

RESEARCH ARTICLE

Drivers for spatial modelling of a critically endangered seabird on a dynamic ocean area: Balearic shearwaters are non-vegetarian

Andrés de la Cruz¹  | Fernando Ramos²  | Gabriel Navarro³  |
Andrés Cózar¹  | Juan Bécares^{4,5}  | Gonzalo Muñoz Arroyo¹ 

¹University Institute of Marine Research (INMAR), Campus of International Excellence of the Sea (CEIMAR), Cádiz University, Cádiz, Spain

²Cádiz Oceanographic Centre, Spanish Institute of Oceanography, Cádiz, Spain

³Department of Ecology and Coastal Management, Institute of Marine Sciences of Andalusia, ICMAN-CSIC, Cádiz, Spain

⁴SEO/BirdLife – Marine Programme, Barcelona, Spain

⁵CORYS – Research and Conservation of Biodiversity, Barcelona, Spain

Correspondence

Andrés de la Cruz, University Institute of Marine Research (INMAR), International Campus of Excellence in Marine Science (CEIMAR), Biology Department, Cádiz University, Puerto Real, Cádiz, Spain.
Email: andres.delacruz@uca.es

Funding information

the Ministry of Science, Innovation and Universities, Grant/Award Number: MEGAN project (Ref. CTM2013-49048-C2-1-R); the ECOFISH project; the Biodiversity Foundation; the Ministry for the Ecological Transition; the Demographic Challenge; the Pleamar Program, co-financed by the FEMP

Abstract

1. Spatial modelling is an important research tool to improve our knowledge about the distribution of wildlife in the ocean. Using different modelling techniques (MaxEnt and a generalized linear mixed model), a predictive habitat suitability model was developed for one of the most threatened seabirds in the world: the Balearic shearwater, *Puffinus mauretanicus*.
2. Models were developed using a 10-year dataset from the Gulf of Cádiz (on the south-western Iberian Peninsula), a key foraging area for Balearic shearwaters during migration and the non-breeding season.
3. Predictive habitat maps strongly matched the observed distribution patterns, pointing to bathymetric features as the main modelling drivers. The species was concentrated on shallow areas (up to approximately 100 m in depth) of the continental shelf, very close to the mouth of the Guadalquivir River. In contrast with previous studies, Balearic shearwater distribution in the highly dynamic Gulf of Cádiz was not correlated with areas of high chlorophyll *a* concentration.
4. This lack of spatial correlation probably arises from the delay between the phytoplankton bloom and the response of the zooplankton and small fish that are preyed upon by Balearic shearwaters, which may result in important displacements of this trophic chain across the Gulf of Cádiz.
5. The analysis presented contributes to a better understanding of the spatial distribution and ecology of the critically endangered top predator in the Gulf of Cádiz and offers important information to improve management plans.

KEYWORDS

chlorophyll, GLMM, Gulf of Cádiz, *Puffinus mauretanicus*, spatial distribution modelling, top marine predators

1 | INTRODUCTION

Species distribution models (SDMs) are increasingly used to understand and predict patterns of biodiversity distribution, emerging as a key tool in ecology and biogeography research (Peterson et al., 2011; Reisinger et al., 2018; Fernandes et al., 2019). SDMs for mobile

organisms are based on tracking or presence records of species and analyse the relationship between these records and the environmental characteristics at such sites (Franklin, 2010). Modelling tools have improved our knowledge about species distribution and consequently the identification of priority conservation areas (Guisan & Thuiller, 2005; Sánchez-Carnero et al., 2016). In the ocean, SDMs

characterize habitats from an oceanographic point of view (Ballance, Pitman & Fiedler, 2006), allowing the distribution of predators to be related to prey availability and oceanographic processes controlling productivity (Hunt & Schneider, 1987).

One of the most challenging aspects is to understand the mechanisms driving the distribution of marine organisms. In the highly oligotrophic open ocean, the appearance of patchy areas of high primary productivity, associated with oceanographic processes such as upwelling, oceanic fronts, or eddies, create aggregation areas where relatively complex trophic webs develop, attracting a high number of top marine predators and resulting in biodiversity hotspots (Malakoff, 2004; Worm et al., 2005; Alves et al., 2018). The increasing development of satellite remote-sensing techniques has revealed the relationships of marine predator distributions, providing remote-sensed estimates of primary productivity (using chlorophyll *a* (CHL-*a*) concentration as a proxy) and sea surface temperature (Polovina et al., 2004; O'Toole et al., 2017; Zainuddin et al., 2017). Top marine predators do not feed on phytoplankton, however. Thus, in the intensely dynamic ocean with rapid and highly variable spatio-temporal changes (Maxwell et al., 2015), it would be expected that there is a decoupling between the processes controlling primary producers and the upper trophic levels of the food web (Le Fèvre, 1987; Renault et al., 2016). This phenomenon would result in a mismatch between primary productivity and the spatial ecology of marine top predators (Grémillet et al., 2008).

Effective management and conservation in the open ocean is highly dependent on understanding basic predator ecology (Game et al., 2009; Marshall et al., 2016; Guerra, 2019) and the processes driving their distribution (Afán et al., 2015; Gladics et al., 2015; García-Barón et al., 2019). The importance of this not only lies in the fact that top predators are key ecological indicators in marine ecosystems (Maxwell et al., 2013; Hazen et al., 2019), but also because many of them are facing severe conservation problems and are subject to protection measures regulated by law, the application of which is not always completely effective (Soulé et al., 2005; Lescroëil et al., 2016).

Much of the planet's biodiversity is found in the ocean and yet the marine environment is clearly under threat and remains mostly unprotected (Jenkins & Van Houtan, 2016; Luypaert et al., 2019). In particular, seabirds are one of the most threatened groups within the marine environment and their populations have declined globally by almost 70% in the last century (Paleczny et al., 2015; Dias et al., 2019). The establishment of marine protected areas (MPAs) has become one of the most pragmatic approaches to mitigate biodiversity loss (Hyrenbach, Forney & Dayton, 2000; Davidson & Dulvy, 2017; Handley et al., 2020), and seabirds are effective proxies for identifying priority conservation sites for themselves and for other taxa (Brooks et al., 2001). Among seabirds, the Balearic shearwater (*Puffinus mauretanicus*) is one of the most threatened species in the world (Oro et al., 2004; Genovart et al., 2016; Birdlife International, 2020). This species, endemic to the Balearic Islands, is listed as Critically Endangered on the International Union for Conservation of Nature (IUCN) Red List (Birdlife International, 2020).

