). The 24 hours pattern of activity (Fig. 5) showed that foraging (F) and travelling (T)
51 600 fixes turned out to mostly occur, for all birds, during the day (**Wilcoxon test, N= 18, T= 0,**
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53 601 **p<0.001**). Foraging fixes (F class) occurred during the whole daytime and immediately after sunset.
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55 602 Travelling started one hour after sunrise. In June, the travelling activity was not performed
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57 603 throughout the day, showing a decrease during the central part of the day (Fig. 5). **The time spent**

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3 604 **by the birds resting on the water during day and night was comparable (Wilcoxon test, N= 18,**
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5 605 **T= 56, p>0.05).**

6 606 The analysis of the spatial distribution of the Resting fixes (Fig. 6) showed that **the mean and**
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8 607 **median score computed on 273 cells containing at least one R fix was 3.18 and 2, respectively.**

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10 608 Only 12 hexagonal cells of the grid obtained **the highest scores** ranging from 9 to 29 (see Materials
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12 609 and Methods for details) **showing that birds were** highly concentrated for resting near their
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14 610 breeding colony and along the Western Sardinian coast, near the Oristano Gulf. Lower
15 611 concentration areas were also observed along the coast of Northern Sardinia (Fig. 6).

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17 612 According to AICc, the most supported model for **foraging** habitat selection among the considered
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19 613 set included all main effects and the interactions between nesting period and bathymetry or distance
20 614 from the colony (Table 2 and 3). This model had a strong support, as the second best model was not
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22 615 truly competitive because its additional parameter did not significantly improve the fit. **Indeed, the**
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24 616 **value of the maximized log-likelihood increased only slightly (-807.19 vs -806.95; see Burnham**
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26 617 **& Anderson 2002) and the two measures of performance (mR² and AUC) did not change**
27 618 **noticeably (Table 2).**

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29 619 As expected, **sea** productivity had a positive effect on the probability of use, irrespective of the
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31 620 reproductive stage (Table 3). **During incubation, birds foraged preferentially in areas relatively**
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33 621 **near to the colony and at shallow sea depths, while during chick rearing they preferred to use**
34 622 **cells located at a greater distance from the colony and did not avoid areas with deeper sea**
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36 623 **(Fig. 7).**

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38 624 The results of the model used to **investigate the variability of sea productivity during the**
39 625 **tracking period revealed a significant effect of the interactions between sampled octad and**
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41 626 **bathymetry or distance from the colony (OCTAD:BATHY and OCTAD:DCOL) (Table 4). As**
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43 627 **expected, cells located near the colony showed a marked productivity decrease late in the**
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45 628 **breeding season; the productivity of cells located far from the colony site was high and did not**
46 629 **show any trend across octads (Fig. 8).**

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50 631 Discussion

51 632 Yelkouan shearwaters showed a strong spatial preference for coastal waters (< 20 km from the
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53 633 coast) that were located within the continental shelf (< 200 m isobaths, neritic zone) and
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55 634 characterized by a high primary productivity. These findings are consistent with what has been
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57 635 described for yelkouan shearwaters breeding in France (Péron et al. 2013, Lambert et al. 2017) as
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59 636 well as for the closely related Balearic shearwater *Puffinus mauretanicus* **within the NW**

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Mediterranean and along the Portuguese coasts during the post-breeding period (**Meier et al. 2015**; Araújo et al. 2017). 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 and 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 and 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 under-exploited 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 towards more distant foraging areas (namely the Gulf of Lion and Northern Tuscany) increased. Notably, the West Sardinian waters, which represented the main foraging area during incubation, were not visited during the chick rearing stage. Two birds travelled 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 and Vidal 2008). Since the French breeding population is relatively small (500-1000 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

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3 669 observation and the role of this gulf as a feeding hotspot for yelkouan shearwaters coming from the
4 670 core of the breeding range.

6 671 As a general pattern, the main foraging areas were largely located in shallow (<200 m depth) areas

8 672 with high nutrient inflows brought to the sea by large rivers, which trigger complex food chains

10 673 (Darnaude 2005; Caddy 2000; Ludwig et al. 2009) and increase local biodiversity (Harmelin-Vivien

11 674 et al. 2009). In particular the Gulf of Lion, owing to hydrographic features that include the **Rhône**

13 675 river run-off and wind-driven coastal upwelling processes, is one of the most productive areas of the

15 676 Mediterranean (Millot 1990) where small epipelagic teleosts (European pilchard *Sardina pilchardus*

17 677 and European anchovy *Engraulus encrasicolus*) are the dominant species in term of fish biomass

18 678 (Banaru et al 2013). As a consequence, a large number of marine predators (whales, dolphins,

20 679 seabirds) are attracted and congregate here, especially during summer (David and Di-Méglio 2013;

22 680 Lambert et al. 2016).

