The importance of Portuguese Continental Shelf Waters to Balearic Shearwaters revealed by aerial census

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Abstract

The Balearic shearwater *Puffinus mauretanicus* is one of the most threatened seabirds in the world. To evaluate the abundance and distribution of Balearic Shearwaters in Portuguese Continental Shelf Waters, during the post-breeding period when migrating birds are outside the Mediterranean Sea, we conducted 5 aerial surveys between 2010 and 2014 (21 survey days covering 62,716 km^2). Following a line transect method, observers recorded a total of 181 Balearic Shearwaters sightings. Using Distance sampling software, we estimated an overall species abundance (2010–2014) of 10,182, ranging between 2338 in 2010 and 23,221 individuals in 2012. During the 2012 post-breeding period, the Portuguese Continental Shelf Waters were used by up to 96.8% of the latest migratory population assessment. Considering Balearic Shearwater estimates per sampling block, there was a preference for the North and Center sectors of the Portuguese coast (respectively, 7058 and 1366 individuals) where several SPAs were already designated. We computed the annual and overall habitat predictive models for Balearic Shearwaters using a maximum entropy algorithm on MaxEnt software. In all models, the Balearic shearwater distribution was best predicted by mean chlorophyll concentration. Balearic Shearwaters are mostly present in shallow shelf and coastal waters particularly in the widest portions of the continental shelf. These areas are strongly influenced by upwelling, which concurs with the chlorophyll concentration being the most important predicting variable. Portuguese Continental Shelf Waters are one of the most important post-breeding grounds to the Balearic Shearwater.

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Responsible Editor: V. Paiva.

Reviewed by undisclosed experts.

Electronic supplementary material

The online version of this article (doi: 10.1007/s00227-017-3089-x) contains supplementary material, which is available to authorized users.

Introduction

The Balearic Shearwater *Puffinus mauretanicus* is included in the Critically Endangered IUCN extinction risk category (BirdLife International 2015). The adult population of this species is declining alarmingly and demographic models predicted its extinction within a few decades (Oro et al. 2004 ; Genovart et al. 2016). The main threats to the Balearic Shearwater population are lack of breeding habitat, predation when breeding and by-catch (Cooper et al. 2003 ; Oro et al. 2004 ; Arcos 2011a ; Abelló and Esteban 2012). Pollution, including light pollution, and fish stock depletion are among the most recently identified threats to Balearic Shearwaters (Boué et al. 2013 ; Rodríguez et al. 2015 ; Costa et al. 2016).

Ruíz and Martí (2004) reported a total population size of 10,000 Balearic Shearwaters and Arcos (2011b) reported 9000–13,000 mature individuals. More recently, Arroyo et al. (2014) presented a conservative range of 24,000–26,500 Balearic Shearwaters leaving the Mediterranean through the Strait of Gibraltar.

Balearic Shearwaters breed in the Mediterranean typically in the Balearic Islands (Spain). After the breeding season in March - July (Ruiz and Martí 2004; Louzao et al. 2006) most of the population disperses to wintering areas in the Atlantic, crossing the Strait of Gibraltar, headed by the non-breeders (Guilford et al. 2012 ; Arroyo et al. 2014), moving northwards into the productive coasts of Portugal (Ramírez et al. 2008 ; Guilford et al. 2012 ; Oppel et al. 2012 ; ICNF 2014), Galicia (Mouriño et al. 2003), Bay of Biscay and south-western France (Yésou 2003 ; Février et al. 2011).

The Balearic Shearwater conservation status and its imminent risk of extinction increase the need to evaluate the population across the species migratory range. Balearic Shearwaters use Portuguese Continental Waters as migratory flyways, stopover sites and wintering areas, especially on the post-breeding and wintering seasons (June–October), although non-breeders are present all year round (Guilford et al. 2012; Oppel et al. 2012; ICNF 2014). In fact, several marine SPAs were recently designated or expanded in Portugal (Decree-Law n. 105/2012, Regulatory Decree n. 17/2015 and Decree-Law n. 204/2015) due to their importance to marine birds, including the Balearic Shearwater.

Seabird distribution studies have been mostly ship-based up until the 1990s when airplane surveys were introduced (Ainley et al. 2012). Presently, aerial surveys are widely used to assess the distribution and abundance of seabirds (e.g. Bretagnolle et al. 2004; Certain and Bretagnolle 2008; Ridgway 2010; Buckland et al. 2012; Péron et al. 2013; Winiarski et al. 2013). Until now, systematic aerial surveys have never been used in Portuguese Continental Waters for assessing marine bird population estimates.

Abundance estimates of migratory species with transnational ranges are complex, involving a large amount of resources. The aerial campaigns reported in the present study were integrated in wider monitoring efforts to evaluate the abundance and distribution of cetaceans and seabirds in Portuguese Continental Waters within the scope of different projects (see http://www.safeseaproject.org , http://www.fameproject.eu , http://www.marprolife.org). Aerial surveys easily cover track lines over a large area in a short period of time, allowing for a standardized and cost-effective census methodology, which provides annually replicable population monitoring data (Camphuysen et al. 2004).

Data collected by aerial surveys can be used to build predictive distribution models allowing for further inferences about a species' use of space within a certain range. Since seabirds are highly mobile species, locations with no observations are not necessarily true absences, and thus presence-only modelling techniques are particularly useful when assessing and predicting seabird habitat use and habitat suitability (Elith et al. 2006, 2011). In addition, modelling and predictive approaches using covariates contribute to optimizing prediction sensitivity (Bretagnolle et al. 2004).

Unbiased abundance estimates and probability distribution maps are essential to understanding the current demographic trends outside the Mediterranean and their relation to the breeding population. The main objective of this study was to evaluate the abundance and distribution of Balearic Shearwaters in

Portuguese Continental Waters during the post-breeding period.