Balearic shearwaters are easily monitored and cross different and very dynamic areas during their migration from their breeding areas in the Mediterranean Sea, transiting the Strait of Gibraltar, and reaching the North Atlantic (Guilford et al., 2012). Moreover, they prey on a variety of species of pelagic fish and other marine organisms (Käkelä et al., 2010). Therefore, their conservation status may reflect the conditions of the environment where they are found, thus acting as an indicator species (Siddig et al., 2016). The population size of Balearic shearwaters is estimated at around 25,000 individuals (Arroyo et al., 2016), and demographic modelling shows a severe decline and predicts extinction within a few decades (Genovart et al., 2016). Balearic shearwaters leave the Mediterranean, heading to the Atlantic Ocean, from mid-May to mid-July, and return to the breeding grounds from late August, peaking in October (Guilford et al., 2012; Arroyo et al., 2016). The Gulf of Cádiz (GoC; Figure 1) is part of its flyway migratory corridor and plays an important role as a foraging area (Arcos et al., 2009). Therefore, the GoC has been identified as a marine Important Bird and Biodiversity Area (IBA) (Arcos et al., 2009) and Special Protected Area (SPA) for its importance for the Balearic shearwater, among other seabird species (Ministerio de Agricultura Alimentación y Medio ambiente, 2014).

Species distribution models have been used extensively to determine the most suitable habitat for the Balearic shearwater (Louzao et al., 2006a; Louzao et al., 2012; Meier et al., 2015; Araújo et al., 2017), and have played a major role in identifying the marine IBA of GoC, and with it the legally-binding SPA, for the protection of the species (Arcos et al., 2012; Ministerio de Agricultura Alimentación y Medio ambiente, 2014). Based on a significant improvement in the monitoring of this species in the GoC, the aim of this study was to advance the understanding of the distribution of the Balearic shearwater, analysing the contemporary oceanographic features influencing the distribution of the species in the region. Considering previous knowledge, we hypothesize that dynamic variables related to ocean productivity drive the occurrence of the Balearic shearwater in the GoC. Consequently, a higher probability of occurrence of Balearic shearwater in areas with higher primary production would be expected (Louzao et al., 2011b; Louzao et al., 2012; Araújo et al., 2017). Alternatively, in very dynamic marine areas, other oceanographic processes could mask the relationships between primary production and the presence of top predators (Croll et al., 2005).

2 | METHODS

2.1 | Study area

The distribution and essential habitat of the Balearic shearwater were studied in the GoC over a period of 10 years, between 2006 and 2018, during the post-nuptial migration period (Table S1). The area surveyed ranged from Cape St. Vincent in the Algarve (off the southern coast of Portugal) to the Atlantic coast of Andalusia (off the south-west coast of Spain) as far as Cape Trafalgar (i.e. from 36°00' to

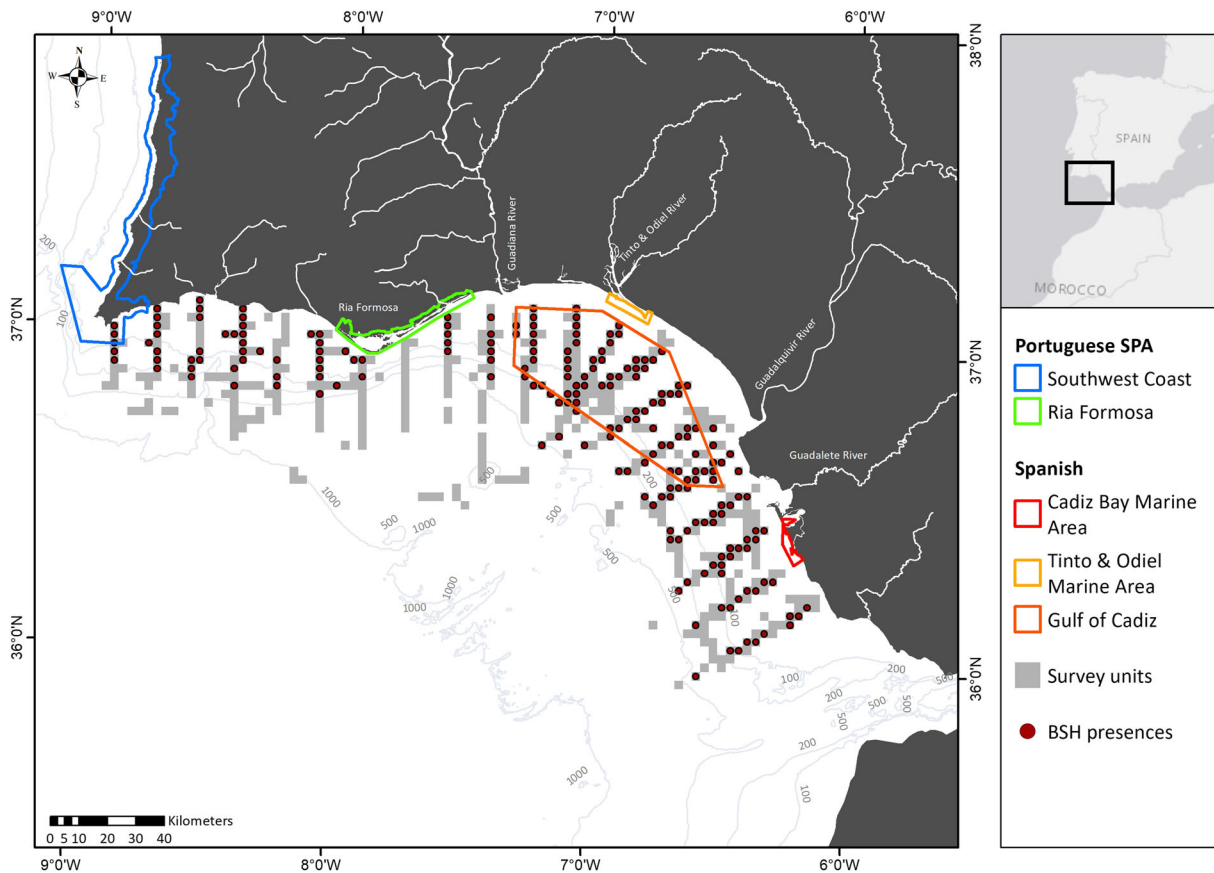


FIGURE 1 Overview of the study area. Red dots represent the presence of Balearic shearwater, *Puffinus mauretanicus*, in the 10-minute survey units (grey squares). Coloured outlines indicate the Special Protection Areas (SPAs) in the Gulf of Cádiz. The main bathymetric profile and main rivers of the area are also indicated

37°00'N and from 5°45' to 9°00'W), encompassing 390 km of coastline and a total area of almost 20,000 km². This area was studied during the annual summer ECOCADIZ acoustic-trawl surveys conducted by the Spanish Institute of Oceanography (IEO), on board the R/V *Cornide de Saavedra* (until 2013) and subsequently on board the R/V *Miguel Oliver*, to acoustically evaluate the small pelagic fish populations over the GoC continental shelf (covering depths of <200 m) (Massé et al., 2018).

