Consistent foraging areas and commuting corridors of the critically endangered Balearic shearwater *Puffinus mauretanicus* in the northwestern Mediterranean

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ARTICLE INFO

ABSTRACT

Unprecedented changes to the marine environment and growth of bio-logging science make detailed study of the movement ecology of threatened marine species timely. Here, we study spatial and temporal patterns of marine space use by a critically endangered seabird: the Balearic shearwater *Puffinus mauretanicus*. Using a suite of bio-logging systems, 67 foraging trips were recorded during incubation periods between 2011 and 2014 from one of the species' largest colonies (Sa Cella, Mallorca). Most birds followed narrow flight corridors to restricted neritic foraging grounds on the Iberian continental shelf. Productive foraging areas along the Catalan coast (NE Spain) were consistent across multiple years and between sexes, indicating extensive use of predictable resources. While our study emphasises the vulnerability of this species to anthropogenic activity in nearshore waters, consistent commuting corridors and foraging grounds represent tractable habitat for protection and offer hope for developing area-based management approaches. Preferred foraging areas showed strong overlap with recently declared Special Protection Areas, strengthening the evidence base for targeted management at these sites.

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1. Introduction

Seabirds are one of the most threatened groups of marine vertebrates (Croxall et al., 2012; Spatz et al., 2014), and while there have been some successes in protecting terrestrial breeding sites, this group spend the majority of their lives at sea where the level of protection afforded is poor (Grémillet and Boulinier, 2009; Lewison et al., 2012). Recent marine conservation measures have largely focused on establishing networks of marine protected areas (MPAs) (Abdulla et al., 2009). While these tools show promise for some taxa (Halpern, 2003; Selig and Bruno, 2010), protection of seabirds and other highly mobile top predators is challenging (Game et al., 2009; Hooker et al., 2011; Ronconi et al., 2012). For example, predictable oceanographic features are potential priority areas for conservation (e.g. Hazen et al., 2013; Scales et al., 2014b), yet few pelagic environments and associated species have been incorporated into existing management frameworks (Game et al., 2009). Furthermore, movement corridors (e.g. migration or commuting) between key marine habitats are ecologically important, but often overlooked, areas in need of protection (Hooker et al., 2011). Initiatives to identify marine Important Bird Areas (IBAs),

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such as the recent inventories of Spain and Portugal (Arcos et al., 2009; Ramírez et al., 2008), and ongoing work in other regions (Lascelles et al., 2012), represent an important step towards improving levels of protection for seabirds. However, comprehensive knowledge of at-sea movements and their spatio-temporal variability is often lacking.

The Mediterranean Sea is under particular pressure from increasing human activity (Bianchi, 2007; Coll et al., 2012; Lewison et al., 2014). This semi-enclosed basin contains high biodiversity, high levels of endemism, and significant extinction threats (Coll et al., 2010). Seabirds are no exception, with several endemic taxa of immediate conservation concern due to their small and declining populations (Zotier et al., 1999). One such species is the Balearic shearwater, Europe's only critically endangered seabird (Arcos, 2011; IUCN, 2014). Breeding is restricted to the Balearic Islands (Ruiz and Martí, 2004), with an estimated breeding population of ∼3200 pairs (although this figure contains considerable uncertainty: Arcos et al., 2012a). This species is experiencing severe decline driven by low rates of adult survival (Oro et al., 2004), likely because of direct and indirect effects of human activity. Although small pelagic fish represent the main prey of Balearic shearwaters (Gutiérrez and Figuerola, 1995), they also feed on fisheries discards, leading to severe risk of bycatch (Arcos and Oro, 2002a; Le Mao and Yésou, 1993; Navarro et al., 2009; Oliveira et al., 2015). Other factors, including unregulated levels of predation by introduced mammals at colonies (Arcos, 2011), climate change (Luczak et al., 2011; Wynn et al., 2007), changes in discard availability (Bicknell et al., 2013), fisheries overexploitation (Arcos et al., 2008) and coastal development (Arcos, 2011) place the long-term survival of this seabird in jeopardy.

Intensive research in the western Mediterranean has provided important insights into the distribution and ecology of the Balearic shearwater in recent years. Vessel-based observations and tracking data have revealed that the species preferentially forages in highly productive, but heavily fished, waters along the Iberian continental shelf and Balearic archipelago (Abelló et al., 2003; Ruiz and Martí, 2004). Additional information on the species' variable foraging habits and oceanographic characteristics of high-density areas has aided interpretation of marine habitat use (i.e. Arcos et al., 2000; Arcos and Oro, 2002a; Louzao et al., 2006, 2012). Despite such attention, this species has been the focus of relatively few tracking studies. Satellite tracking on Mallorca and Menorca (Bartumeus et al., 2010; Ruiz and Martí, 2004), and more recently on Eivissa (Louzao et al., 2012) has provided insights into at-sea movements of birds from known colonies. Nevertheless, detailed multi-year information on foraging movements of confirmed breeders is lacking, and little is known about at-sea behaviours outside of the chick-rearing period.

Following identification of marine IBAs in Spanish waters (Arcos et al., 2009), the Spanish Government is engaged in affording protection to these sites under the European Union Birds Directive (2009/147/EC). A network of Special Protection Areas (SPAs) covering nearly 50,000 km² was designated in July 2014 as part of the Natura 2000 network, and efforts to establish management plans are now underway (Boletín Oficial del Estado, 2014). Of 39 new SPAs, 20 sites were considered relevant for conservation of Balearic shearwaters, including 14 sites used during the breeding period. There is now a need to validate the importance of these conservation areas for breeding birds of known origin, and to assess their stability of use over time.

We undertook the first multi-year tracking study of incubating Balearic shearwaters from one of the largest known colonies on Mallorca, with the aim of generating detailed information on the movement ecology of this species of relevance to conservation management. We aimed to: (i) identify the main commuting and foraging areas of breeding birds, (ii) determine levels of inter-annual variability in foraging distributions, (iii) determine the extent to which current Special Protection Areas (SPAs) overlap with at-sea distribution and behaviour and (iv) test previously unexplored environmental controls of observed commuting and foraging strategies.