24 681 Most seabirds occurring in the Gulf of Lion are supposed to originate from colonies situated 150-

25 682 500 km away, because the surrounding area offers few opportunities for rocky island-nesters to

27 683 breed (Carboneras 2013). Food richness and seasonal availability may well account for the long

28 684 distance travels of Tavolara's yelkouan shearwaters late in the breeding season and fits with the

30 685 general pattern of other predators migrating in this gulf at the same time. As shown by our analysis,

32 686 the departure toward farthest feeding areas is also concurrent to, and could be explained by, the

34 687 shortness of food resources closer to the natal colony during the highly demanding chick rearing

35 688 period. We should also remark that some of the Sardinian hotspots fall near river mouths, such as

37 689 the **Tirso** in the Oristano Gulf and the Coghinas on the northern coast, and this may explain the

39 690 high levels of productivity recorded in spring time during the incubation period that may have

41 691 allowed individuals to find sufficient food resources relatively near to the colony.

42 692 From a behavioural point of view, the decision of undertaking long distance foraging trips might

44 693 entail the adoption of a dual-foraging strategy (Chaurand and Weimerskirch 1994; Weimerskirck et

46 694 al. 1994). The paucity of data from consecutive trips of a same individual (Table 1) and the absence

47 695 of tracks simultaneously involving both members of a pair prevent us from confirming whether the

48 696 bimodal pattern of trip duration, particularly obvious during the chick rearing period, could be

49 697 safely interpreted as a dual strategy. Among seabirds, a dual foraging strategy has been explained as

51 698 the need to alternate short trips for searching food for the chick with long trips for self-provision

52 699 (Weimerskirck et al. 1994; Stahl and Sagar 2000; Terauds and Gales 2006). Such a pattern has been

53 700 associated to conditions of low/insufficient prey availability in the vicinity of the colonies for

54 701 several species, such as the closely related Manx shearwater *Puffinus puffinus*, (Riou et al. 2011,

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3 702 Fayet et al. 2015, Tyson et al. 2017), Cory's shearwater *Calonectris borealis* (Granadeiro et al.
4 703 1998; Magalhães et al. 2008), Scopoli's shearwater *Calonectris diomedea* (Cecere et al. 2014). In
5 704 the case of Tavolara's birds, the need to cope with increased food requirements and decreasing
6 705 productivity in foraging areas used during incubation may force parents to perform longer trips to
7 706 richer (albeit distant) feeding areas such as the Gulf of Lion. **We believe that this is the main**
8 707 **reason for the long trips rather than a dual foraging strategy per se.**

9 708 The location of seabird colonies has been positively associated to areas of high minimum food
10 709 availability across years (Sandvik et al. 2016). Direct flights across the open sea to predictably rich
11 710 and shallow feeding areas along the North Mediterranean coasts during the chick rearing period
12 711 show that adult yelkouan shearwaters from the Tavolara colony can efficiently adapt their foraging
13 712 range to seasonal changes of marine productivity. Under increasingly frequent scenarios of food
14 713 shortage, the ability to shape their foraging strategy according to productivity changes (as suggested
15 714 by the recent northerly shift in the foraging areas of manx and balearic shearwaters; Wynn et al.
16 715 2007; Guilford et al. 2008) may allow yelkouan shearwaters to maintain their breeding philopatry
17 716 even when the colonies are misplaced with respect to the most profitable feeding locations (cf.
18 717 Grémillet et al. 2008).

19 718 Concerning the daily time budget, fixes of yelkouan shearwaters breeding at Tavolara were
20 719 classified as indicating "resting" activities in 50.1% of the cases and "foraging" activities in 35.7%
21 720 of the cases. **Péron** et al. (2013) obtained similar findings at their study colonies on the French
22 721 Mediterranean coast. Feeding turned out to be almost totally diurnal. The birds mostly travelled in
23 722 the first hours of the day (soon after their morning rafts) and in the evening, before and after sunset.
24 723 This overall activity pattern agrees with data collected **on the closely-related balearic shearwater**
25 724 **(Meier et al. 2015) and on the** manx shearwater (Dean et al. 2013; Fayet et al. 2015). Such
26 725 findings could help to interpret and standardize the raft census methodology which is already in use
27 726 for population size assessment.

28 727 During their excursions at sea, the tracked birds spent most of the time resting on the sea surface,
29 728 particularly at night, in the early morning and during the central hours of the day. Early morning
30 729 rafts, after leaving the colony, had been specifically described by Raine et al. (2010), and could
31 730 allow information exchanges before heading to different diurnal feeding areas. The rather high
32 731 proportion of time spent "resting" in water has been associated to other additional functions, such as
33 732 prey digestion (Ropert-Coudert et al. 2004), resting during feeding trips (Shamoun-Baranes et al.
34 733 2011), waiting for a proper time to enter their nest (Shiomi et al. 2012), either in proximity of the
35 734 colony or at more distant sites (Raine et al. 2010; Dean et al. 2013; Borg et al. 2016). A sit-and-wait

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3 735 feeding strategy in areas rich of food (Freeman et al. 2013; Yoda et al. 2014) and the location of
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5 736 productive areas by odour transported by the ocean flow (Nevitt and Bonadonna, 2005) have been
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7 737 proposed as possible additional explanations, when this behaviour takes place within the feeding
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9 738 areas.