This is an important area for seabirds, with five SPAs designated under the 1979 Birds Directive (2009/147/EC) (European Commission, 2009) as part of the Natura 2000 network. The Spanish areas include the GoC (ES0000500), the Tinto and Odiel rivers (ES0000501), and the Bay of Cádiz (ES0000502) (Ministerio de Agricultura Alimentación y Medio ambiente, 2014), and the Portuguese areas include the south-west coast (PTZPE0015) and the Ria Formosa (PTZPE0017) (Figure 1).

The GoC region is characterized by strong seasonality and important synoptic meteorological events (Prieto et al., 2009), which largely control chlorophyll *a* concentrations and suspended material (Caballero et al., 2014). In this basin important river flows (Guadiana, Guadalquivir, Tinto-Odiel, etc.) fertilize the coastal fringe, maintaining high concentrations of chlorophyll *a* throughout the year (Navarro & Ruiz, 2006). The shelf zone between Trafalgar and Santa Maria Capes

embraces favourable features and sustains a high concentration of fish eggs, larvae (Baldó et al., 2006), and small pelagic fish (Ruiz et al., 2009).

2.2 | At-sea data collection and processing

Vessel-based surveys were conducted in early summer (from June to early August; Table S1). During the surveys, seabirds were counted on one or both sides ahead of the vessel, depending on census conditions and following the standard European Seabirds at Sea (ESAS) protocols (Tasker et al., 1984; Camphuysen & Garthe, 2004). Snapshot counts were used to count flying birds (Tasker et al., 1984). All observations were registered during good weather conditions and summed into 10-min survey units with the vessel travelling at a constant speed of 10 knots in order to standardize the measurements over several years. A binary value of '1' was assigned to each 10-min sequence in which the presence of the Balearic shearwater was recorded (hereafter referred to as 'presence') (Figure 1), whereas sequences where no Balearic shearwater were observed were coded as '0' (hereafter referred to as 'absence'). This presence/absence was considered as the dependent (response) variable. Data on abundance (i.e. density) were not considered in this research.

2.3 | Environmental variables description and selection

A set of ecologically relevant predictors (static and dynamic) were selected to characterize the marine environment as proxies for the physical and biological processes potentially driving the Balearic shearwater distribution in the GoC, based on our previous knowledge of habitat selection in the species (Louzao et al., 2006a; Louzao et al., 2012; Araújo et al., 2017). The ecological basis for choosing the variables is presented in Table S2. Static (physical) variables (i.e. bathymetry, slope, distance to isobaths, and distance to main coastal geographic features) were extracted and derived from the EMODnet Bathymetry portal (<http://www.emodnet-bathymetry.eu>; Marine Information Service, 2016). Dynamic oceanographic data, monthly chlorophyll *a* concentration, and monthly sea surface temperature were extracted from Aqua MODIS satellite imagery via at a spatial resolution of 4×4 km (<https://oceancolor.gsfc.nasa.gov>), and turbidity was derived using remote-sensing reflectance from Aqua MODIS following the method described by Caballero et al. (2014) (Table S2). When the survey took place over a period of 2 months a new layer, with the average of both months, was calculated.

Collinearity between variables was investigated by estimating pairwise Spearman's rank correlation coefficients in R (R Development Core Team, 2020). When a pair of environmental variables was highly correlated ($|R_s| > 0.65$), the most ecologically relevant variable was chosen to be tested in the model (Table S3).

2.4 | Distribution models performance

A comprehensive ecological modelling approach was followed to investigate the influence of environmental factors on the occurrence of Balearic shearwater by developing an SDM. For this purpose, the performance of two modelling procedures was compared.

2.5 | Annual distribution models

First, the effects of environmental variables on the presence of Balearic shearwater were investigated separately by year (annual distributions models), using the maximum-entropy modelling technique, MaxEnt (Phillips, 2017; Elith et al., 2011). This approach has fewer information requirements, allows an estimation of the explanatory power of each environmental variable, and is easily integrated with the graphical representations in the geographic information system (GIS), providing predictive distribution maps based on the occurrence probability for each year, which has made it one of the most widely-used methods to perform SDMs (Elith et al., 2006; Elith & Leathwick, 2009). Before running annual models, all data were prepared to be read by MAXENT software. One of the requirements of MAXENT is that all spatial information must be presented in the same format (i.e. with the same number and size of cells and the same

geographic extension) for both the presence data for the species and for the environmental variables to be tested in the model. To obtain easily interpretable results, the predictive layers included in the model were restricted to the sampled area. Models were evaluated for each year using default datasets, randomly selecting a bootstrapping sample of 25% as test data, and removing duplicate values per cells to minimize autocorrelation biases and linear and quadratic relationships with a cloglog output for easier interpretation. In order to reduce the sample bias, a 'bias file' was used to represent the sampling effort each year. MAXENT predictions were calculated 10 times in order to obtain an average prediction and coefficient of variation for the predictions (Edrén et al., 2010). The area under the receiver operating characteristic curve (AUC) was used to assess the predictive performance of each model (Fielding & Bell, 1997). The range of AUC values varies from 0 to 1 (i.e. ranging from negligible to perfect discriminatory power). An AUC of 0.5 indicates that the performance of the model is equal to that of a random prediction, whereas values between 0.5 and 1 indicate the following performance classification: 1.0–0.9, excellent; 0.9–0.8, good; 0.8–0.7, reasonable; 0.7–0.6, poor; and 0.6–0.5, unsuccessful (Engler, Guisan & Rechsteiner, 2004).

2.6 | Overall model

Data for the 10 years were pooled to investigate the overall effect of explanatory factors on the distribution of the species (overall model). In order to choose the best model to analyse presence-absence data (Brotons et al., 2004), generalized linear mixed models (GLMMs) with a binomial error distribution and logit link function were used (Zuur et al., 2009), with the help of the 'glmer' function from the LMER4 package for R (R Development Core Team, 2020). The factor *year* was settled as a random effect, and the variables retained after collinearity analysis (see above) were included as fixed factors in the GLMM model procedure. Logarithms of distance variables were calculated in order to avoid convergence problems and scale variable warnings. Model selection was made using Akaike's information criteria (Akaike, 1973) to identify the most robust (i.e. including variables with the strongest impact on outcomes) and parsimonious (i.e. avoiding over-fitting) models following a forward stepwise selection approach (Burnham & Anderson, 2002). When the differences of AIC values between models were low (i.e. $\Delta AIC < 2$), models with fewer variables were selected in order to maintain the most parsimonious model (Burnham & Anderson, 2002).