2. Materials and methods

2.1. Study site and field methods

The study was conducted at one of the largest Balearic shearwater breeding colonies (Sa Cella cave; ∼6.3% of the global population), situated on the western tip of Mallorca, Spain, during March–April 2011–2014 (Fig. 1; 39°36′N, 02°21′E). To investigate at-sea movements and activity patterns, 61 incubating birds were fitted with both i-gotU GPS loggers (modified GT-120: 11.2–15.4 g) and British Antarctic Survey geolocators (MK18 or MK14: 1.4–1.9 g) during 82 deployments over 4 years. To validate behavioural information collected with GPS and geolocators, a subset of 22 individuals were also fitted with 2.7 g time–depth recorders (TDRs: Cefas Technology Ltd, Lowestoft, UK) in 2013 and 2014.

Targeted birds were temporarily removed from the nest and GPS loggers were attached to contour feathers on the back using Tesa tape (details in Guilford et al., 2008), while geolocators and TDRs were mounted on plastic leg rings attached to the tarsus (details in Guilford et al., 2012). GPS devices were configured to obtain hourly positions, while TDRs collected pressure readings at 1-s intervals. Geolocators provided a measure of time spent on or in the water, by recording the number of 3-s blocks in a 10-min period that the device was immersed. The total weight of combined bio-loggers and attachments was ≤4.7% of the body mass of birds (mean: 4.2 ± SD 0.3%; body mass: 508 ± 33 g), and was thus within the 3–5% limit recommended by most authors (Phillips et al., 2003; Wilson et al., 2002).

To reduce potential detrimental effects to the birds, bio-loggers were deployed for the duration of one foraging trip and, upon return to the cave, birds were caught and devices removed. On three occasions birds evaded recapture after a single trip and two or more trips were recorded. Feather loss was low-to-negligible in all cases, and birds were handled on average for 19 (±SD 6) minutes during device deployment and 23 (±SD 6) minutes during recovery. Birds were sexed from DNA extracted from blood (Vetgenomics, Spain) or feathers (Avian Biotech, UK) collected during device recovery.

2.2. Ethics statement

All research work was performed under relevant permits issued by the Government of the Balearic Islands (Permit numbers: CAP04/2010, CAP31/2011, CEP04/2012, CEP03/2013, CEP15/2014), in accordance with regional legislation (BOIB 97 Decret 65/2004) and following established field procedures that minimise colony disturbance (see Guilford et al., 2012).

To assess potential impact of tag attachment, breeding success (measured by egg hatching and chick fledging success of a pair) was recorded for both experimental birds and a set of unhandled closely matched control nests within the colony (see Section 3.1). To minimise disturbance, individuals were only tagged once during a season.

2.3. Data analysis

2.3.1. Data processing

Geolocator activity data were processed using BAStrak software (British Antarctic Survey, Cambridge, UK). To account for the
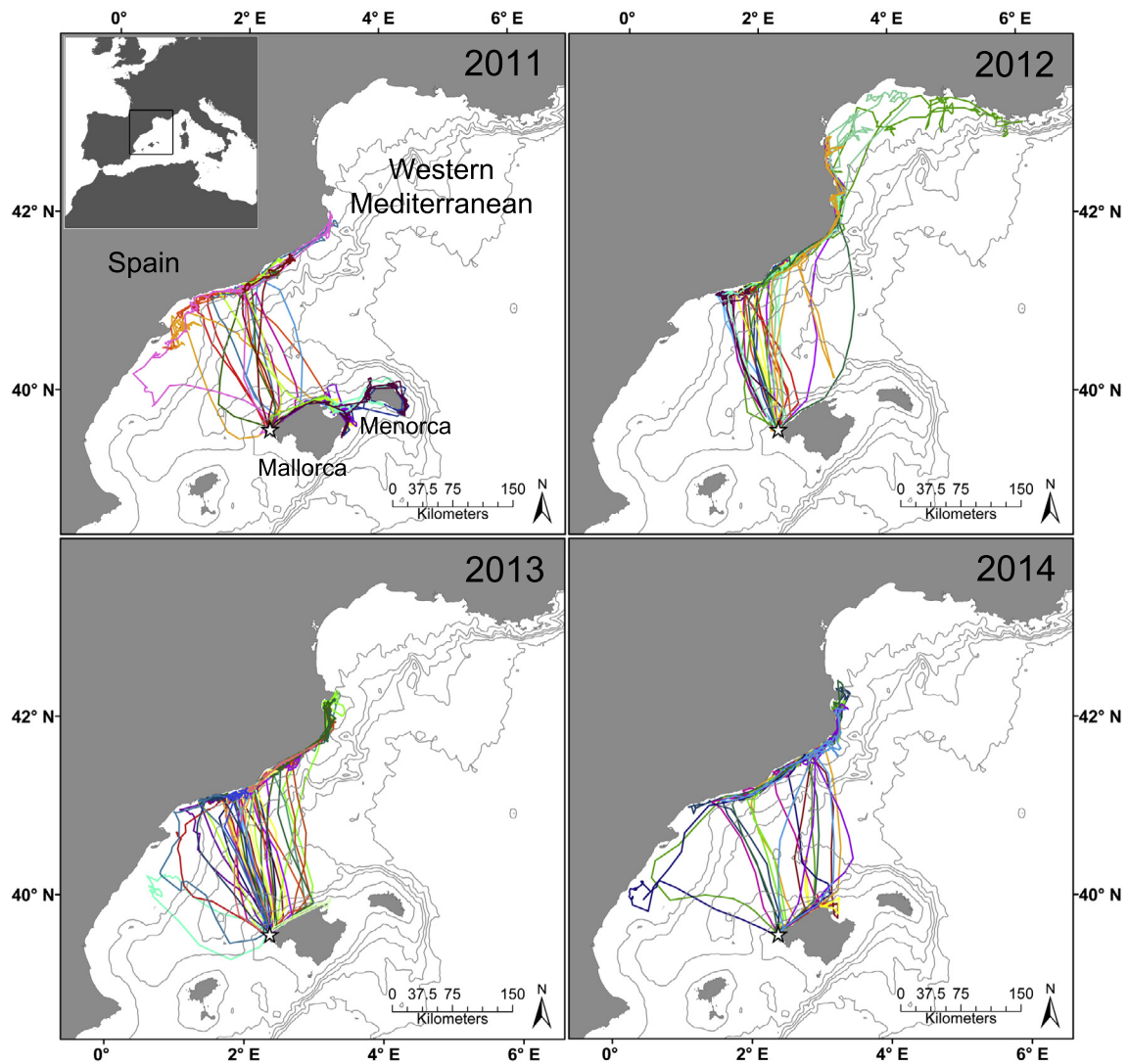
Fig. 1. Balearic shearwater foraging trips recorded during incubation periods in 2011 (n = 16), 2012 (n = 14), 2013 (n = 23) and 2014 (n = 14). Individual trips are coloured in unique shades within each year, and only complete foraging trips are displayed. Isobaths are denoted with grey lines (200 m, 1000 m, 1500 m, 2000 m and 2500 m; GEBCO 30-arc second bathymetry data) and the colony location is indicated with a star. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

mismatch in recording intervals of GPS loggers and geolocators, activity data were matched to 1-h GPS track segments (Mean ± SD segment duration: 60.0 ± 6.7 min) after having been split from 10-min blocks into 1-min units. GPS track segment break-points would often occur part way through a 10-min block, so in this way 1-min values from the same block could be partitioned either side of the break. The proportion of time spent immersed within each track segment was then calculated.