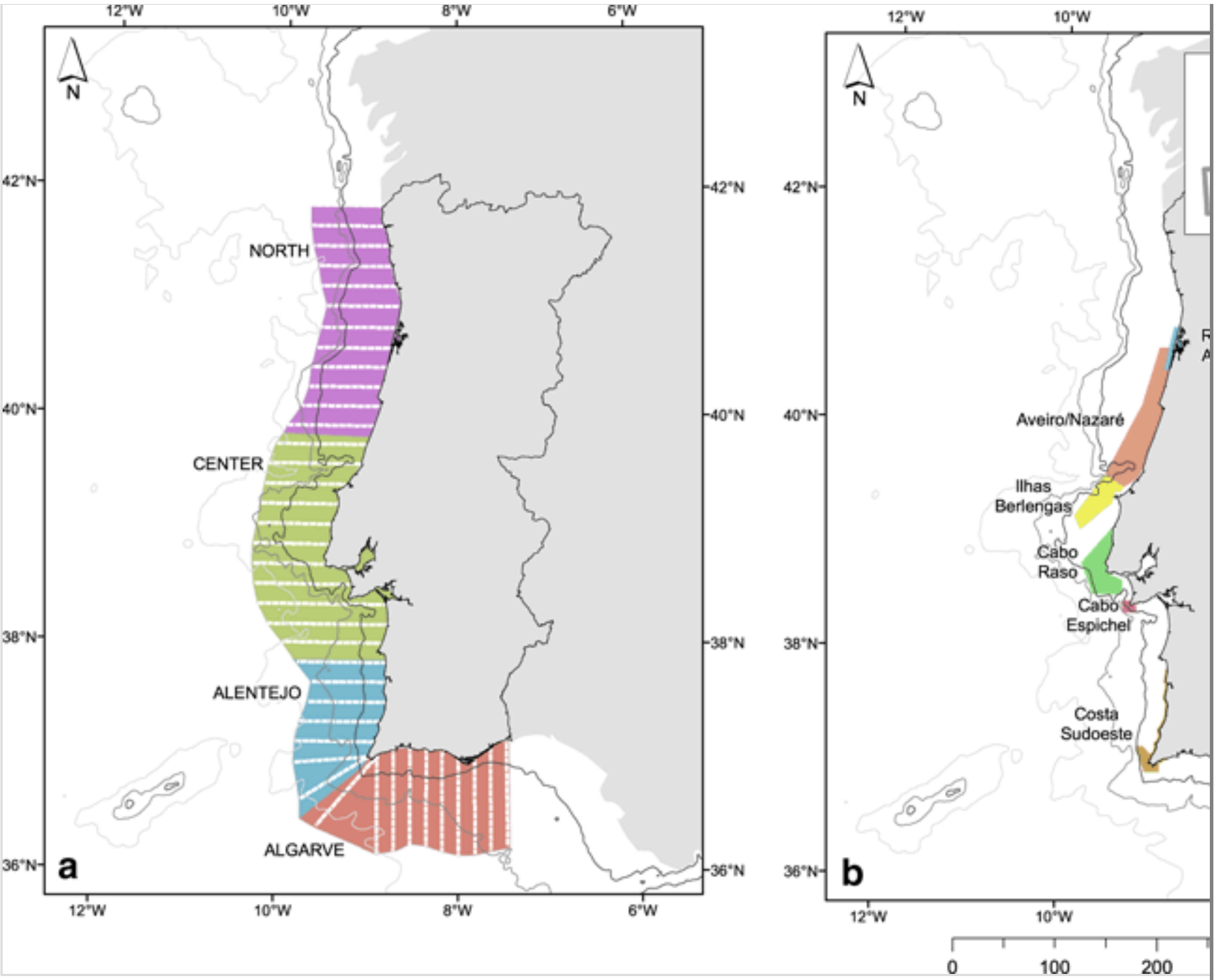
Methods

Study area

The study was conducted within Portuguese Continental Waters (latitude ranging from 36.5°N to 41.5°N and longitude extent defined by a 50 nm buffer along the coastline). The study area (62,716 km^2) represents 18.97% of the Portuguese EEZ (327,667 km^2, including a 23,728 km^2 continental shelf area). We divided the study area into four regions (see Fig. 1 a).

Fig. 1

a Overview of the study area showing the North, Center, Alentejo and Algarve blocks; theoretical line transects (*dashed white line*); **b** Marine SPAs: Ria de Aveiro, Aveiro-Nazaré, Berlenga, Cabo Raso, Cabo Espichel and Costa Sudoeste. Bathymetric profile of the area showing the 200 m (*dark grey line*), 1000 m (*grey line*) and 3000 m isobaths (*light grey line*)



Presently, 6 large marine SPAs (Ria de Aveiro, Aveiro-Nazaré, Berlenga, Cabo Raso, Cabo Espichel and Costa Sudoeste) have been created or expanded (Fig. 1 b) taking into account the occurrence, distribution and reproduction of several seabird species, totaling a marine area of 6188 km^2 (26% of the national continental shelf area).

Data acquisition

In this study, we used the standard line-transect Distance Sampling technique (Buckland et al. 2001 ; Thomas et al. 2010), which allows for inter-annual replication. Aerial surveys using parallel transects (perpendicular to the coast) were shown to be the most efficient design in the study area (http://www.fameproject.eu ; http://www.marprolife.org). Therefore, flights were carried out during September and October 2010, September 2011, September 2012, October 2013 and September 2014 (Table 1) along a set of parallel 50 nm-long transects (approximately) separated from each other by a distance of 10 nm and perpendicular to the coast (Fig. 1a), since transect direction should be parallel to any hypothetical gradients within strata (Buckland et al. 2001). All the inflight procedures and optimal flight conditions were based on internationally tested methodologies for line transect surveys (Bretagnolle et al. 2004; Camphuysen et al. 2004; Certain and Bretagnolle 2008). Flight surveys were conducted under standardized criteria: average flight speed of 100 knots (185 km/h), altitude above ground level (AGL) of 500 ft (150.4 m), visibility range >5 km and Beaufort sea state ≤3. In addition, all the selected planes met the following specifications: high-wing aircraft equipped with two bubble windows and twin engine.

Table 1

Aerial survey characterization

Campaign	Flight dates	Survey duration	Area (km^2)	Transect length (nm)	Number of transects	Average Beaufort
2010	27, 28 September, 20, 21 October	12h38m	62,716	1398.30	36	1.81
2011	21–24, 26 September	16h44m	62,716	1705.43	39	2.05
2012	6–9 September	16h26m	62,716	1683.01	40	1.31
2013	7–10 October	17h07m	62,716	1723.40	40	2.06
2014	2–5 September	14h33m	62,716	1510.80	38	2.09

Survey duration, time used for each survey

Area total area covered annually, *Transect length* total transect length surveyed annually, and average Beaufort per campaign

For all observations, the perpendicular angle from the track line to the location of sitting or flying birds was measured using a hand-held clinometer and the individual/flock position was registered using several handheld GPS units in redundancy. The survey team consisted of two trained observers, one data recorder and a pilot (Trenkel et al. 1997; Noer et al. 2000; Perkins et al. 2005).

Environmental data

Many environmental variables have been implicated in explaining seabird distribution (Lieske et al. 2014). In the present study, we sought abiotic and biotic variables (available at ecologically relevant spatial and temporal scales), which are known important predictors of seabird distributions. Therefore, the following eco-geographical variables (EGV) were selected (preliminary modeling trials, see Table S1): Bathymetry and Sea Surface Temperature (SST), assumed as proxies for physical processes or features driving prey distribution; Chlorophyll Concentration (Chl), an index of marine productivity (Afán et al. 2014); Slope, assumed as a proxy for upwelling and known to influence seabird distributions (Nishizawa et al. 2015).

Bathymetry data were obtained from the NOAA's National Geophysical Data Center (ETOPO2; http://www.ngdc.noaa.gov/mgg/image/2minrelief.html , assessed on 05/02/16) with a very fine spatial resolution (~1.852 km grid) and resampled to a spatial resolution of 4 km^2 (to match Sea Surface Temperature and mean Chlorophyll Concentration spatial resolution). To resample Bathymetry data, the *Nearest neighbour assignment* technique was used in the ArcGIS 10.3 tool *Resample*. In addition, the Bathymetry data were used to calculate Slope using the ArcGIS *Slope* tool. In addition, mean Sea Surface Temperature and mean Chlorophyll Concentration of the respective surveyed month were obtained from Aqua-MODIS satellite imagery (spatial resolution = 4 km^2), available from http://oceancolor.gsfc.nasa.gov/ (assessed on 05/02/16). In 2010 an average was calculated for September and October SST and Chlorophyll data.

A reduced number of eco-geographical variables (EGVs) were used for two main reasons. First, some of the initially tested EGVs were highly correlated (Table S1). For those correlated EGV pairs the most ecologically relevant EGV was selected. Second, the use of a reduced number of EGVs avoids model over-fitting to training data. The potential of overfitting increases as model complexity increases (Phillips et al. 2006). Simple models (fewer parameters, simpler relationships) should be favored over complex ones (more parameters, more complex functions: overfit) when modelling potential distributions (Rodda et al. 2011).

Data processing

Distance Sampling (line transects) allows estimating density and/or abundance of objects using distance values from a line to those objects' detections (Buckland et al. 2001 ; Thomas et al. 2010). Line transects allow for a proportion of objects to be missed leading to unbiased density estimates and also allowing for a more efficient use of data (larger sample sizes, same effort), specially at relatively low object densities (Camphuysen et al. 2004).