2.7 | Spatial autocorrelation bias

Spatial autocorrelation (i.e. where locations close to each other show values that are more similar than for locations that are more distant) is a general statistical property of ecological variables observed across geographic space (Legendre, 1993; Dormann et al., 2007) that

may be an important source of bias in most spatial analyses (Segurado, Araújo & Kunin, 2006). The occurrence of this spatial autocorrelation in the residuals of distribution models means that the key assumptions of residuals being independent and identically distributed is violated, which can inflate the probabilities of falsely rejecting the null hypothesis (type-I error) (Segurado, Araújo & Kunin, 2006; Dormann et al., 2007; Peres-Neto & Legendre, 2010). In these cases, spatial distribution models may overestimate the importance of environmental factors (Legendre, 1993; Dale & Fortin, 2002), generating an artificial matching between species distribution and modelling drivers (Legendre et al., 2002; Dormann et al., 2007). In this study the spatial autocorrelation of the residuals of the best models was assessed by calculating the Moran's auto-correlation index (I) (Moran, 1950), using the 'ape' library in R (Paradis, Claude & Strimmer, 2004). Moran's I ranges from '-1' (perfect dispersion) to '+1' (perfect correlation), with values around zero indicative of a random spatial pattern. For each survey unit, the coordinates (latitude and longitude) of the initial unit were computed.

3 | RESULTS

3.1 | At-sea survey

One hundred and four vessel-based survey days were conducted in early summer in the GoC (Table S1), covering 2,003 survey units and more than 333 hours of observation over the 10 years of the study. Balearic shearwater were present in 420 units. Overall, most of the shearwaters were seen on the continental shelf off the coast of the Bay of Cádiz and near the mouth of the River Guadalquivir (Figure 1).

3.2 | Annual distribution models

After collinearity analysis, the following parameters were retained to be tested against Balearic shearwater presence: 'Bathymetry', 'Distance to Guadiana River mouth', 'Distance to Guadalquivir River mouth', 'Distance to 200-m isobath', 'Chlorophyll a concentration (CHL- a)', and 'sea surface temperature (SST)' (Table S3).

All annual distribution models for every single year of the study showed either a reasonable or good performance, with an average of 0.790 ± 0.06 AUC (Table 1) and, in all cases static predictors contributed substantially more to model performance than dynamic predictors. Moreover, the contribution of the different factors was quite consistent throughout the years of the study. Bathymetry was the most explanatory variable in the majority of the annual models (average contribution $36.60 \pm 25.37\%$; Table 1). The probability of occurrence was maximum in shallow water, up to depths of approximately 100 m, and rapidly decreased beyond 200 m (Figure 2). The distance to the Guadalquivir river was the second factor most contributing to the performance of the models in the majority of the years ($20.35 \pm 16.56\%$; Table 1), with higher occurrence probability near its mouth (Figure 2). In some years (i.e. 2013 and 2015), the higher probabilities of occurrence moved to the west, near Portuguese waters, and then the 'Distance to Guadiana River mouth' or the 'Distance to 200-m isobath' (shelf break) acquired a more relative contribution (Figure 2; Table 1). These results show a remarkably consistent distribution of the Balearic shearwater in summer in the GoC, covering shallow waters near the coast, between the mouths of the Guadiana and Guadalquivir rivers, and extending towards the Bay of Cádiz, as reflected by most of the annual models (Figure 3).

Dynamic oceanographic variables only contributed marginally to the development of annual models. As an indicator of primary

TABLE 1 MaxEnt analysis with the average results of 10 replicates

Survey	Test AUC	SD	Bathymetry	Dist. from Guadalquivir	Dist. from Guadiana	Dist. from 200-m isobath	CHL-a	SST
2006	0.851	0.038	60.87	16.93	3.94	13.00	2.53	2.73
2007	0.752	0.060	56.17	13.72	7.55	12.85	9.63	0.08
2009	0.798	0.047	46.66	18.94	4.12	12.68	11.67	5.94
2010	0.894	0.031	17.82	15.37	9.59	35.91	17.79	3.53
2013	0.724	0.054	2.09	17.97	50.14	10.13	14.43	5.23
2014	0.774	0.041	15.10	18.40	22.60	33.62	10.17	0.11
2015	0.763	0.060	35.49	5.52	45.63	3.62	3.44	6.29
2016	0.728	0.065	83.34	1.39	10.29	3.53	1.30	0.14
2017	0.781	0.034	34.80	35.22	13.53	4.75	3.93	7.78
2018	0.840	0.049	13.70	60.06	13.06	10.05	2.99	0.15
Averaged annual value	0.790	0.048	36.60	20.35	18.05	14.01	7.79	3.20
SD	0.056		25.37	16.56	16.64	11.56	5.72	2.99

Note: Mean test AUC, its standard deviation (SD), and heuristic estimate for environmental parameters of the models analysed (bathymetry, distance to Guadalquivir River mouth, distance to Guadiana River mouth, distance to 200-m isobath, CHL-a; and SST), relative contribution (%) in each year, and overall surveys are shown. First predictors with major contribution are showed in bold and second predictor in *italics*.