TDR data were processed in the 'diveMove' package in R (Luque, 2007). Depth measurements were calibrated using a 'moving quantile' zero-offset correction method (details in Luque and Fried, 2011), and classified using a dive threshold of 1 m. Dives were matched to 1-h track segments for behavioural classification purposes. All analyses were carried out in R version 3.0.2 (R Core Team, 2013), Matlab R2013a (Mathworks, USA) and ArcGIS version 10.0 (ESRI, USA).

2.3.2. Foraging distributions and SPAs

Multiple bio-logging systems were used to identify areas likely to be associated with foraging (Appendix A). A filtering method was developed on a subset of 18 birds for which simultaneous dive,

GPS and immersion data were obtained, before applying to the full GPS dataset. Track segments likely to be predominantly associated with commuting flight (speed of movement >7 ms^{-1}) and rest (night-time locations between 21:00 and 06:59 Central European Summer Time (CEST)) were discarded, based on speed distributions with and without dives, and on temporal patterns of dive and immersion activity (see Appendix A). Filtering retained 54% of locations and 98% of dive time in the test dataset, and 56% of locations in the full 4-year dataset.

The distribution of foraging birds was plotted with the subset of retained locations, using fixed kernel density estimation (KDE) in the Geospatial Modelling Environment (Beyer, 2012) (cell size: 1 km^2). Only GPS fixes falling between two consecutive track segments assigned to the foraging class were used in KDE. To avoid pseudo-replication caused by multiple trips from the same individual, a single track per individual per year was randomly selected (repeat tracks were used in other analyses). Covariance bandwidth matrices were obtained using the plug-in estimator (Wand and Jones, 1994) in the 'ks' package in R (Duong, 2013; see Appendix Table A.1. and Fig. A.4. for bandwidth matrices and a comparison of bandwidth optimisers). To quantify spatial overlap between

foraging distributions and protected waters off Spain and France, we determined the proportion of foraging locations falling within SPAs and all designated MPAs.

For each foraging trip, the total distance travelled, maximum trip range and total trip duration were calculated. To compare between tracking periods and between sexes, linear mixed-effects models (LMMs) with a random individual intercept were fitted using the 'lme4' package in R (Bates et al., 2013). Full models and models without a fixed effect were then compared using likelihood ratio tests. Owing to insufficient sample sizes, within-year comparisons between sexes were limited to 2013 and 2014.

2.3.3. Foraging consistency

Inter-annual consistency in foraging areas was evaluated by measuring the overlap of kernel density estimates, within 50% and 90% kernel density contours. 50% contours were used to compare core foraging areas, while 90% contours provided a more encompassing estimate of foraging range (Börger et al., 2006). Site fidelity was measured using the Volume of Intersection (VI) Index (Seidel, 1992), a statistical measure of overlap between two utilization distributions (calculated implementing R functions from Fieberg, 2014). The VI index ranges from zero to 1, where zero signifies no overlap and 1 signifies identical density areas (Fieberg and Kochanny, 2005). The same method was used to compare foraging areas between the sexes in 2013 and 2014.

2.3.4. Route fidelity and commute efficiency

To test for individual consistency in outbound routes to foraging grounds, median nearest neighbour distances (Freeman et al., 2011) between the outbound paths of tracks were calculated for (a) pairs of tracks from the same individual collected in separate breeding seasons and (b) pairs of tracks from different individuals collected in separate breeding seasons for all bird combinations. LMMs were then fitted on nearest neighbour distances with a random individual intercept and fixed group (a and b) effect.

To determine orientation efficiency (the strength with which individuals actively oriented towards mainland foraging areas or back to the colony) we calculated the straightness index (ratio of the beeline distance to the path distance travelled) of outbound and inbound track sections for birds that commuted to the Catalan coast off the Spanish mainland. The track locations at which birds began actively orienting towards their goal (the orientation distance), and the subsequent commute sections of track, were determined using a backward path analysis (BPA) (Bonadonna et al., 2005; details in Appendix B). To validate the directionality of the track section chosen by BPA, linear regression was performed on the retained portion of each track. The outbound goal was defined as the location after the bird reached the mainland foraging area (<30 km from the coast where 99% dive activity fell) and subsequently dropped its speed to <7 ms^{-1}. The 10 km radial boundary from the colony was used as the inbound goal as rafting predominantly occurred within this distance.

2.3.5. Activity patterns

Trip activity budgets were determined based solely on geolocator activity data. To retain high-resolution activity data, immersion values were matched to 10-min interpolated GPS tracks (interpolation using piecewise cubic hermite polynomials, following Tremblay et al., 2006). Data were then grouped into three classes according to the proportion of time spent immersed within a track segment. Sensitivity tests indicated that grouping levels within the tested range had little effect on mapped distributions (see Appendix Table C.1). Final immersion activity classes were validated using the TDR test dataset and were believed to broadly identify the following behaviours: Low ($\leqslant$0.05 time) = track segments associated with sustained commuting flight (segments

containing dive activity: 0.9%), Moderate (>0.05 – <0.95 time) = segments predominantly associated with foraging and search behaviours (segments containing dive activity: 47.9%), High ($\geqslant$0.95 time) = segments associated with rest or water-based foraging behaviours (segments containing dive activity: 10.3%). Activity budgets were determined based on the proportion of time spent in the three classes throughout a foraging trip.

The proportion of total dive time falling within each hour of the day and the number of dives falling within 2 m depth bins were calculated for the subset of TDR-tracked individuals. To plot maps of dive activity, dive data were matched to the nearest 10-min interpolated GPS locations, and the number of dives hour^{-1} were calculated within cells over a 10 × 10 km grid. This cell size provided data at an appropriate spatial scale for foraging movements and protected area management considerations (both covering areas >100 km^2), while accounting for dive location uncertainty.