10 739 Since most of population estimates of this species rely on counting birds rafting near or heading to
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12 740 colonies, we evaluated **the spatial distribution of resting areas**. The location of coastal patches
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14 741 selected for rafting suggests an important role of the waters surrounding Tavolara island as a resting
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16 742 area before and after visiting the colony. The other selected patches coincide with some of the most
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18 743 important feeding areas: mouth of Coghinas river (North Sardinia), Alghero (Northwest Sardinia)
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20 744 and Oristano (West Sardinia). The latter area is the main feeding destination of yelkouan
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22 745 shearwaters from Tavolara during the incubation stage. An attractive effect of non-home colonies
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24 746 (as suggested by e.g. Bourgeois and Vidal 2008; Borg et al. 2015) did not emerge from our data,
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26 747 although one of the resting spots is close to known colonies (Alghero, Northwest Sardinia).
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28 748 Travelling toward distant feeding localities could also be interpreted as an indirect consequence of
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30 749 bluefin tuna *Thunnus thynnus* overfishing in the Italian waters (Sardinia included). Since the
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32 750 traditional tuna trapping fisheries were almost completely replaced by industrial fishing, bluefin
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34 751 tuna started to be harvested at a rate exceeding the reproductive capabilities of the existing stock
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36 752 (Longo and Clark 2012) and, in a few decades, the stocks have collapsed to the current low
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38 753 abundance (MacKenzie et al. 2009; ICCAT 2010). Tunas drive small fishes toward the surface and
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40 754 are considered as "facilitators" for seabirds to whom they are strongly associated both in tropical
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42 755 and temperate seas (Le Corre and Jaquemet 2005; Veit and Harrison 2017). **In late spring in the
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44 756 Mediterranean Sea tunas, during their migration, get close to the coasts when yelkouan
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46 757 shearwaters are raising chicks. Then the drop of tuna population may have reduced the
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48 758 feeding opportunities for shearwaters, forcing them to move further. Because the yelkouan
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50 759 shearwater is an endemism confined to the Mediterranean and Tavolara island hosts around
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52 760 half of its global population, our findings suggest that, beside direct threats (mortality due to
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54 761 by-catch and overfishing of prey species: Gaudard 2018), conservation measures to be
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56 762 enforced at sea should address the full sustainability of all fisheries across an area
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58 763 encompassing the foraging hotspots identified (namely the Oristano and Alghero waters, the
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60 764 Bonifacio Strait and the Gulf of Lion).**

55 765 In conclusion, despite the limitations associated with the relatively low number of marked
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57 766 individuals, some relevant patterns of the spatial ecology of the yelkouan shearwater could be
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59 767 described. Their main value seems that of referring to the globally most important colony known to
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3 768 date. Studies on different populations are strongly needed in order to assess and implement an
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5 769 effective pan-Mediterranean conservation strategy for this endemic and charismatic taxon.
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17 776 Author contributions

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19 777 NB, MZ conceived the project; NB, MZ, FP, AN and GS co-ordinated the data collection; GC, DG,
20 778 AM, AG and EP performed data management/analyses and drafted part of the manuscript; FP and
21
22 779 MZ drafted the manuscript and FP **and EP** guided the final writing with contributions from all
23
24 780 authors. NB supervised all phases of the project since its beginning. All authors read and approved
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26 781 the final manuscript.
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29 783 Conflict of interest

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31 784 The authors have no conflicting interests.
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34 786 Ethical approval

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36 787 All procedures performed in this study were in accordance with the ethical standards of the
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38 788 institution or practice at which the studies were conducted.
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Table 1. Characteristics of the tracks obtained from GPS data loggers mounted on yelkouan 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 beeline between the maximum distant point reached and the colony is reported as Distance from Tavolara, while the Total Travelled 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 travelled 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	CR	11/06/2012 03:37:00	17/06/2012 23:41:00	7	2012	c	60	162	141	941
TJ3270	T19*	CR	18/06/2012 03:43:00	18/06/2012 23:42:00	1	2012	c	60	21	69	
	T06	I	27/03/2013 07:23:00	03/04/2013 22:19:00	8	2013	c	20	511	225	1266
	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*	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	CR	11/06/2012 03:03:00	13/06/2012 00:56:00	2	2012	c	60	47	107	406
	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*	CR	19/04/2012 07:21:00	19/04/2012 22:56:00	1	2012	c	60	17	26	
TA2236	T08	I	26/03/2013 06:41:00	30/03/2013 21:41:16	5	2013	c	20	309	120	189
	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
TJ3290	T03	I	26/03/2013 04:33:00	01/04/2013 22:58:00	7	2013	c	20	465	184	1041
	T04	I	23/03/2013 07:29:00	30/03/2013 22:49:00	8	2013	c	20	506	144	1249
TA2228	T09	I	25/03/2013 03:35:00	31/03/2013 23:38:00	7	2013	c	20	468	120	1073
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	1097
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	1387	579	2341
	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	2601
TJ3271	T34	I	17/04/2015 04:47:00	21/04/2015 00:00:00	4	2015	c	20	270	206	658

For Peer Review

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; Δ 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 the best model.