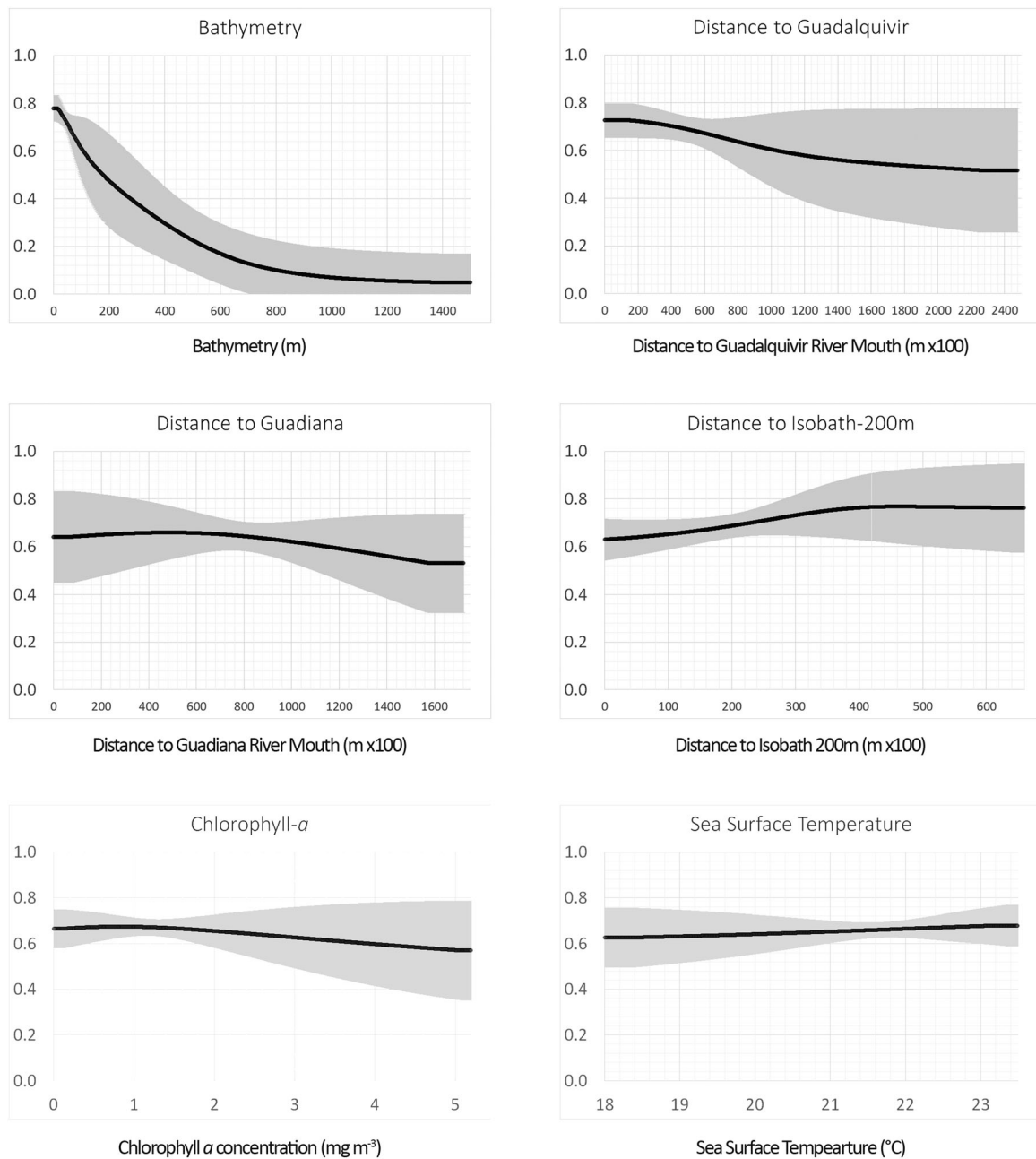


FIGURE 2 Averaged annual model response curve showing the predictor variables. The curves show the mean response of 10 replicated MAXENT runs over the 10-year dataset (black line) and the mean \pm standard deviation (grey)

production, CHL-a contributed only $7.79 \pm 5.72\%$ (Figure 2; Table 1) to the averaged model and the response curve showed a negative effect, with a higher probability of Balearic shearwater presence for low CHL-a ($<1 \text{ mg m}^{-3}$). The contribution of SST was also found to be minimal ($3.20 \pm 2.99\%$) and hardly showed any effect (Figure 2; Table 1).

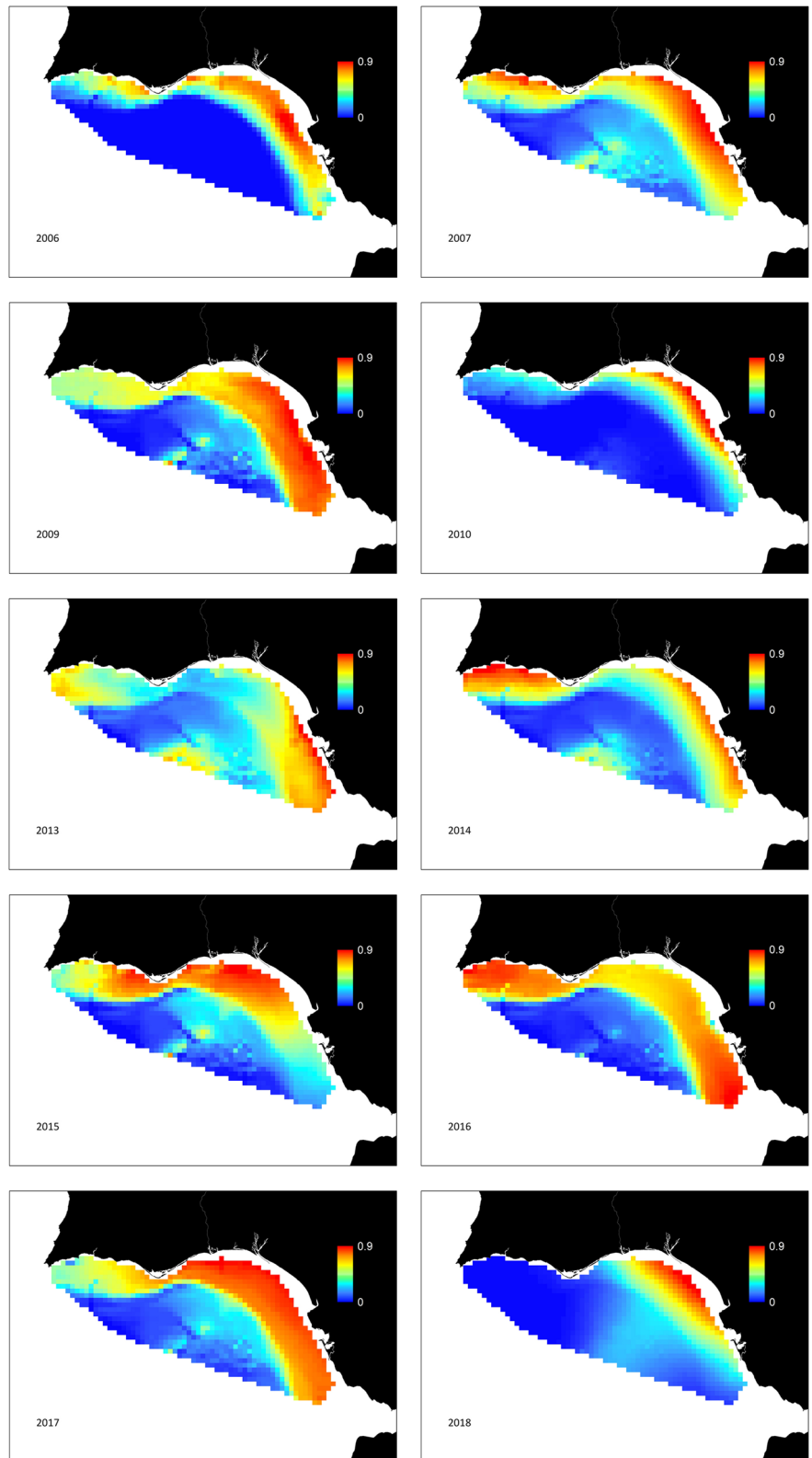
3.3 | Overall model

In order to analyse the general distribution in the GoC and compare with annual models, an overall model was constructed, compiling the

data for the 10 years of study. Thus, 63 models were tested, setting *year* as a random effect, and incorporating the variables with significant effects following a forward stepwise procedure (Table S4). Fourteen models showed statistically significant effects and are presented in the Table 2. The values of Moran's *I* were close to zero and significant in all cases, suggesting that spatial autocorrelation did not bias the results of the models.