2.3.6. Meteorological controls of foraging strategy

Binomial Generalized Additive Models (GAMs) with a logit link function were used to test the influence of the local wind field and lunar cycle on the choice of which foraging area birds headed to at the beginning of an outbound trip (Hastie and Tibshirani, 1990). GAMs were fitted with the mgcv package in R (Wood, 2006). 6-hourly 0.125° gridded 10 m U and V wind component data fields were obtained from European Centre for Medium-Range Weather Forecasts (ECMWF) operational models (ECMWF, 1995; provided by UKMO through BADC: https://badc.nerc.ac.uk/home/). Data on the fraction of the moon illuminated each day were provided by the U.S Naval Observatory & Astronomical Applications Department (http://aa.usno.navy.mil/data/). Wind fields from the operational model were validated through a comparison with re-analysis model data (see Appendix Fig. D.1). Zonal and meridional wind fields were converted to total wind speed (ms^{-1}) and direction (wind vector azimuth, degrees) values before environmental data were matched to GPS locations. Mean values for each covariate within the outbound track sections of individual foraging trips were then calculated. Foraging site was used as the binomial response variable in the model (0 = Balearic Islands, 1 = Mainland Spain), and mean environmental covariates were tested as fixed effects. Birds were assigned to two foraging areas based on the distribution of median track distances from the colony during the first trip day (Appendix Fig. D.2). Generalized Additive Mixed-Effects models (GAMMs) were initially run to account for any dependence introduced by multiple tracks from the same individual. However, the level of between-group variability was not sufficient to warrant incorporating individual as a random effect (Appendix Table D.1). Model selection was undertaken using a manual forwards stepwise-selection method involving comparison of model Akaike Information Criteria (AICc).

For birds that commuted directly to the mainland, the outbound track section was defined as that falling 10 km from the colony and 30 km from the mainland (see Section 2.3.4). For birds remaining around the Balearic Islands (for the entire trip or >6 h prior to mainland travel) the first 6 h of track (corresponding to the minimum mainland commute duration) were used.

3. Results

3.1. Impact of device attachment

89% of tracked pairs and 69% of control pairs bred successfully (Appendix Table E.1). In two of four years all tracked pairs hatched and fledged young, and in a third year all but one chick hatched and fledged. There was no evidence to suggest that experimental nests had significantly lower hatching or fledging success than

controls; overall, tracked birds were more successful (Fisher's exact tests, Hatching: $p > 0.05$, power = 0.55, Fledging: $p = 0.006$, power = 0.90; Appendix Table E.1). See Appendix E for a comparison of trip characteristics of birds carrying different device loads.

3.2. Foraging distributions and SPAs

77 (94%) instrumented birds were recaptured, and 69 (84%) GPS loggers recovered, yielding 67 complete foraging trips from 50 individuals (2011 = 16, 2012 = 14, 2013 = 23, 2014 = 14; Appendix Table E.3). 64 (96%) tracked birds foraged north of the colony, with only three individuals showing initial southerly-directed movement (Fig. 1). Shearwaters used two coastal areas in the northwestern Mediterranean: waters along the Iberian continental shelf and those around the Balearic Islands (Fig. 2). Foraging birds utilized small proportions of the total area of sea available within their median or maximum foraging trip ranges (median: 214 km radius, 10.7% area; maximum: 491 km radius, 7.0% area; Fig. 2), and were absent from accessible stretches of coast both west and south of the colony.

Birds ranged maximum distances of between 75.6 km and 491.1 km from the colony, travelling total distances of between 203 km and 2109 km, with trip durations of between 15.6 and 309.2 h (Table 1). Movements were predominantly coastal: 92% of all track locations occurred within 20 km of the shoreline and 91% fell over water depths <100 m (Fig. 1).

All birds visited Spanish SPAs during foraging trips, while only 5 birds during 6 trips visited French SPAs. 61% of foraging locations fell within designated SPAs (60% within Spain, and 1% within France), 63% overlapped with all listed Natura 2000 sites, and 65% overlapped with areas designated as some form of MPA, regardless of whether the Balearic shearwater was a listed feature (Appendix Fig. F.1). The majority of high-use areas overlapped with conservation sites; however, frequented stretches of coast between

Table 1
Foraging trip characteristics of Balearic shearwaters tracked during incubation from Sa Cella, Mallorca between 2011 and 2014. The mean (±SD) trip range, trip duration and total distance travelled is shown for each study year and sex. Chi-square values, degrees of freedom (subscript numbers) and *p*-values summarise likelihood ratio tests used to compare full LMMs (containing a random 'individual' intercept term and 'year' or 'sex' as a fixed effect) with LMMs containing no fixed effect. In the absence of repeated measures for individuals, one-way ANOVA tests (summarised by *F* values) were used to compare trip metrics between males and females for single tracking periods in 2013 and 2014. Years with matching superscript letters showed significant differences at the 5% level (Tukey's all pairs comparison test). *p*-values < 0.05 are given in bold.

Tracking season	n	Trip range (km)	Trip duration (h)	Total distance (km)
2011	16	185.7 (±53.1)[a]	153.5 (±58.5)	771.1 (±261.8)
2012	14	288.2 (±101.1)[a]	162.7 (±65.7)[a]	956.1 (±479.2)
2013	23	223.5 (±55.6)	114.2 (±38.3)[a]	696.2 (±191.1)
2014	14	228.2 (±98.8)	157.1 (±36.3)	818.2 (±321.0)
χ^2_3	–	11.845 ($p = \mathbf{0.008}$)	11.147 ($p = \mathbf{0.011}$)	5.467 ($p = 0.141$)
Male (all yrs)	27	219.8 (±67.2)	140.2 (±45.0)	749.9 (±240.3)
Female (all yrs)	25	243.4 (±77.7)	139.6 (±40.6)	800.8 (±251.7)
χ^2_1	–	1.257 ($p = 0.26$)	0.025 ($p = 0.88$)	0.459 ($p = 0.50$)
Male (2013)	8	210.1 (±38.8)	114.5 (±19.7)	684.5 (±141.1)
Female (2013)	13	241.8 (±53.0)	123.6 (±38.8)	745.7 (±179.2)
$F_{1,19}$	–	2.137 ($p = 0.16$)	0.376 ($p = 0.55$)	0.670 ($p = 0.42$)
Male (2014)	8	237.0 (±97.1)	171.4 (±34.8)	881.3 (±323.4)
Female (2014)	6	216.5 (±109.1)	138.0 (±31.1)	734.1 (±326.5)
$F_{1,12}$	–	0.137 ($p = 0.72$)	3.438 ($p = 0.09$)	0.705 ($p = 0.42$)

Barcelona and Cap de Creus fell largely within unprotected waters (Fig. 2).