Distance considers several assumptions for the collected data, namely: all objects on the line are detected; the detections are made at their initial locations; distance measurements are exact; cluster sizes are recorded without error and sampled plots are representative of the entire survey region (Buckland et al. 2001 , 2008).

In the present study, we used the line transect method, assuming that all individuals in the line are detected [the detection probability is 1 at zero perpendicular distance, $g(0) = 1$] and the probability of detection falls off smoothly from 1 as a function of distance from the track line. This function is known as the detection function (Buckland et al. 2012). The assumption that all animals in the line are detected may be violated for two main reasons: (1) animals are missed because they are submerged (availability bias) and (2) observers fail to detect animals at the surface (perception bias). Availability bias should be minimal for seabird species that spend most of their time on the surface (Ronconi and Burger 2009). The abundance and density estimates presented were uncorrected for both biases.

All abundance values were estimated using Conventional Distance Sampling (CDS) (Buckland et al. 2001) in DISTANCE software. The model combinations half-normal key with cosine adjustments, half-normal key with Hermite polynomial adjustments and hazard-rate key with simple polynomial adjustments (Thomas et al. 2010) were tested to calculate abundance values (to find the detection function with the best fit - lower Akaike Information

Criterion, AIC) (Marques et al. 2007; Thomas et al. 2010). The group size effect on the detection probability was tested by fitting a regression of group size log against the detection probability. When estimating abundance, the regression's mean value is used instead of the observed mean group size, if significant at $\alpha = 0.15$. The coefficient of variation (CV) and 95% confidence intervals (CI) were estimated by bootstrapping (999 replicates) within strata, using transects as sampling units (Buckland et al. 2001).

Flock size data did not fit normality (assessed using Shapiro–Wilk's test) even after data transformation. Therefore, the Kruskal–Wallis test was used to assess significant differences between the numbers of Balearic Shearwater individuals per flock.

As for the predictive modeling of Balearic Shearwater distribution, we considered six scenarios: one scenario relative to each annual campaign between 2010 and 2014, and another relative to all years combined (overall model). To compute the overall model, we used the average values of the dynamic EGVs for each surveyed month. All occurrence locations were also included as training data in this model.

We computed the annual and overall habitat predictive models for Balearic Shearwaters using a maximum entropy algorithm on MaxEnt 3.3.3 and obtained predictive distribution maps based on occurrence probability. The maximum entropy algorithm provides clean, effective predictive model fits and can also handle small sample sizes (Phillips et al. 2006; Wisz et al. 2008; Kumar and Stohlgren 2009). MaxEnt performs well when compared to other presence-only modeling techniques and to models using both presence and absence data (Elith et al. 2006, 2011). However, much like other machine-learning techniques, MaxEnt can assign a higher probability of occurrence to a certain area rather than the actual occurrence in that area (Meirinho et al. 2014). Ensemble techniques were not postulated, since we aimed at final results that could be straightforward, easily used and replicated by conservation planners and managers. For all these reasons, nowadays MaxEnt stands out as one of the most valuable tools to achieve such results (Porfirio et al. 2014), and, therefore, it was chosen among other similar machine-learning techniques. Detailed descriptions of MaxEnt and its mathematical computations are given in Phillips et al. (2004, 2006).

Model performance was compared using different sets of predictive variables. Correlations were tested (Pearson correlation for pairwise comparisons using ENMtools software - downloaded from https://github.com/danlwarren/ENMTools on 15/02/2016, Warren et al. 2010), so that strongly correlated variables were not included in the same set of variables. For every highly correlated pair of variables ($|r|>0.7$), the least relevant variable was excluded from further analyses (Table S1). To evaluate the models, datasets were subsampled by randomly selecting 75% of the sample points as training data and 25% as test data. MaxEnt was set to remove duplicate presence records from the same grid cell to minimize autocorrelation biases and the default option "Auto-Features" was used to select the functional forms. Five replicate models were conducted for each of the six scenario datasets.

The area under the receiver operating characteristic curve metric (AUC) was used to test each model discriminative abilities (Peterson et al. 2007). The percentage contributions of each variable and their response curves were also analyzed. These percent contribution values are only heuristically defined: they depend on the particular path that the MaxEnt code uses to get to the optimal solution, and a different algorithm could get to the same solution via a different path, resulting in different percent contribution values. The response curves illustrate how the logistic prediction changes with the fluctuation of each environmental variable, while keeping all other environmental variables at their average sample value (Phillips 2006).

Results

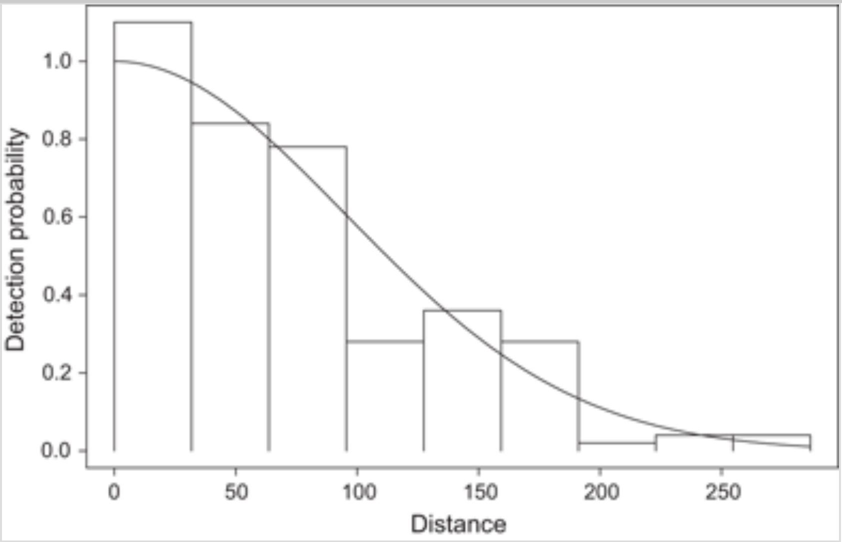
Balearic Shearwater abundance estimates 2010–2014

We completed 21 survey days, consistently covering an area of 62,716 km^2 each year (Table 1). According to the Beaufort scale the average sea state for all surveyed years was 1.86, ranging from 1.31 (2012) to 2.09 (2014). The total time of survey effort was 77h28 m flight hours (only Beaufort ≤3 periods were considered).

Exploratory analyses of detection functions indicated detection probabilities below 0.2 for distances over 191 m from the center line (Fig. 2). However, despite the lower detection probability for distances over 200 m from the center line, we verified that truncation did not improve the detection function quality. Therefore, the detection function was estimated using the total number of flock sightings.

Fig. 2

Global detection function fitted to the distance data ($n = 187$, Balearic Shearwater sightings) using the model combination half-normal key with Hermite polynomial adjustments (distance in meters)



Due to its lower AIC value (1971.99), the half-normal key with Hermite polynomial adjustments was the best model combination using data from all sampled years (Fig. 2), when comparing to models using the Half-normal key with cosine adjustments (AIC = 1973.04) and the Hazard-rate key with simple polynomial adjustments (AIC = 1975.12). Because there was no obvious decrease in detection near the line, we assumed that all birds were detected. In fact, flights were operated according to standardized criteria (speed and altitude), which ensure that observers detect flying or sitting Balearic Shearwater flocks before any evasive movements in relation to the airplane. To a certain extent, the perception bias was avoided by flying when the Beaufort scale was below or equal to 3. Nonetheless, we assume that some birds may not have been accounted for, leading to underestimated abundances.