Model	k	logLik	Δ 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		

Table 3. Estimated parameter (Coeff), with SE, Wald 95% confidence interval (95% CI), and variable testing (the type II Wald χ^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: 3288; 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 χ^2	df	P
(Intercept)	3.55	0.30	2.96 - 4.15			
STAGE[chick rearing]	-2.82	0.34	-3.5 - -2.15	5.34	1	0.02
BATHY	4.32	0.44	3.45 - 5.19	192.88	1	<0.0001
DCOL	-1.28	0.12	-1.51 - -1.05	11.15	1	0.0008
PROD	-0.84	0.20	-1.22 - -0.45	17.94	1	<0.0001
STAGE[chick rearing]:BATHY	-3.04	0.45	-3.93 - -2.16	45.07	1	<0.0001
STAGE[chick rearing]:DCOL	1.36	0.13	1.10 - 1.62	107.09	1	<0.0001

Table 4 - Estimated parameter, with corresponding SE, Wald 95% confidence interval (95% CI), , and variable testing (the type II Wald χ^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 χ^2	df	P
(Intercept)	0.80	0.05	0.70 - 0.90			
OCTAD				634.08	4	<0.0001
89 vs 81	0.00	0.05	-0.11 - 0.10			
105 vs 81	0.77	0.06	0.66 - 0.89			
161 vs 81	0.96	0.05	0.87 - 1.05			
169 vs 81	0.97	0.05	0.86 - 1.07			
BATHY	0.03	0.02	-0.01 - 0.06	75.91	1	<0.0001
DCOL	-0.10	0.05	-0.20 - 0.00	6.33	1	0.01
OCTAD:BATHY				393.08	4	<0.0001
89:BATHY vs 81:BATHY	-0.01	0.02	-0.04 - 0.02			
105:BATHY vs 81:BATHY	-0.11	0.02	-0.15 - -0.08			
161:BATHY vs 81:BATHY	-0.21	0.01	-0.24 - -0.18			
169:BATHY vs 81:BATHY	-0.22	0.02	-0.25 - -0.19			
OCTAD:DCOL				81.39	4	<0.0001
89:DCOL vs 81:DCOL	0.05	0.05	-0.05 - 0.16			
105:DCOL vs 81:DCOL	0.29	0.05	0.19 - 0.39			
161:DCOL vs 81:DCOL	-0.10	0.05	-0.19 - -0.01			
169:DCOL vs 81:DCOL	-0.09	0.05	-0.19 - 0.02			

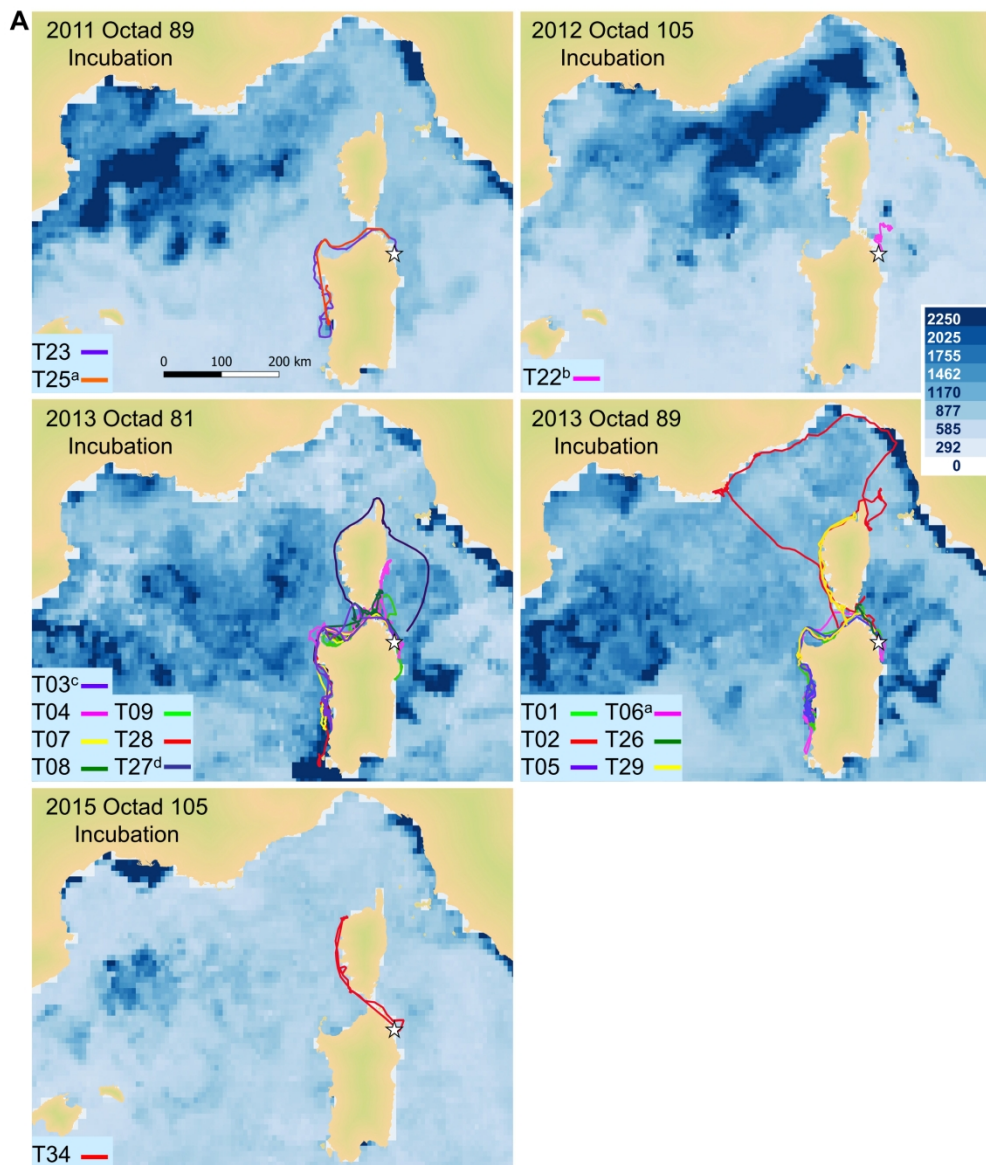
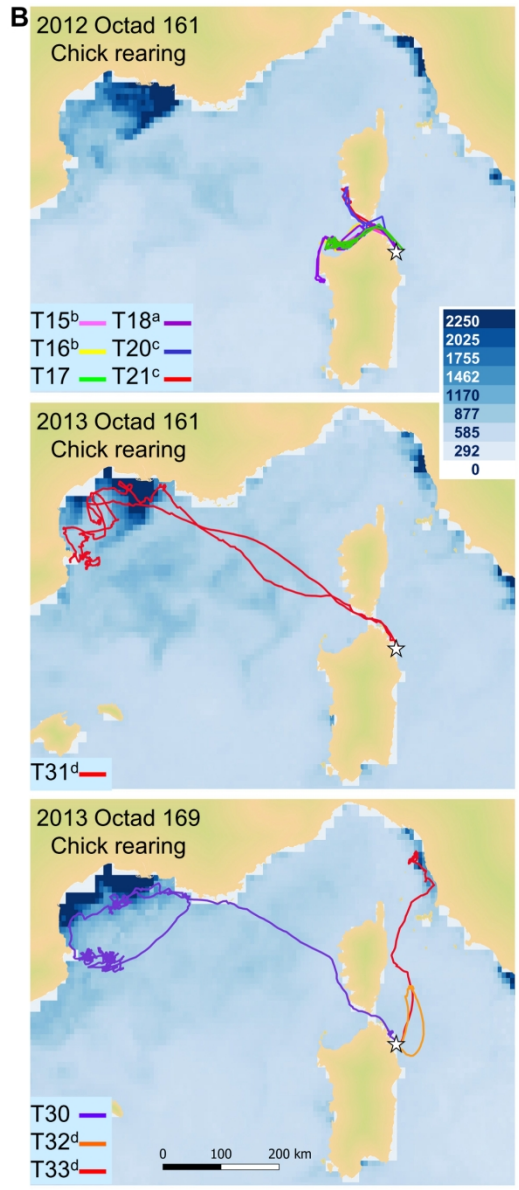