3.3. Foraging consistency

Foraging areas overlapped among years (90% probability contours: VI index = 0.22–0.64; Table 2). Core foraging areas were
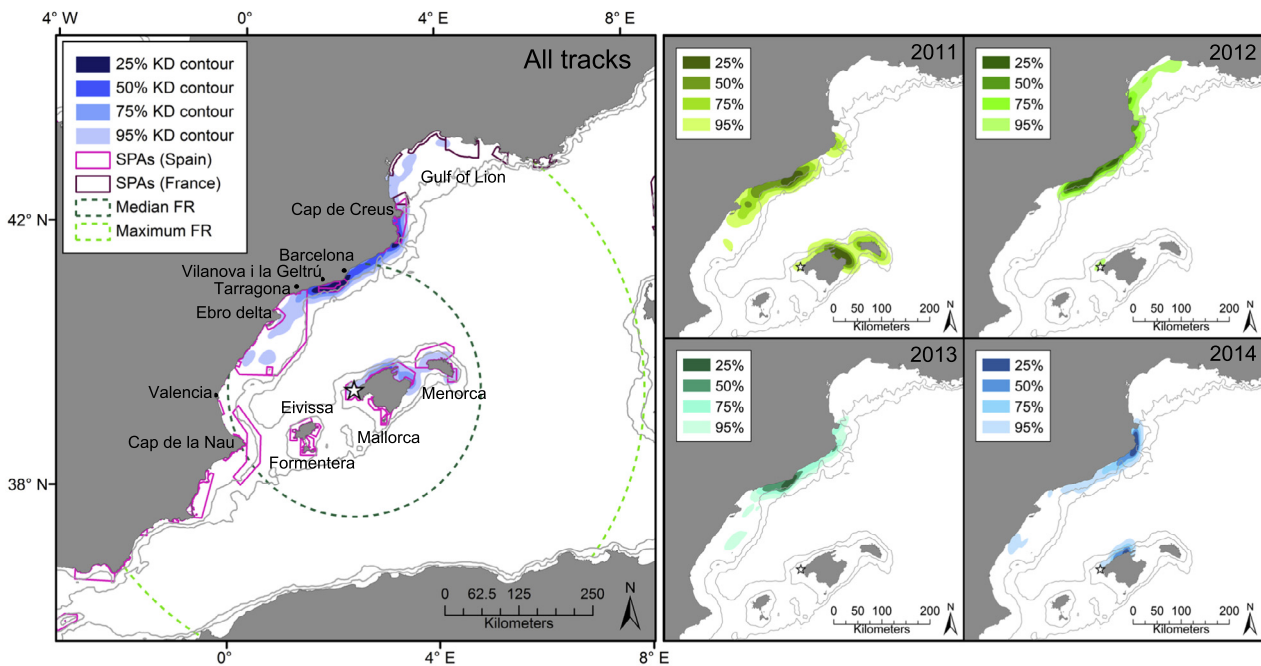

Fig. 2. Kernel density estimates (25%, 50%, 75% and 90% kernel density contours) of GPS locations likely to be associated with foraging behaviour for 63 Balearic shearwaters tracked from Sa Cella, Mallorca during incubation periods (March–April) between 2011 and 2014 (2011: *n* = 15, 2012: *n* = 12, 2013: *n* = 22 and 2014: *n* = 14, no within-year repeated measures). Pink and purple boxes show Natura 2000 Special Protection Areas (Spain = Pink, France = Purple; Sources: European Commision, 2014, Ministerio de Agricultura, Alimentación y Medio Ambiente, 2014); Green dotted lines show median (dark green) and maximum (light green) foraging ranges (FR). 200 m and 1000 m isobaths (GEBCO 30-arc second bathymetry data) are denoted with grey lines and the colony location is indicated with a star. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Pairwise overlap of 50% and 90% kernel density (KD) contours for the tracked Balearic shearwater population between years. Foraging area overlap was compared with the volume of intersection (VI) index (Seidel, 1992).

Year	VI index	
	50% KD contour	90% KD contour
2011–2012	0.36	0.37
2011–2013	0.36	0.41
2011–2014	0.04	0.22
2012–2013	0.49	0.64
2012–2014	0.14	0.34
2013–2014	0.00	0.27

more variable, but there was still considerable overlap (50% probability contours: VI index = 0.00–0.49).

There was some variation in foraging distributions because of inter-individual differences during 2011 and 2014 (Fig. 1 and 2). In both years, a small number of birds remained exclusively around the Balearic Islands (2011: $n = 7$; 2014: $n = 4$). A second group also foraged locally prior to commuting to the mainland ($n = 7$). In other years, all birds except one engaged in direct commuting trips. Foraging trips were significantly shorter in 2013 than in 2012, and trip range differed significantly between 2011 and 2012. There were no significant differences in total trip distance between years (Table 1).

Male and female foraging areas overlapped substantially in both 2013 and 2014 (VI index: 2013 50% = 0.26, 90% = 0.46; 2014 50% = 0.63, 90% = 0.68; Appendix Fig. F.2), with no significant differences in trip range, trip duration and total distance (Table 1).

3.4. Route fidelity and commute efficiency

Tracked birds commuted to Catalonia along consistent routes (Median nearest neighbour distances: *within years* – between individual: 15.8 km (IQR 9.3–48.7); *between years* – within individual: 30.6 km (IQR 9.8–54.3), between individual: 40.0 km (IQR 16.3–61.3)) (Fig. 3a, Appendix Fig. C.1). Intra-individual variation in route fidelity was similar to inter-individual variation (LMM, $\chi^2_1 = 0.358$, $p = 0.549$). 85% of birds undertook commuting trips, and the orientation efficiencies of these individuals were high during both outbound and inbound track sections (Straightness index, outbound: 0.98 ± 0.03, inbound: 0.96 ± 0.04; Orientation distance, outbound: 161 ± 23 km, inbound: 183 ± 26 km; Appendix Table B.1).