When single predictors were considered (mod01–mod06, Table 2), static features (bathymetry and distance to Guadalquivir River mouth) performed better than dynamic features (CHL-a and SST). The most parsimonious and best-fitting multivariate model

FIGURE 3 Annual averages of 10 replicated MaxEnt models for the Balearic shearwater, *Puffinus mauretanicus*, in the Gulf of Cádiz. Warmer colours show areas with better-predicted conditions



(mod28, Table 2) also included SST, although the contribution of this variable with respect to the bivariate model (mod8, Table 2) was relatively small. According to the best-fitting model the probability of occurrence of Balearic shearwater decreases markedly towards deeper waters (primary fixed factor), as the distance away

from the mouth of the Guadalquivir River increases (secondary fixed factor), and also decreases as the SST drops (a tertiary fixed factor) (Figure 4). Any of the models that included a significant effect of CHL-a showed a poorer fit than models including the predictors described above.

TABLE 2 Biologically relevant explanatory variables used for the overall distribution modelling of the Balearic shearwater and associated oceanographic processes

Model	Single variables	Estimate	SE	P	Deviance	df.resid	AIC	ΔAIC	I	P (I)
mod01	log_bat	-1.47	0.18	<0.001	1960.1	2,108	1966.1	42.7	0.05	<0.001
mod03	log_guadalq	-1.75	0.21	<0.001	1964	2,108	1970	46.6	0.04	<0.001
mod04	log_iso200	0.84	0.13	<0.001	1991.2	2,108	1997.2	73.8	0.05	<0.001
mod05	CHL-a	0.29	0.09	0.002	2027.3	2,108	2033.3	109.9	0.06	<0.001
mod06	SST	0.11	0.05	0.018	2031	2,108	2037	113.6	0.05	<0.001
mod08	log_bat	-1.10	0.19	<0.001	1927.7	2,107	1935.7	12.3	0.04	<0.001
	log_guadalq	-1.23	0.22	<0.001						
mod16	log_guadalq	-1.47	0.22	<0.001	1942.1	2,107	1950.1	26.7	0.04	<0.001
	log_iso200	0.60	0.13	<0.001						
mod17	log_guadalq	-1.83	0.21	<0.001	1946.1	2,107	1954.1	30.7	0.03	<0.001
	CHL-a	0.41	0.10	<0.001						
mod18	log_guadalq	-2.37	0.27	<0.001	1949.8	2,107	1957.8	34.4	0.04	<0.001
	SST	-0.23	0.06	<0.001						
mod21	CHL-a	0.34	0.09	<0.001	2018.5	2,107	2026.5	103.1	0.05	<0.001
	SST	0.14	0.05	0.004						
mod28	log_bat	-1.12	0.19	<0.001	1913.4	2,106	1923.4	0	0.04	<0.001
	log_guadalq	-1.83	0.28	<0.001						
	SST	-0.23	0.06	<0.001						
mod38	log_guadalq	-1.59	0.22	<0.001	1935	2,106	1945	21.6	0.03	<0.001
	log_iso200	0.46	0.14	0.001						
	CHL-a	0.28	0.10	0.007						
mod39	log_guadalq	-2.09	0.28	<0.001	1927.8	2,106	1937.8	14.4	0.04	<0.001
	log_iso200	0.60	0.13	<0.001						
	SST	-0.23	0.06	<0.001						
mod56	log_guadalq	-2.15	0.28	<0.001	1922.6	2,105	1934.6	11.2	0.03	<0.001
	log_iso200	0.48	0.14	<0.001						
	CHL-a	0.24	0.10	0.021						
	SST	-0.21	0.06	<0.001						

Note: The shaded model (mod28) indicates the best model of Balearic shearwater occurrence in the GoC. Only models with significant variables are presented in the table with their AIC values. ΔAIC represents the difference in AIC with respect to the best model. The Moran index (I) shows the spatial autocorrelation of the model residuals and the P (I) evaluates their significance. Distance variables are log-transformed, using logarithm base 10.

Abbreviations: bat, bathymetry in metres; CHL-a, chlorophyll *a* concentration in mg m⁻³; df.resid, residuals of degrees of freedom; d_guadalq, Euclidean distance from Guadalquivir River mouth in metres; iso200, Euclidean distance from 200-m isobath in metres; SST, sea surface temperature in °C.

Figure 5 shows that the predicted optimal areas for the species during the summer in the GoC are found in shallow waters near the coast, between the mouths of the Guadiana and Guadalquivir rivers, and extend towards the Bay of Cádiz. This pattern is consistent with the results obtained in the annual models (Figure 3).

4 | DISCUSSION

Understanding how animals select their habitat and foraging resources therein is a crucial component of basic and applied ecology (Chudzińska et al., 2015). The prediction of the distributions of species is central to diverse applications in ecology, evolution, and

conservation science (Elith et al., 2006). In particular, with species facing a high degree of global threat, distribution modelling may allow effective conservation strategies to be undertaken (Maiorano et al., 2019; Schank et al., 2019). The relatively long-term dataset analysed (including 10 years from a period of 13 years) accounts for some interannual variability (Tummon et al., 2015), whereas previous studies of the distribution of this species covered more limited time periods (Arcos et al., 2009; Louzao et al., 2012). Increasing the number of sampling years allowed an increased number of sampling units, thus providing the number of presences and absences needed to obtain better model performance with more reliable and robust results (Araújo & Guisan, 2006; Brotons, Herrando & Pla, 2007; Meynard, Leroy & Kaplan, 2019). Furthermore, as the choice of modelling