Fig. 1 Tracks of yellow shearwaters GPS tagged from 2011 to 2015 at Tavolara Island, Sardinia, IT (white star). The blue shades show sea net primary productivity (expressed as $\text{mg C} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) grouped according to Octads (8 days periods) in 2011-2015. Each panel contains the tracks obtained in the octad for which sea productivity was calculated and included in the analysis (see Table 1). T indicate 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.

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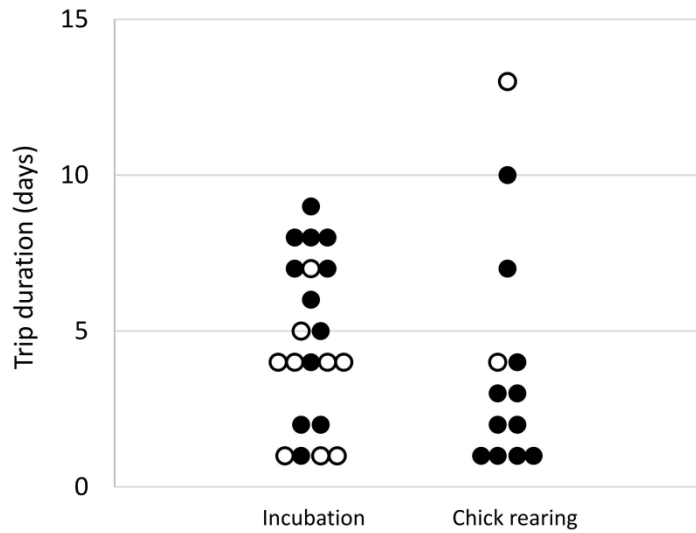


Fig. 2. Trip duration in days estimated from yellow shearwaters tracks (N=34) recorded during incubation and chick rearing stages from 2011 to 2015 at Tavolara Island (Sardinia, IT). Open dots represent incomplete tracks.