3.5. Activity patterns and diving behaviour

Birds spent on average 53.4 ± 6.6% of trip time engaged in high immersion activity, which is likely to represent rafting or foraging from the surface (Appendix Table C.2). High on-water activity took place most frequently during the night and least frequently during crepuscular hours, when peak numbers of track segments associated with low on-water time occurred (Fig. 3). Comparatively little time was engaged in low immersion behaviour indicative of bouts of sustained flight (7.2 ± 3.9%). Periods of moderate immersion activity likely to be associated with foraging behaviours and slower pre-commute flight accounted for a significant proportion of trip time (39.4 ± 5.0%), and were largely in daylight hours (Fig. 3, Appendix Table C.2).
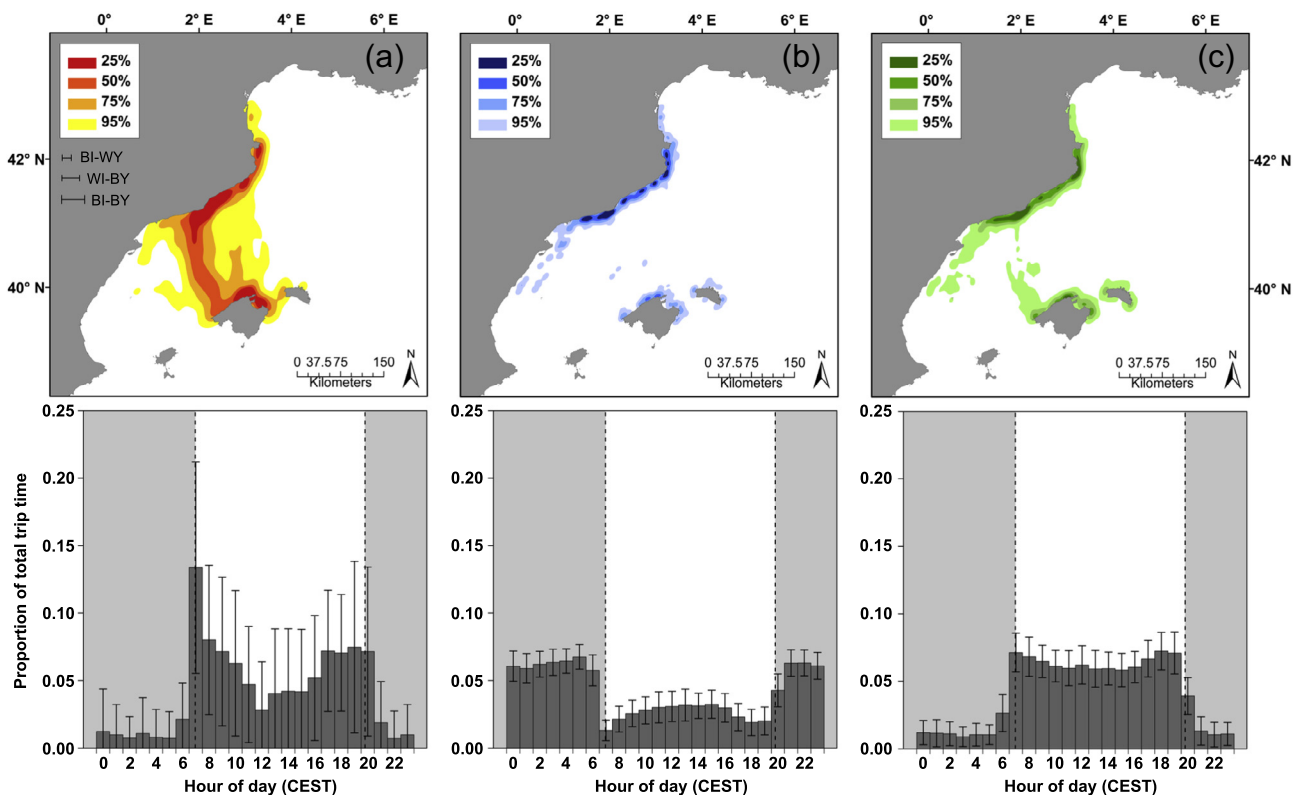

Fig. 3. Kernel density estimates of locations associated with track sections in which birds spent (a) ⩽5% time immersed (*low*), (b) ⩾95% time immersed (*high*) and (c) >5 to <95% time immersed (*moderate*) (KDE bandwidth selector: Plug-in, cell size = 1 km², $n = 60$). Plots below maps show mean (±SD) daily distributions of total time spent in each immersion category for individuals. Dotted lines indicate the average dawn and dusk time of all GPS locations during tracking periods (CEST) (07:27 and 20:18, respectively). Scale bars in Fig. 3a show median nearest neighbour distances of outbound commutes between paired tracks from (BI-WY) different individuals within years, (WI-BY) the same individual between years and (BI-BY) different individuals between years.
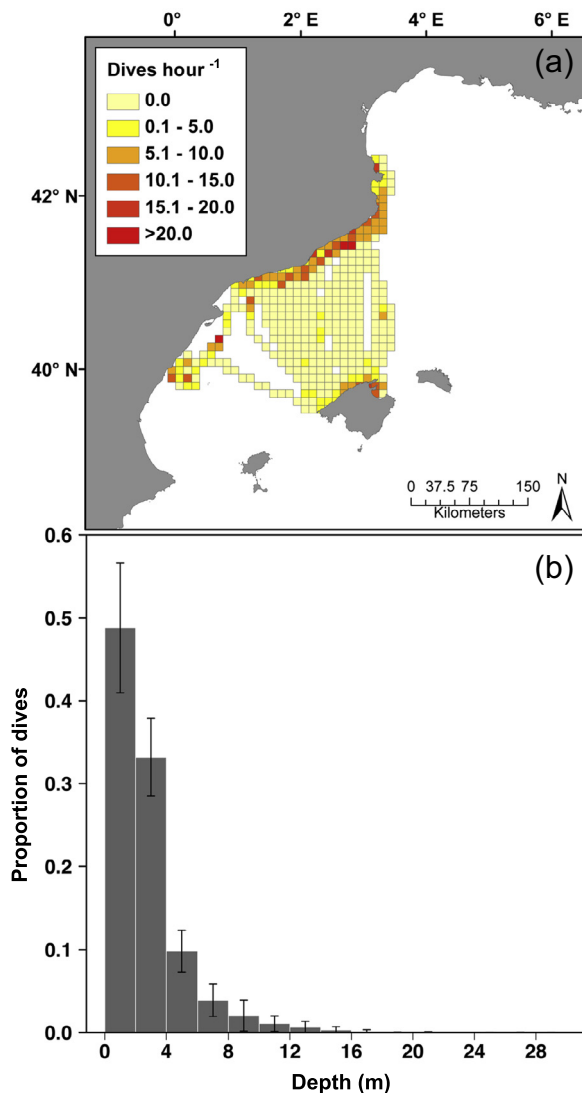
Fig. 4. (a) Dive rate (dives hour^{-1}) of Balearic shearwaters (n = 18) within 100 km^2 grid cells in the northwestern Mediterranean and (b) the mean (±SD) proportion of dives per trip within 2 m depth bins (n = 19,480).