The overall average flock size was 2.86 birds (Table 2a; Fig. 3). The annual flock size varied from 1.28 individuals in 2010 to 4.11 individuals in 2012. The lowest flock size value observed in 2010 is mainly associated to a high number of single animal observations. There were no significant differences between years in the number of individuals per flock (Kruskal–Wallis test, $H_4 = 8.949$, $p = 0.062$). In all analyzed data frames the observed group size value was always chosen over the expected value.

Table 2

(a) Balearic Shearwater flock sightings, average flock size, abundance (*n*) and density (n km^{-2}) and (b) Balearic Shearwater flock sightings, average flock size, abundance (*n*) and density (n km^{-2})

	Number of flock sightings	**Average flock size (CV%)**	**Abundance (95% CI low–high)**	**Density (95% CI low–high)**	**C.V. (%)**
(a) Survey year					
2010	18	1.28 (12.34%)	2338 (1099–4271)	0.037 (0.019–0.076)	34.92
2011	25	3.00 (20.55%)	6250 (3128–12,055)	0.100 (0.050–0.230)	34.73
2012	67	4.11 (10.51%)	23,221 (10,423–49,279)	0.370 (0.163–0.951)	40.17
2013	36	3.36 (15.09%)	8053 (1922–1,935,329)	0.128 (0.030–0.638)	82.88
2014	41	2.54 (12.92%)	9783 (4962–18,475)	0.156 (0.081–0.344)	33.75
Overall	187	2.86 (14.79%)	10,182 (4902–20,449)	0.162 (0.072–0.418)	26.58
(b) Survey blocks					
North	138	3.52 (7.82%)	7058 (3313–16,331)	0.429 (0.201–0.993)	41.83
				0.068	

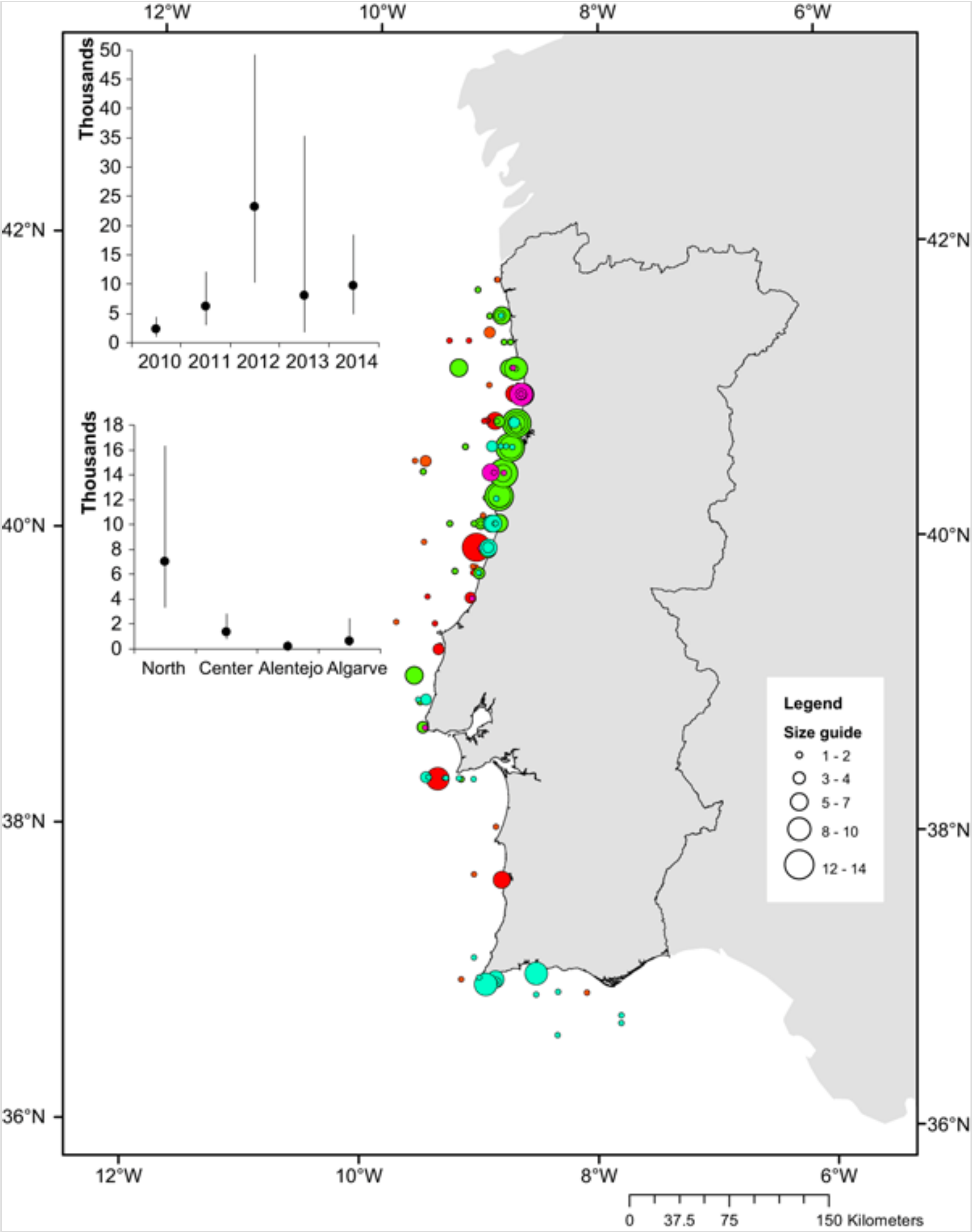
Centre	33	2.03 (14.93%)	1366 (754–2795)	(0.037–0.138)	33.85
Alentejo	5	2.0 (38.73%)	187 (63–628)	0.019 (0.006–0.064)	58.56
Algarve	11	3.18 (28.69%)	638 (182–2442)	0.039 (0.011–0.150)	72.07

Coefficient of variation (CV) and 95% abundance and density confidence interval (CI) calculated using bootstrapping (999 replicates) per surveyed year

Coefficient of variation (CV) and 95% abundance and density confidence interval (CI) calculated using bootstrapping (999 replicates) per surveyed area (considering the 5-year dataset)

Fig. 3

Balearic Shearwater sightings during aerial surveys in 2010 (*orange*), 2011 (*red*), 2012 (*green*), 2013 (*pink*) and 2014 (*cyan blue*). The *circle size* indicates number of individuals per flock. *Graphics* indicate annual and survey block abundance (*bars* represent low–high 95% confidence interval values)



The lowest values of Balearic Shearwater sightings were observed in 2010 (9.6% of total sightings) and the highest values were observed in 2012 (35.8%) (Table 2a; Fig. 3). In addition, the Balearic Shearwater abundance in Portuguese Continental Waters varied between 2338 individuals (CV = 34.92%)

in 2010 and 23,221 individuals (CV = 40.17%) in 2012, whereas densities ranged between 0.037 individuals km^{-2} in 2010 and 0.370 individuals km^{-2} in 2012 (Table 2a). The overall abundance estimate (considering the 5-year data) was 10,182 (CV = 26.58%) and the overall density amounted to 0.162 individuals km^{-2}.

Most Balearic Shearwater sightings were recorded in the North block of the surveyed area (138 sightings) representing 73.79% of all sightings. The lowest number of Balearic Shearwater sightings was recorded in the Alentejo Region representing only 2.67% of all sightings (Table 2b; Fig. 3). Accordingly, the Balearic Shearwater abundance was higher in the North block (an average of 7058 individuals; CV = 41.83%) and lower values were observed in the Alentejo block with an average of only 187 individuals (CV = 58.56%) (Table 2b).