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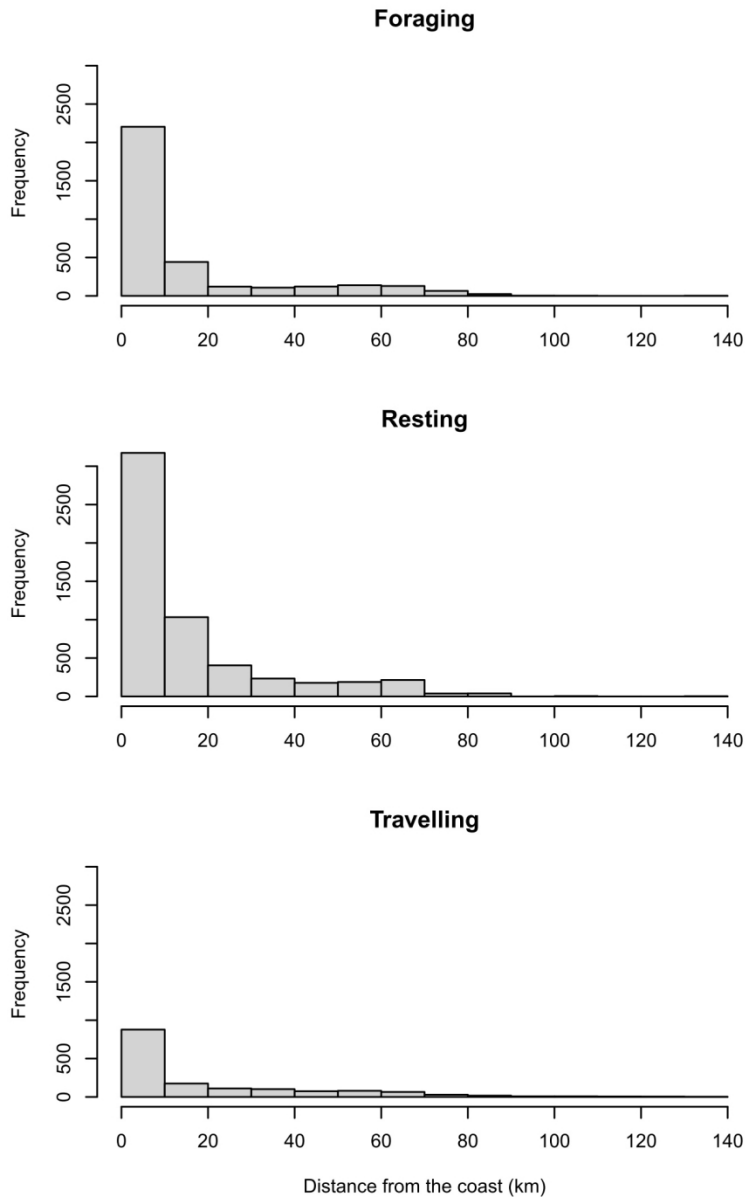


Fig. 3 Frequency distribution of the distances from the coast of fixes belonging to the three behavioural categories (Feeding, Resting, Travelling) obtained from GPS tagged yelkouan shearwaters at Tavolara Island (Sardinia, IT) from 2011 to 2015. The reported data refer to the tracks of all animals in both breeding stages (incubation and chick rearing).

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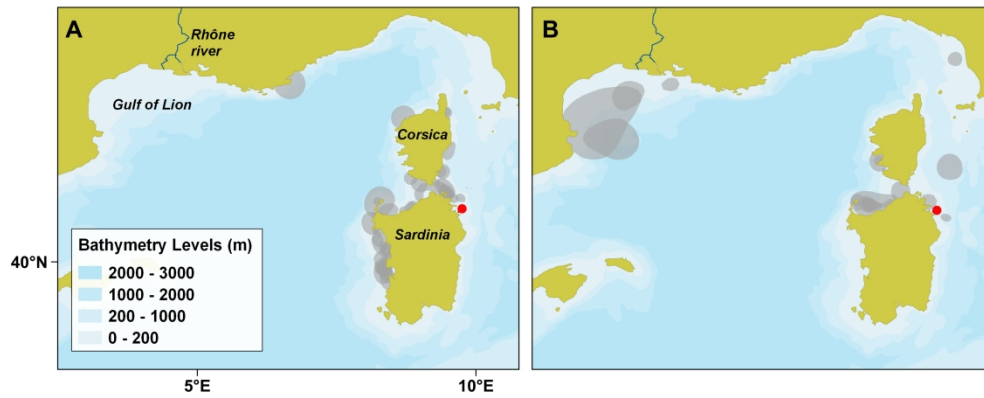


Fig. 4 Foraging core areas with a different percentage of volume contour per individual (median: 55%; IQR: 50%-55% volume contours) obtained from the distribution of the fixes categorised as F (feeding activity) of yellow shearwaters GPS tagged from 2011 to 2015 at Tavolara Island (red dot; Sardinia, IT).
A: Incubation period (n tracks = 17, n individuals = 16); B: Chick rearing period (n tracks = 10, n individuals = 6).