We recorded 19,808 dives from 19 birds during 20 foraging trips in 2013 and 2014. Dives were recorded for one individual in both years and only one of the two tracks was used for analysis. Simultaneous GPS and immersion data were obtained for 18 individuals. Dives took place in both of the foraging areas identified with GPS and activity data (Fig. 4a). Birds dived almost exclusively during the daytime and crepuscular hours, with a high proportion of dive time preceding dusk (Appendix Fig. A.2a). Birds predominantly dived within the top 4 m of the water column (proportion of dives per trip ⩽4 m = 0.63–0.93; Fig. 4b), although reached depths of up to 28 m. The majority of dives lasted ⩽10 s (66–98% of trip dives; maximum duration = 69 s).

3.6. Meteorological controls of foraging strategy

The probability of birds remaining in waters around the Balearic Islands was greater during southerly winds than northerlies (p = 0.002, Fig. 5a), and during lower wind velocities (p = 0.003, Fig. 5b). The optimal model, containing wind speed and wind direction, explained a considerable amount of deviance in the data (% deviance = 43.7, r^2 = 0.481; Appendix Table D.2). Lunar phase was not found to be a significant predictor variable.

See Appendix Fig. G.1. for additional maps of chlorophyll-a (chl-a), sea-surface temperature (SST) and thermal frontal activity during different tracking periods.

4. Discussion

Through combined use of multiple tracking systems, our study demonstrates that Balearic shearwaters undertake direct commuting flights from their island colony to spatially restricted neritic foraging areas near the mainland coast. These foraging areas are remarkably consistent across multiple years and between sexes. Such findings highlight the potential benefits of site protection within the Balearic shearwater's breeding range, and the value of detailed tracking data in MPA evaluation and refinement processes.

4.1. Foraging and commute consistency

Many seabirds show foraging site fidelity (Patrick et al., 2014; Ramos et al., 2013; Weimerskirch, 2007), typically attributed to use of stable or persistent oceanographic features such as shelf breaks and fronts (Hyrenbach et al., 2000; Scales et al., 2014a). Here, Balearic shearwaters repeatedly foraged along the Catalan continental shelf, known for predictable meso-scale hydrographic features (Millot, 1999; Salat, 1996), elevated productivity (Estrada, 1996; Sabatés et al., 2007) and large spawning aggregations of small pelagic fishes (Palomera et al., 2007). These neritic waters are influenced by interactions between the southward flowing northern current and shelf-slope topography (La Violette et al., 1990; Salat, 1996), which in addition to riverine inputs from sources such as the Ebro delta, and localized wind-driven upwelling, result in persistent enhanced productivity during the spring (Estrada, 1996). Such oceanographic features may help to explain observed foraging distributions. While prior studies have identified the importance of these coastal shelf waters, and their oceanographic characteristics, for Balearic shearwaters (Abelló et al., 2003; Arcos et al., 2012b; Arcos and Oro, 2002a; Louzao et al., 2006), the consistency with which breeding adults of known provenance return to these areas has not been previously shown. Our findings suggest that birds forage on prey (either small shoaling pelagic fish or fisheries discards) with relatively predictable distributions within coastal Catalan waters (Louzao et al., 2009).

Balearic shearwaters varied in their use of waters close to the Balearic Islands, suggesting that resources may be more ephemeral here. Lower levels of spring–summer productivity around the Balearic archipelago (Bosc et al., 2004; Estrada, 1996), and variability in the north Balearic front (García et al., 1994; La Violette et al., 1990) may reduce prey predictability, with consequences for shearwater foraging. Furthermore, local wind conditions may influence the choice of foraging area, as results indicated that birds had an increased probability of heading east along the Mallorcan coast to forage in southerly winds and lower wind velocities. We tentatively suggest that this could be due to a sheltering effect along the elevated northern coasts of Mallorca and Menorca during such conditions, or to enhanced foraging opportunities associated with coastal wind-driven upwelling. Inter-annual differences in trip characteristics were largely attributable to extended movements into the Gulf of Lion in 2012, and local foraging in 2011. Inter-annual variation in environmental conditions (Appendix G), is likely to have influenced observed foraging distributions, although a quantitative investigation of environmental drivers is still required.

At-sea surveys and predictive models indicate that waters around the Ebro Delta, Cap de la Nau and, to a lesser extent, southern Mallorca are key Balearic shearwater foraging grounds (Louzao
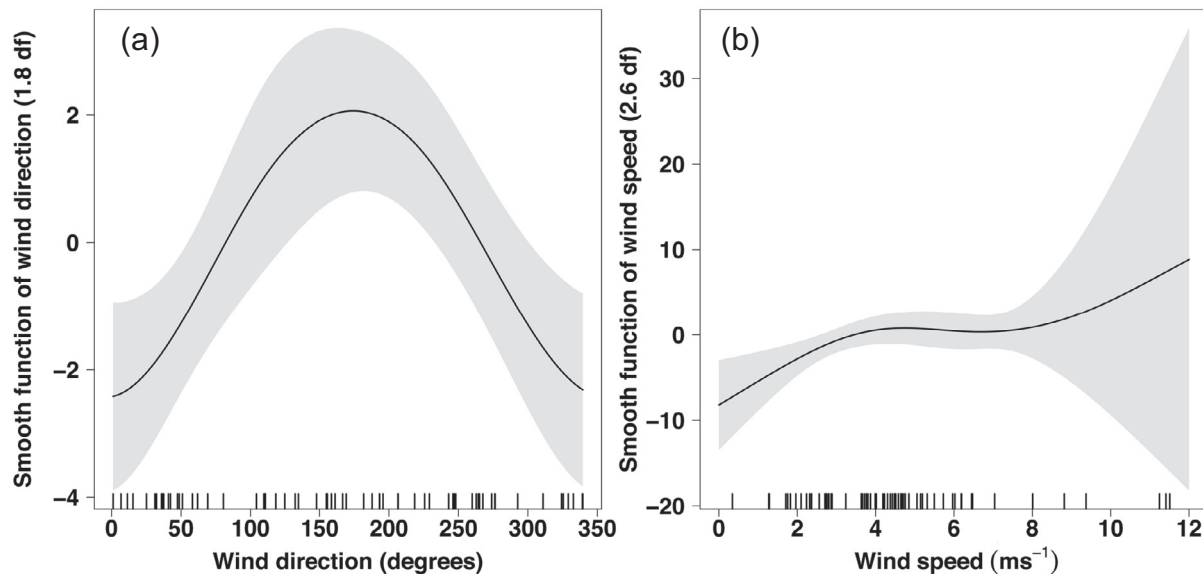
Fig. 5. Estimated smooth terms from the binomial GAM used to model the probability of Balearic shearwaters heading to foraging grounds off Catalonia as a smooth function of (a) wind direction (°; cyclic smooth term) and (b) wind speed (ms^{-1}; thin plate regression spline smooth term). The solid line represents the smoother, shaded areas represent 95% confidence bands and vertical lines along the x-axis indicate values of the explanatory variables ($n = 65$).