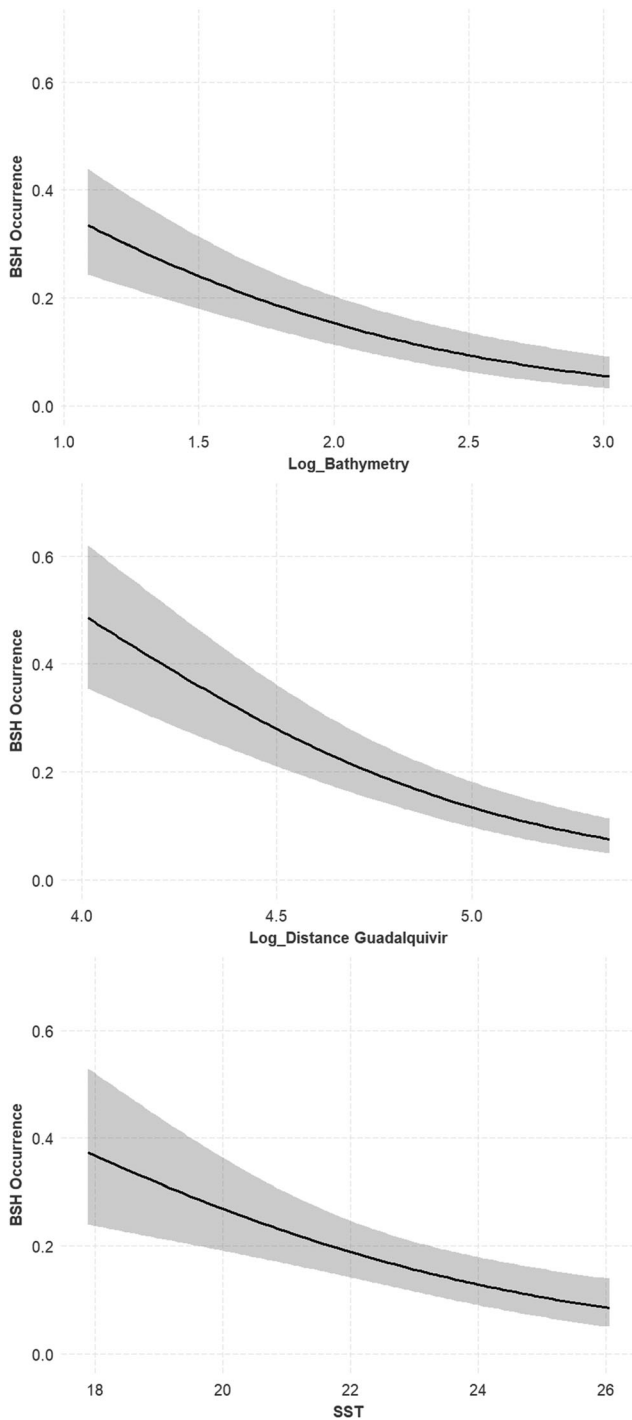


FIGURE 4 Representation of response curves illustrating the relationship between predictions for the occurrence of the Balearic shearwater (BSH) and the main fixed factors in the best-fitting generalized linear mixed model. The area shaded in grey represents the 0.95 confidence interval

method may influence the resulting predicted distribution (Araújo & New, 2007; Oppel et al., 2012), the predictions of two widely accepted methods of SDM, MaxEnt (Elith et al., 2011) and GLMM (Jamil et al., 2013), were combined. Both approaches provided similar and consistent results over time, supporting a relatively high

confidence in the habitat selection pattern of the Balearic shearwater in the GoC, thus increasing the relevance of this area for the conservation of this species (Araújo & Williams, 2000).

The results revealed the zone of the continental shelf with relatively shallow coastal waters in the vicinity of the Guadalquivir River mouth as the key area for the Balearic shearwater. Previous studies have shown that shallow waters close to the coast along the Iberian continental shelf are suitable areas for the presence of the Balearic shearwater (Louzao et al., 2006a), and this particular geographical pattern has been described recently (Arroyo, De la Cruz & Delgado, 2020). Their tendency to feed near coasts has also been studied previously (Arcos & Oro, 2002; Arcos et al., 2012), as well as their migratory movements closely following the Spanish Mediterranean coast (Mateos et al., 2010). Moreover, population concentrations close to large river mouths, in response to nutrient-loaded run-off, have also been reported for the species (Louzao et al., 2006a).

The association of Balearic shearwaters with the Guadalquivir River estuary reflects the notably high biological productivity of this area (Ruiz, Macías & Navarro, 2017). This highly altered estuary acts as a nutrient pump, where the high-water turbidity constrains the primary production and, consequently, most of the nutrients reach the shallow shelf surrounding the Guadalquivir River mouth (Caballero et al., 2014; Ruiz, Macías & Navarro, 2017). These processes, together with warm temperatures during the summer period, maintains a persistently high CHL-a in these areas, whereas the rest of the shelf and the basin experience severe oligotrophic conditions (Navarro & Ruiz, 2006; Prieto et al., 2009). Moreover, the development and maintenance of phytoplankton blooms are strongly influenced by meteorological forces resulting from both the wind regime and episodes of high rainfall, which determine river discharges (Prieto et al., 2009). Thus, these nutrient-rich waters create a suitable environment for spawning and the subsequent development of the early life stages of pelagic fish species, such as anchovy (*Engraulis encrasicolus*) (Catalán et al., 2006; Ruiz et al., 2006), sardine (*Sardina pilchardus*) (Baldó et al., 2006), and several demersal fish species (Catalán et al., 2006), that constitute the main prey for the Balearic shearwater (Louzao et al., 2006b; Käkälä et al., 2010).

There is a fairly large body of evidence that shows that areas of high CHL-a concentrate a huge number of marine top predators, including predatory fish (Novianto & Susilo, 2016), cetaceans (Panigada et al., 2008; Gill et al., 2011; Breen et al., 2016) and seabirds (Weimerskirch et al., 2005; Louzao et al., 2012). Moreover, previous studies have succeeded in using CHL-a as the main explanatory variable in niche models for the Balearic shearwater (Louzao et al., 2006a; Louzao et al., 2012; Araújo et al., 2017). Chlorophyll a may be indicative of the trophic linkage from phytoplankton to zooplankton and the small fish preyed upon by Balearic shearwaters. If high biological productivity is at the base of the recurrent use of this area by the species, why then are significant relationships not found with oceanographic variables connected to productivity and, in particular, with CHL-a? The answer may rely on the fact that, in highly dynamic marine areas, the spatio-temporal lag between the phytoplankton blooms and its translation to higher trophic levels of