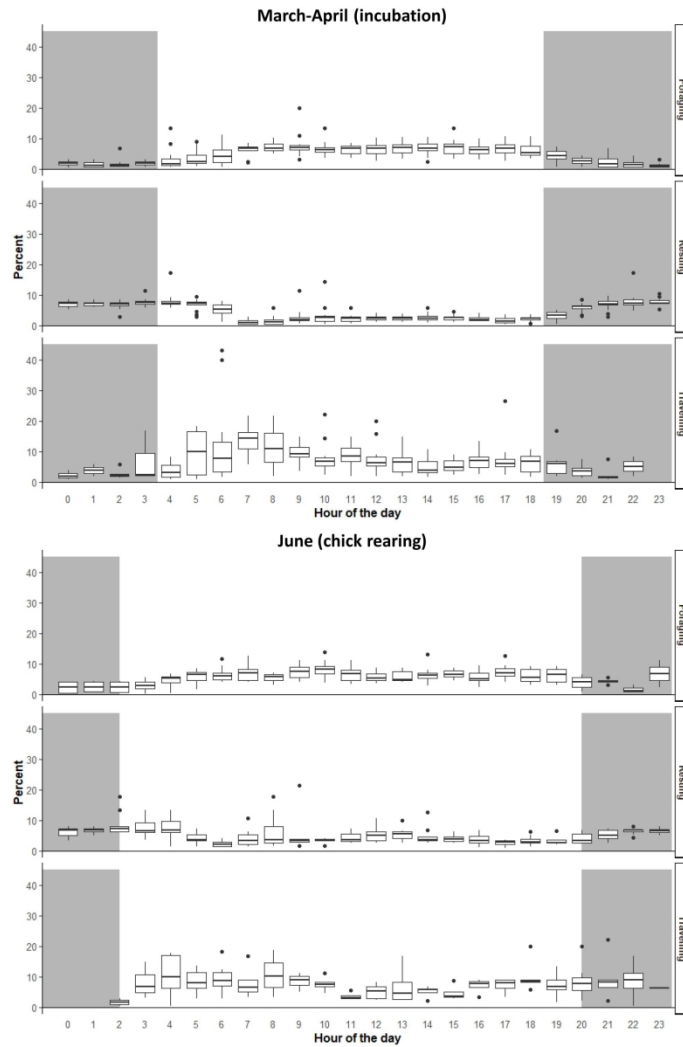


Fig. 5 Daily distribution (in %) of fixes classified as Foraging, Resting and Travelling in the 24 h. The mean nautical dawn and dusk were used to identify the night-hours (grey shadow in the graph) for the two periods considered: March-April (incubation): 18:30-3:30; June (chick rearing): 20:00-2:00.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

209x297mm (300 x 300 DPI)

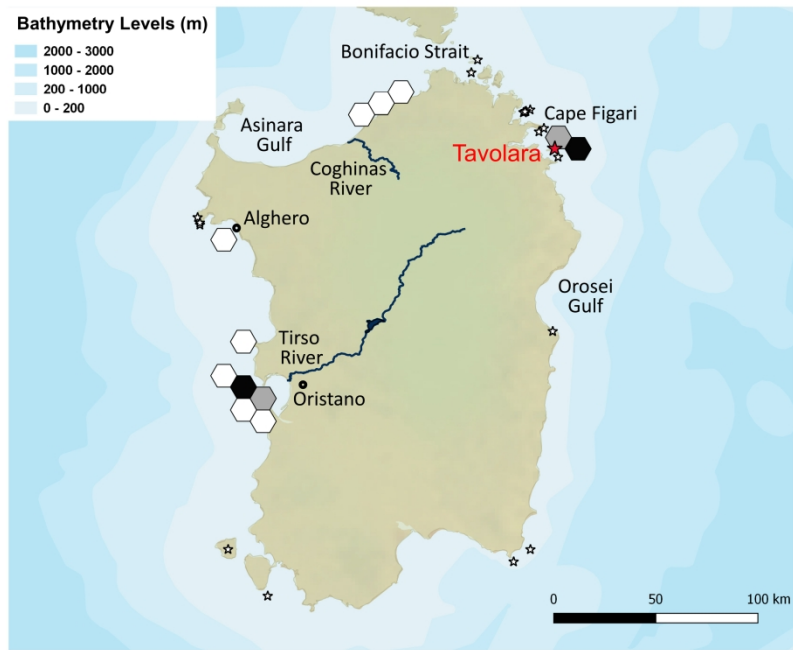
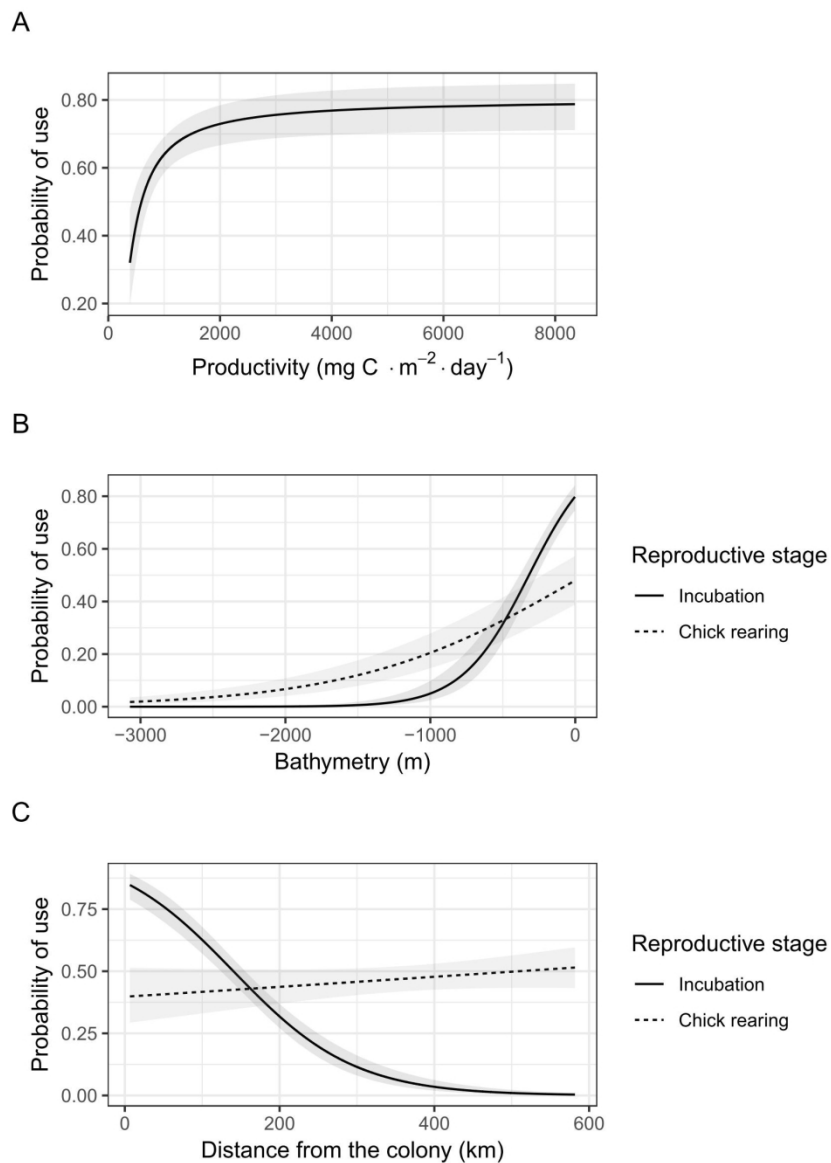