Balearic Shearwater distribution models

Predictive distribution models for Balearic Shearwaters showed a good performance (AUC = 0.804 in 2010 to AUC = 0.994 in 2013) (Table 3). Mean Chlorophyll concentrations presented the highest contribution to explaining annual Balearic Shearwater occurrence probability. Bathymetry, slope and mean SST presented varying contributions over the years (Table 3).

Table 3

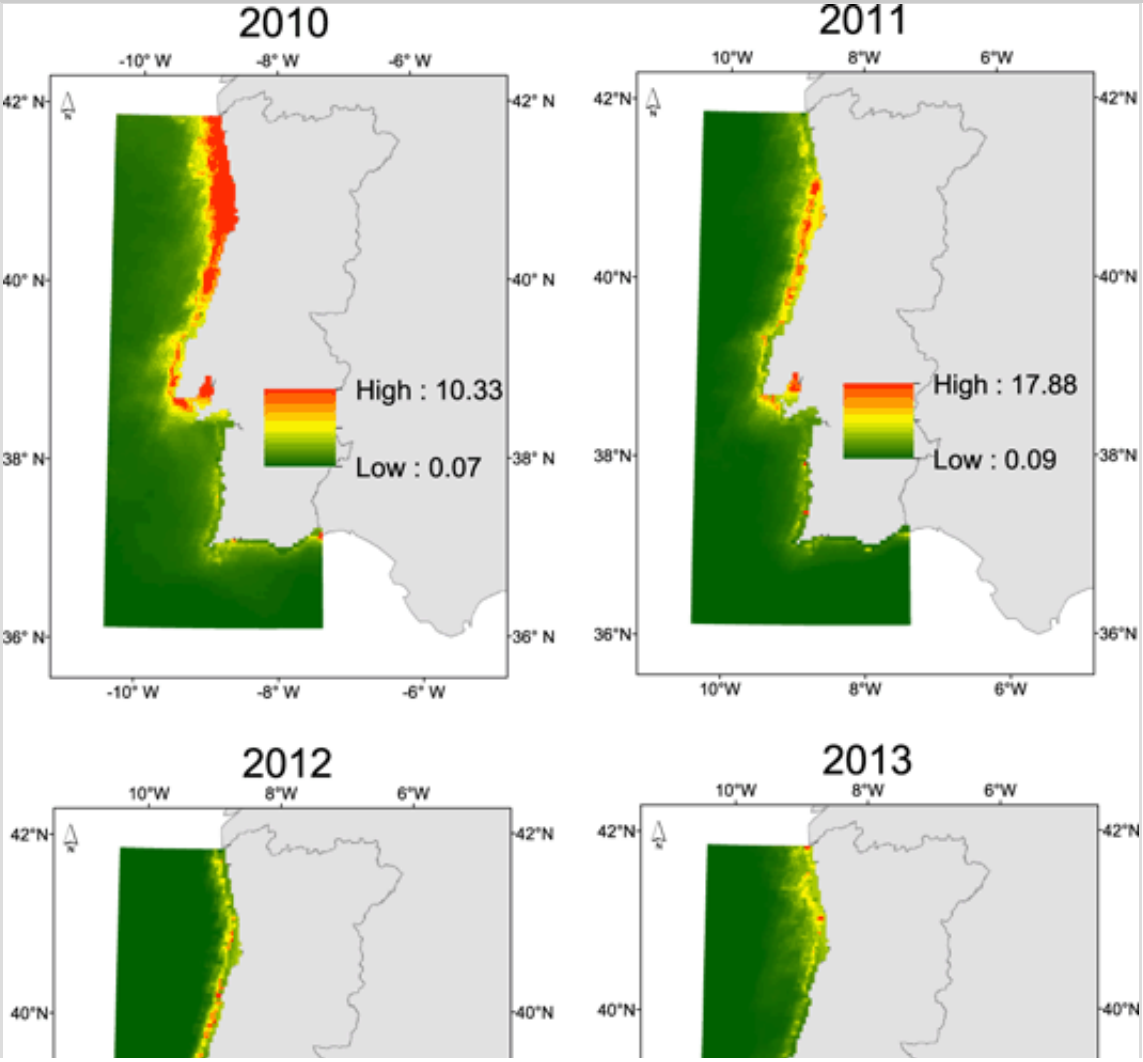
Average test AUCs and standard deviations of bootstrap replicate runs (5 replicates), and heuristic estimate of EGVs (Chl, Bathymetry, Slope and SST) relative contributions (%) to annual and overall models

Campaign	AUC (SD)	Chl	Bathymetry	Slope	SST
2010	0.804 (0.018)	57.4	22.3	19.1	1.2
2011	0.960 (0.014)	68.2	3.2	2.3	26.4
2012	0.940 (0.014)	60.2	6.8	17.1	15.8
2013	0.994 (0.006)	68.7	7.5	12.4	11.4
2014	0.919 (0.009)	68.6	16.6	9.5	5.3
Overall	0.929 (0.013)	51.6	14.5	7.2	26.7

Chlorophyll mean concentration response curves indicate an occurrence probability peak at Chlorophyll concentrations around 2.5 mg m^{-3} in 2010, 2011 and 2012 (see Figs. 4, 5). When Chlorophyll concentrations increase to around 6 mg m^{-3}, occurrence probability does not increase. Therefore, high occurrence probabilities occur at median values of Chlorophyll, as well as at high values of Chlorophyll. An anomaly was detected in 2013 and 2014, when occurrence probabilities increased steeply, peaking at Chlorophyll concentrations around 2 mg m^{-3}, followed by a steep decrease. The overall model reflects an average behavior of the occurrence probability when all years are analyzed.

Fig. 4

Chlorophyll mean concentration (mg m^{-3}) for each surveyed month. 2010 represents an average from September and October