et al., 2012, 2006). However, few of our tracked birds visited these productive areas, despite falling within observed foraging ranges (Fig. 2). Unused areas may instead be important for other Balearic shearwater populations. While colony segregation has been recorded for some seabirds (i.e. Wakefield et al., 2013) it is currently unclear whether this is the case for the Balearic shearwater (although see Louzao et al., 2011).

Direct commuting flights over narrow corridors of the Catalan Sea were characteristic of Balearic shearwater foraging trips across study years. The straightness and consistency of this commute phase indicates that this species uses prior knowledge (Ward and Zahavi, 1973) to access predictable foraging grounds. Commuting is common amongst seabirds (Weimerskirch, 2007), but the efficiencies recorded here are high, and either equal or surpass those reported for other species (Benhamou et al., 2003; Bonadonna et al., 2005; Pettex et al., 2010; Regular et al., 2013). The restricted commuting corridors of tracked birds hold conservation relevance as they fall within an area of prevalent anthropogenic activity, where low-flying Balearic shearwaters may be at increased risk from offshore developments and associated barriers to movement (Masden et al., 2010). These flyways therefore represent tangible offshore targets for protection in the Catalan Sea.

4.2. Activity patterns and their relevance to management

Simultaneous deployment of GPS, geolocators and TDRs revealed strong diel patterns in Balearic shearwater activity, as with other *Puffinus* shearwaters (Aguilar et al., 2003; Dean et al., 2013; Péron et al., 2013; Raymond et al., 2010; Ronconi et al., 2010). Birds were mostly active during daylight hours and dived predominantly within the top 4 m of water column. A greater proportion of dives were undertaken to shallower depths and for shorter durations than previously reported for this species during the chick-rearing period (Aguilar et al., 2003). Moreover, maximum depths were shallower than published allometric relationships with body mass indicate are possible (Burger, 2001), suggesting exploitation of relatively shallow prey. Such knowledge is valuable given that sizable fishing fleets, operating to exploit a range of pelagic and demersal species, frequent similar coastal areas to

foraging Balearic shearwaters (Lleonart and Maynou, 2003; Pertierra and Lleonart, 1996), and may influence the species' movements (Bartumeus et al., 2010). Observations of peak bird activity around crepuscular hours, when seabird-longline interactions can become heightened (Laneri et al., 2010), support recommendations for restrictions on the timing of longline settings (Belda and Sánchez, 2001). While night-setting may not successfully mitigate bycatch for all scavenging seabirds in the western Mediterranean (Arcos and Oro, 2002b; Laneri et al., 2010; Sánchez and Belda, 2003), our findings suggest that gear setting outside of the periods around dawn and dusk could reduce Balearic shearwater bycatch.

4.3. Area-based management and wider conservation implications

The restricted movements exhibited by tracked Balearic shearwaters in this study emphasise the species' vulnerability to fisheries-induced mortality and acute pollution events within high-use areas. Nevertheless, high foraging area fidelity and association with well-defined coastal features indicate that site management has considerable potential to contribute to protection within the species' breeding range. Many existing marine protected areas within the western Mediterranean are multi-use areas (Abdulla et al., 2009) that confer limited protection to species like the Balearic shearwater from at-sea threats. Large, newly designated SPAs present new opportunities to tackle threats within important foraging habitat. The highest density areas of tracked birds in this study align closely with new SPAs along the Catalan coast and around the Balearic Islands, strengthening the evidence base for targeted management strategies at these sites. We suggest that further unprotected foraging habitat of incubating shearwaters, identified between Barcelona and Cap de Creus, may represent a high priority for protection during future assessments.

The extent to which observed movements can be generalised to other breeding phases and colonies is unknown, highlighting clear requirements for future multi-colony and cross-season tracking. Continued monitoring of Balearic shearwater movements to establish the efficacy of MPA design will be crucial for effective conservation outcomes, as has recently been discussed for a range of seabird species (e.g. see Ronconi et al., 2012 and references

therein). For example, adaptive management approaches (Hooker et al., 2011) may become important should Balearic shearwaters adjust their foraging movements in response to future management-driven changes in fisheries activity (Bartumeus et al., 2010; Laneri et al., 2010). Furthermore, it is likely that integrated management strategies within the Mediterranean, incorporating both area-based and non-area-based measures, will be required to tackle the range of pressures currently threatening the Balearic shearwater. The critical status of this species requires a wider conservation strategy to compliment MPA approaches, incorporating regional regulations focused on the most acute threats (i.e. bycatch and oil spills).

While this study has conservation relevance for Europe's most threatened seabird, several other seabirds of high conservation concern forage in the northwest Mediterranean including yelkouan shearwaters *Puffinus yelkouan* (Péron et al., 2013) and Audouin's gulls *Larus audouinii* (Christel et al., 2012). Although marine IBA and SPA designation processes took these species into account, the importance of the region for a range of other sensitive vertebrates (including sea turtles: Cardona et al., 2009, sharks: Mancusi et al., 2005, large pelagic migratory fish: Block et al., 2005, and marine mammals: Gonzalvo et al., 2008) calls for moves towards collaborative research efforts, multispecies assessments and management strategies that extend beyond national borders. Our ability to foster such approaches may ultimately determine whether there is a future for marine apex predators in the Mediterranean.

5. Role of the funding sources

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2015.05. 012.

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