Fig. 6 Resting sites of yelkouan shearwaters GPS tagged from 2011 to 2015 at the Tavolara Island (Sardinia, IT). Score of use in cells of a 10 km spaced hexagonal: white, grey and black cells represent a score ranging from 9-15, 16-22 and 23-29 respectively. See Materials and Methods for details. Stars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

297x209mm (300 x 300 DPI)



45 Fig. 7 Plots of the effects of sea productivity (A; bathymetry = -100 m, distance from the colony = 100 km
46), of the interaction between reproductive stage and bathymetry (B; distance from the colony = 100 km, sea
47 productivity = $2000 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) and of the interaction between reproductive stage and distance
48 from the colony (C; bathymetry = -100 m, sea productivity = $2000 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) on the probability
49 of use of a given $9 \times 9 \text{ km}$ cell. Shaded areas = 95% Confidence bands. Results from the best Generalized
50 Linear Mixed Model developed to describe foraging habitat selection of yelkouan shearwaters tagged at the
51 colony of Tavolara Island (Sardinia, IT) from 2011 to 2015 (error distribution: binomial; random intercepts:
52 bird ID and track ID nested within bird ID). Number of considered cells: 3288; Number of birds: 21; Number
53 of tracks 27. See Table 3 for numerical results.

54 147x203mm (300 x 300 DPI)

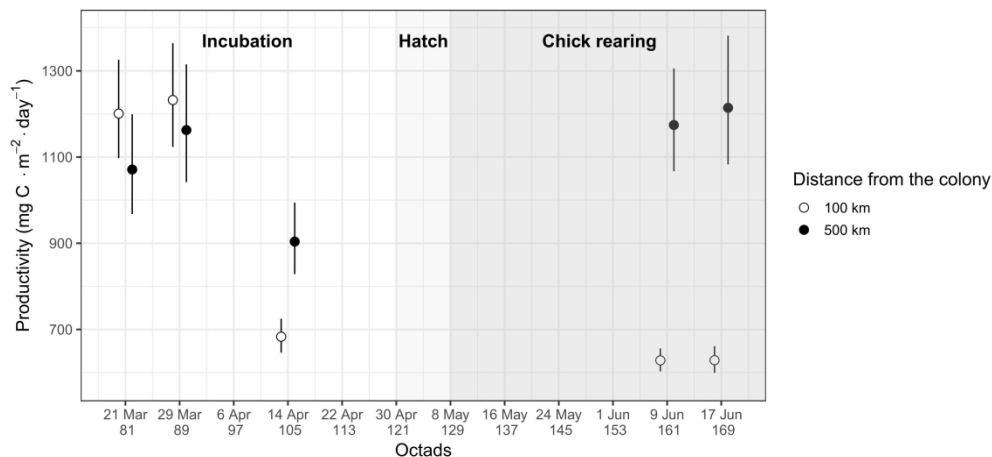


Fig. 8 Plot of the effects of octads and distance from the colony on sea productivity estimated at bathymetry = -100 m. Error bars = 95% Confidence Intervals. Results from the linear mixed model (LMM) analysing the inverse-transformed sea productivity in the cells with at least one foraging fix in the 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.

274x128mm (300 x 300 DPI)