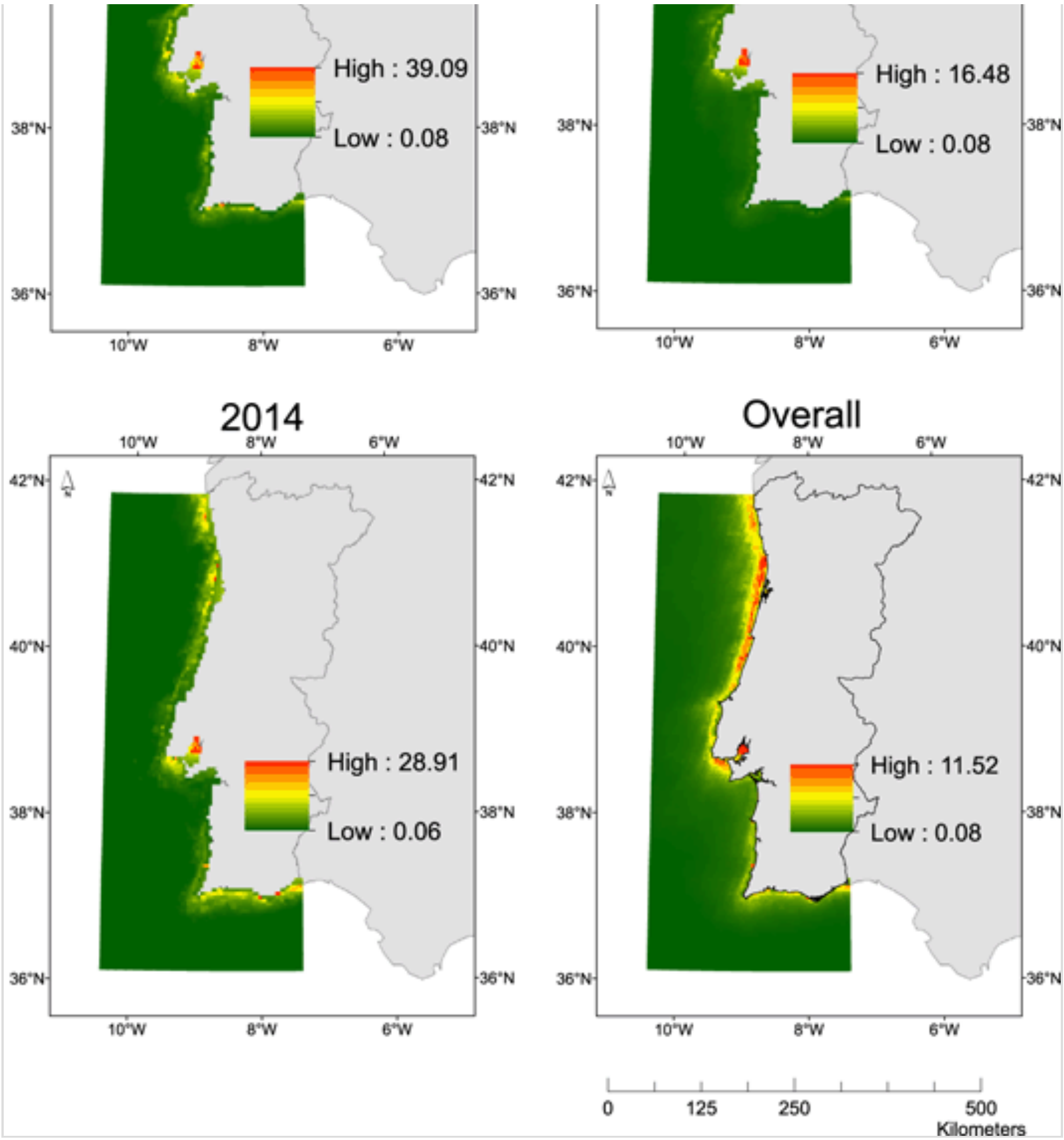
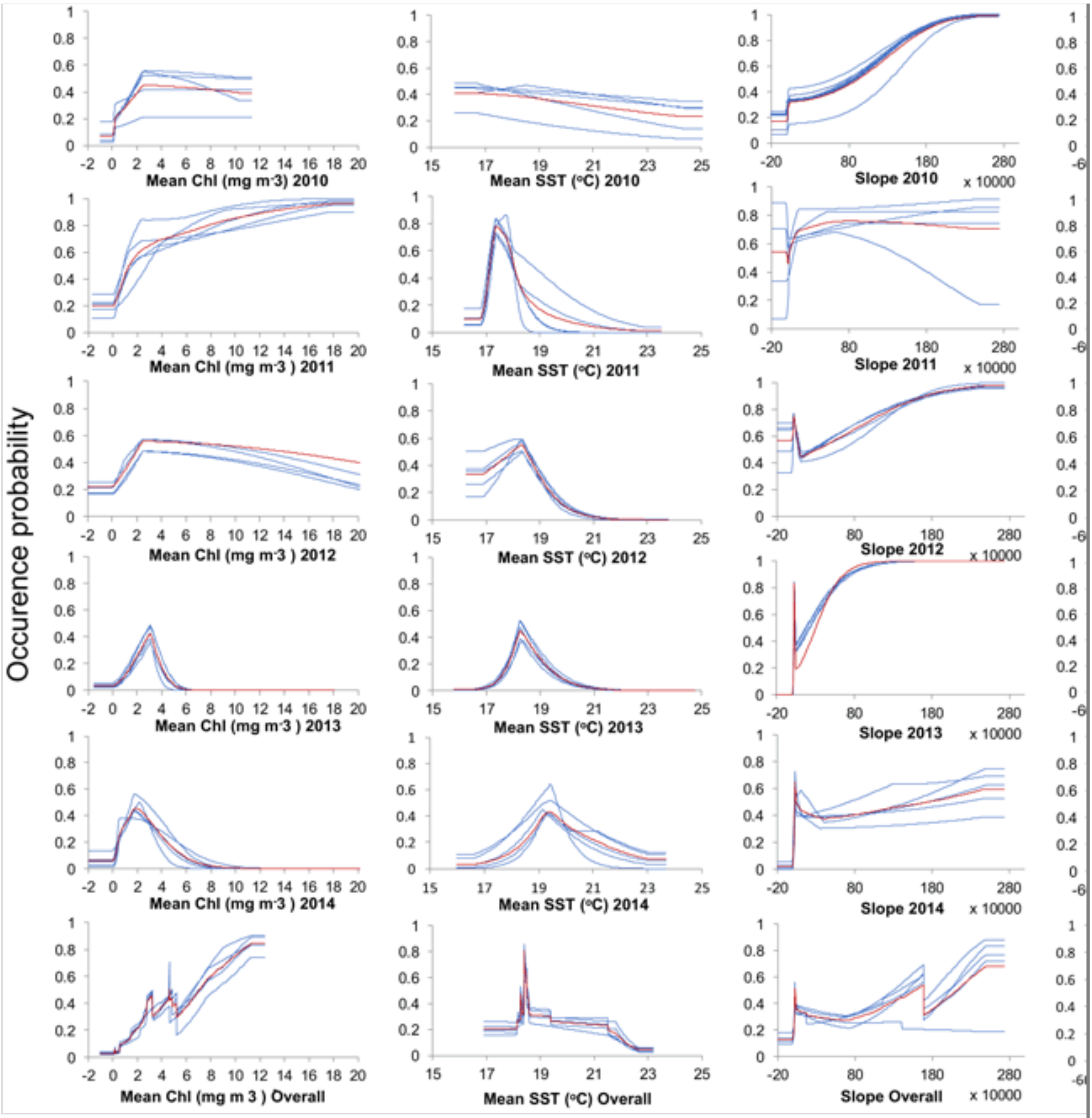


Fig. 5

Response curves of Balearic Shearwater occurrence probability (*blue lines* show the output of 5 replicates, while the *red line* represents the mean value) to variation of EGVs (Mean Chl, Mean SST, Slope and Bathymety). *Curves* show the logistic prediction of occurrence probability using a particular variable while keeping other environmental variables at their average sample value

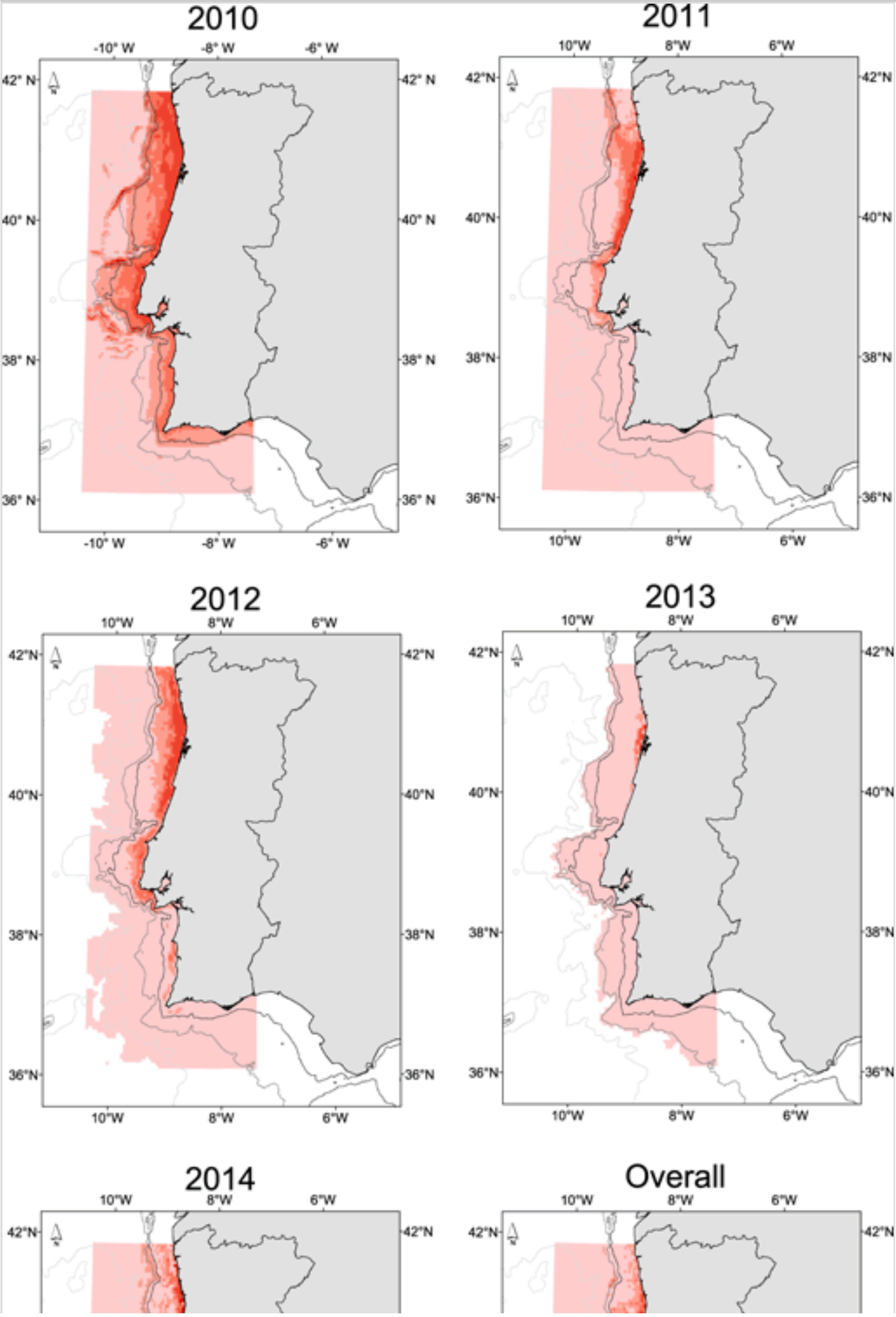


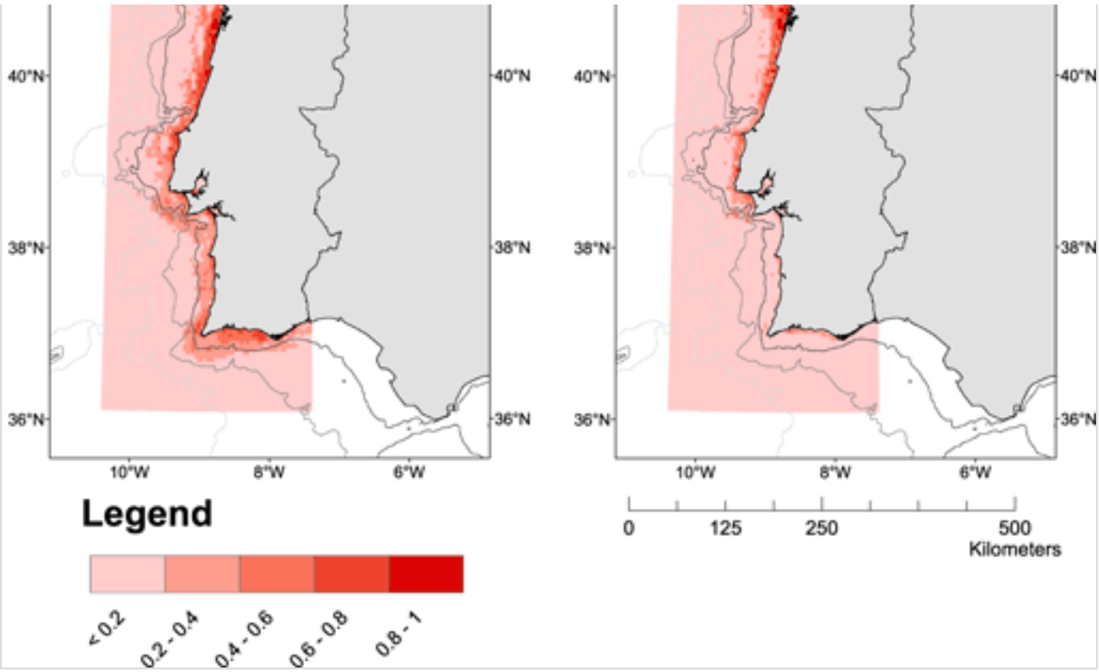
Concerning mean SST, the response curve peaks vary between 15.88 °C in 2010 and 19.31 °C in 2014 (17.35 °C in 2011, 18.26 °C in 2012, 18.23 °C in 2013 and 18.41 °C in the overall set) (Fig. 5 and S1).

Shearwater occurrence probability decreased with bathymetry, with the peak for all models between −79 and −5 m (Fig. 5, S2). Species occurrence was mostly associated to smooth slope responsive curves, except for steeper areas (e.g. submarine canyons) (Fig. 5, S3). These results indicate that occurrence probability was generally higher in wider areas of the continental shelf (Fig. 6).

Fig. 6

Annual and mean (2010–2014) habitat suitability maps for Balearic Shearwaters. Bathymetric profile of the area showing the 200 m (*dark grey line*), 1000 m (*grey line*) and 3000 m isobaths (*light grey line*)





Discussion

Abundance estimates

Based on coastal migration counts, Arroyo et al. (2014) reported 24,000–26,500 Balearic Shearwater individuals annually passing the Strait of Gibraltar from May to July between 2007 and 2010. The present study, using aerial census data collected during September/October when migrating birds are at their post-breeding period outside the Mediterranean Sea, reveals an average annual abundance of 10,182 individuals in Portuguese Continental Waters between 2010 and 2014. The highest annual abundance value was observed in 2012 with an estimate of 23,221 individuals in Portuguese waters representing between 87.6 and 96.8% of the Balearic Shearwater population migrating out of the Mediterranean estimated by Arroyo et al. (2014). In fact, this percentage may be even higher if abundance values were underestimated due to perception bias (arising from possibly unaccounted individuals). Our protocol relies on the assumption that all birds on the line are detected, which may lead to an overestimation of the detection function and an underestimation of abundance values. Due to airplane logistic constrains, the double-observer methodology was not used, which would have contributed to asserting detection accuracy near the transect line (Buckland et al. 2001). Although the perception bias was not estimated, it can be considered constant over the study campaigns given that the same plane, observers and field protocol were used (Panigada et al. 2011).

The relatively high value registered in 2012 contrasts with the lowest abundance value in 2010 (2338 individuals; CV = 34.92%). The progressive and periodical migratory fluxes back to breeding zones or farther north in the Atlantic probably contribute to the registered inter annual variation. Whereas some individuals may stay in Portuguese Continental Waters during the post-breeding period (ICNF 2014), others disperse northwards before returning to their breeding grounds (Mouriño et al. 2003; Yésou 2003; Wynn and Yésou 2007; Février et al. 2010; Darlaston and Wynn 2012; Guilford et al. 2012; Jones et al. 2014). In fact, the Balearic Shearwater northwards expansion became more pronounced since the mid-1990s and long-term increases in Balearic Shearwater abundance in the British Isles were correlated with an increasing regional SST index, and with both anchovy and sardine probabilities of occurrence (Luczak et al. 2011). It is postulated that the increase in sea temperature may have triggered a Balearic Shearwater increase across its northern range by having influenced plankton composition and their fish prey, indicating a climate-driven range expansion of Balearic Shearwaters in the northeast Atlantic through trophic cascade processes (Wynn et al. 2007; Luczak et al. 2011).

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Apparently climate driven changes were also detected in foraging distributions of Cory’s shearwaters breeding in mainland Portugal (Berlenga colony) in 2010 and 2011 in relation to previous years (with pre-laying foraging excursions distancing 700 km from the colony in 2007 and nearly 4000 km in 2011) (Paiva et al. 2013a, b). According to Paiva et al. (2013a, b) these changes were probably due to the extremely low SSTs registered in 2010 and 2011 leading to a lower availability of plankton to upper strata of the food web and strong upwelling leading to low recruitment of pelagic fish species inhabiting the Portuguese coast. The lower SSTs and consequent lower prey availability reported by Paiva et al. (2013a, b) may have also contributed to the lowest Balearic Shearwater abundances registered in our study in the same years (2010 = 2338 individuals, CV = 34.92%; 2011 = 6250 individuals, CV = 34.73%). In fact, prey distribution is a well-established key factor regulating Balearic Shearwater abundance and distribution in non-breeding areas (Yésou 2003).

The inter annual variability of Balearic Shearwater abundance values may also be related to primary productivity irregular patterns across sampling years, as shown by Chlorophyll concentration values. In our study, the lowest Balearic Shearwater abundances match periods of lowest maximum Chlorophyll concentrations (Fig. 4). In fact, the maximum Chlorophyll concentration in 2010 was 10.33 mg m^{-3} whereas the maximum Chlorophyll concentration in 2012 was 39.09 mg m^{-3} (highest Balearic Shearwater abundance, 23,221 individuals). Low Chlorophyll concentration maximum values were also registered in 2011 and 2013 (between 16.5 and 17.9 mg m^{-3}) when Balearic Shearwater abundances were lower (6250 and 8053 individuals, respectively).

Considering Balearic Shearwater estimates per sampling block, values confirm a preference for the North and Center sectors of the Portuguese coast where several SPAs were already designated (SPAs Ria de Aveiro, Aveiro-Nazaré, Berlenga, Cabo Raso, Cabo Espichel). In addition, the SPA Costa Sudoeste was recently enlarged to include Cabo de S. Vicente, where Balearic Shearwaters can be observed in large numbers during migratory fluxes.

Previous studies on Balearic Shearwater local abundance within Portuguese Continental Waters reported over 1000 birds between Aveiro and Figueira da Foz in 2002 (Petronilho et al. 2004), over 1000 birds around Lisbon in 2004 (Poot 2005), and 3500–8700 birds in the 3 marine IBAs Berlengas, Figueira da Foz and Cabo Raso between 2005 and 2007 (Ramírez et al. 2008). Whereas these values represent direct counts of land-based or ship-based surveys using ESAS methodologies, in the present study we used Distance sampling methodologies, allowing for coefficient of variation and confidence interval estimates. Therefore, our results cannot be directly compared with previous estimates for the population in Portuguese waters. Our approach provided the first Balearic Shearwater abundance estimates in Portugal using a standardized method. Considering some of the possible bias affecting abundance estimates (animals that have migrated farther north or that have already migrated back to reproduction areas) the values reported in this study for the Balearic Shearwater population using Portuguese Continental Waters are conservative and are most likely underestimated.

Species distribution models

The correlation between Balearic Shearwater probability distributions and physiographic, oceanographic and remotely sensed data has been the subject of several studies in Portuguese Continental Waters with different analytical techniques (e.g. Guilford et al. 2012; Oppel et al. 2012; Meirinho et al. 2014). We used the maximum entropy algorithm (MaxEnt) to assess late summer/autumn Balearic Shearwater habitat preferences based exclusively on aerial survey data. MaxEnt provides effective model fits, even with small sample sizes (Phillips et al. 2006; Wisz et al. 2008; Kumar and Stohlgren 2009), being well suited to temporarily absent species, with few observations over a large area of suitable habitat (Thaxter et al. 2011). MaxEnt outputs, as any heuristic model result, should be considered as proxies for reality. For a more accurate model evaluation, results must be validated with future studies providing data from opportunist platforms, individual tracking or dedicated surveys.

In the study area, the Balearic Shearwater is mostly present in shallow shelf and coastal waters particularly in the widest portions of the continental shelf. These areas are strongly influenced by upwelling (Fiúza 1983), which explains Chlorophyll as the most important predicting variable. Chlorophyll was also identified as the most important environmental variable in Balearic Shearwater habitats in the western Mediterranean (Louzao et al. 2006, 2012). As mentioned earlier, chlorophyll concentration may provide a proxy for areas of enhanced biological production (see Solanki et al. 2005), thus contributing to defining prey distribution (i.e. juvenile pelagic fish in this case). In turn, prey distribution is a very important factor in regulating Balearic Shearwater abundance and distribution in non-breeding areas (Yésou 2003). However, it is important to remark that during the late summer/autumn (when census were performed), irregular duration and strength of upwelling phenomena are expected (Mason et al. 2005). Therefore, productivity fluctuations within high occurrence probability areas contribute to shearwater inter-annual distribution changes (see Fig. 6). In the present study, the consistently selected preferential habitats occurred between Porto and Figueira da Foz, surrounding Berlenga Island and Cape Raso. These regions correspond to recently designated or enlarged marine SPAs in Portugal (see ICN 2014).

Seabird at-sea distributions strongly depend on where they breed (Le Corre et al. 2012) and the colony effect (Hyrenbach et al. 2007). However, the at-sea distributions of migratory seabird species with low flight costs (e.g. Pennycuick

2002) depend on adequate and abundant food resources. Searching for high productivity areas may be crucial to meet seabird energy demands during the post-breeding period in Atlantic waters where feeding resources are dispersed, when compared with the predictable resources around the breeding colonies in the Mediterranean. It is possible that Balearic Shearwaters use a memory-based foraging strategy (Davoren et al. 2003a, b), in conjunction with the Procellariforms' olfactory capacity to identify peaks of DMS (dimethylsulfide), a compound associated with areas of high productivity (see Cunningham and Nevitt 2005).

Although our study spans a 5-year period, we did not attempt to evaluate abundance trends, largely due to sample size limitations. We plan to further increase this dataset by maintaining the aerial census scheme over the next years. Our results are in line with the Balearic Shearwater abundances recently estimated by Arroyo et al. (2014), and demonstrate that Portuguese Continental shelf waters are used by a large proportion of the population. Overall, the study area seems to be one of the most important post-breeding grounds for the species.

Acknowledgements

This work was partly funded by the Portuguese Wildlife Society and projects SafeSea EEA-Grants, FAME (Proj. 2009-1/089) and European Commission's Life Programme (MarPro NAT/PT/00038). This study was also partly supported by the Portuguese Foundation for Science and Technology (FCT) with Grants SFRH/ BD/30240/2006 to M. Ferreira and SFRH/BD/32841/2006 to P. C. Rodrigues. C. Eira is supported by FCT through CESAM UID/AMB/50017/2013 co-funded by FCT/MEC and FEDER, within PT2020 and Compete 2020 and S. Monteiro is financed by a Grant (BPD/0043/AMB/50017) from UID/AMB/50017/2013. This work was also partially supported by the strategic programme UID/BIA/04050/2013 (POCI-01-0145-FEDER-007569) funded by FCT and by ERDF (COMPETE2020). The authors thank observers and airplane pilots who contributed to this work.

Compliance with ethical standards

Conflict of interest All authors declare they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Electronic supplementary material

Below is the link to the electronic supplementary material.

Supplementary material 1 (PDF 3536 KB)

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