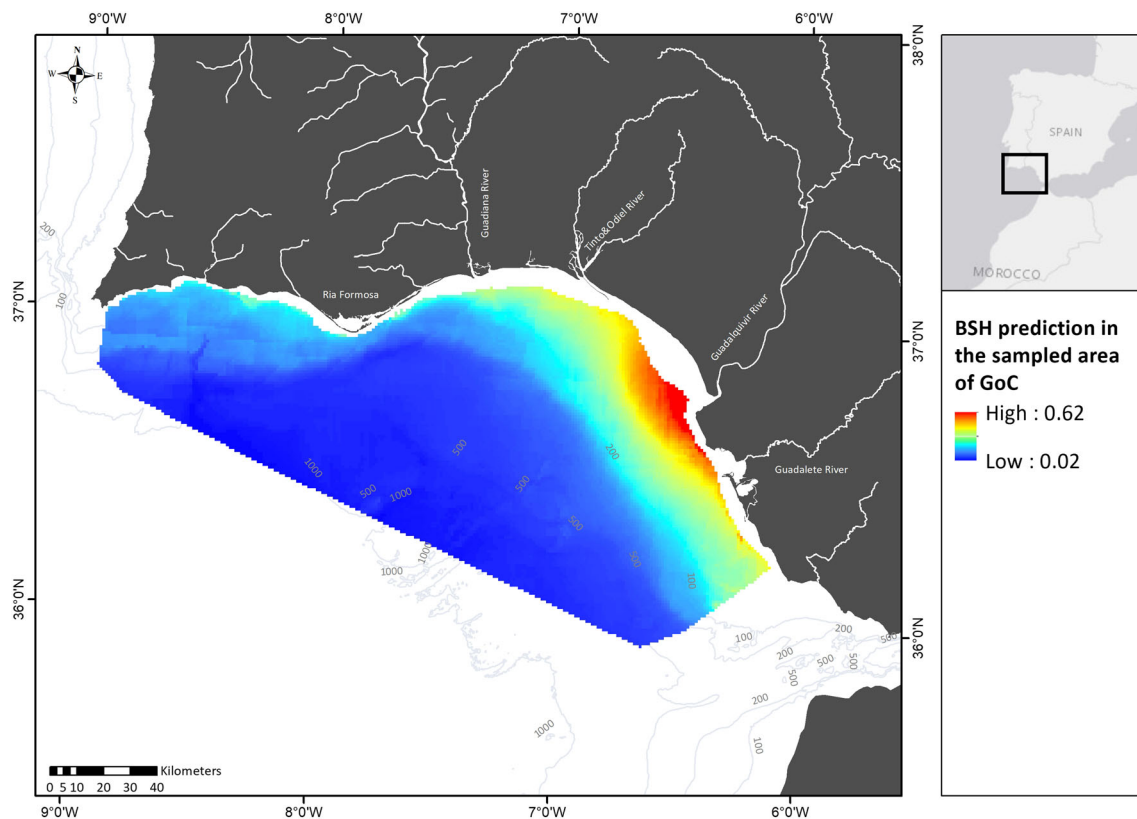


FIGURE 5 Prediction of Balearic shearwater (BSH) occurrence in the study area from the best-fitting generalized linear mixed model calculated exclusively for the sampled area

the food web can obscure the effect of CHL-a on top-predator occurrence (Croll et al., 2005; Pirotta et al., 2011). The plume of nutrients fertilizing the GoC from the Guadalquivir River is displaced by the coastal currents as a function of the wind, turning from the north west to the south east (or vice versa) in a few days, with a prevalence of the eastward direction, towards the Cape Trafalgar and the Strait of Gibraltar, caused by the predominance of westerly winds in the summer (García Lafuente & Ruiz, 2007; Gomiz-Pascual, 2017). This process has been estimated to take approximately 1–2 weeks to reach the Trafalgar area (Gomiz-Pascual, 2017), causing a notable spatiotemporal decoupling between CHL-a peaks and the availability of zooplanktivorous fish. This decoupling makes CHL-a a weakly effective tracer for the concurrent location of prey available for the Balearic shearwater. Moreover, the existence of a prominent point source of nutrients in the GoC would explain why a static variable like the distance to the river mouth becomes a better predictor than monthly averaged CHL-a in the model. Although the presence of Balearic shearwater appears to be more regular to the north of the Guadalquivir River estuary, it can be found across the whole sea area close to the estuary, tracking the fish-rich areas derived from the fertilization pulses around it.

In the best-fitting overall model, SST showed a marginal effect, with an increased probability of Balearic shearwater occurring in colder waters in the study area. This result appears to challenge the finding that warm and biologically productive waters near the

Guadalquivir River mouth are highly suitable for the reproduction of fish species such as the anchovy (Navarro & Ruiz, 2006; Ruiz et al., 2006; Ruiz et al., 2009). Moreover, the effect of intense easterly winds leads to lower SSTs and oligotrophic conditions, diverting the early stages of anchovies away from favourable conditions (Ruiz et al., 2006). Further research is required to unravel the relationships between dynamic variables and Balearic shearwater prey availability. On the other hand, the Balearic shearwater may exploit demersal fish available from trawl fishing (Arcos & Oro, 2002; Louzao et al., 2006b; Käkälä et al., 2010). The GoC is a heavily exploited fishing area (Torres et al., 2013). Fisheries involve numerous trawlers, purse seiners, and artisanal boats (Jiménez, Sobrino & Ramos, 2004). Bottom-trawl fishing provides substantial quantities of demersal prey to seabirds (Louzao et al., 2011a), with most of the fish discards being consumed by seabirds (Arcos & Oro, 2002). The association of the Balearic shearwater with trawlers might also interfere with the local distribution patterns (Mateos & Arroyo, 2011).

This study reveals that although in many cases primary productivity may be a good indicator of the foraging areas for top predators, the decoupling in the translation processes across the different trophic links can break up this relationship, particularly in dynamic ecosystems like the GoC. Information about the immediate prey is generally scarce, however, and focusing on this trophic linkage appears to be fundamental to advance the understanding of the distribution of marine predators.

4.1 | Management and conservation implications

Techniques of environmental niche modelling for habitat selection are an essential management tool for conservation purposes in the marine environment, particularly to delineate core areas for conservation (Lascelles et al., 2016). Top marine predators are critical components in ecosystems, as well as acting as ecological indicators used to identify and prioritize areas for conservation. They are generally long-lived, wide-ranging organisms that forage at high trophic levels, reflecting the influence of long-term and large-scale changes in ecosystems (Piatt & Sydeman, 2007; Rajpar et al., 2018). Changes in abundance and distribution of marine predators often result from alterations in the structure and function of the ecosystem (Springer et al., 2003; Estes et al., 2011; Siddig et al., 2016). Moreover, many of these marine top predators are vulnerable to cumulative impact from human activities, such as by-catch from fisheries, emergent pollution, or climate change, among others (Maxwell et al., 2013; Provencher et al., 2019; Trew et al., 2019).

The Balearic shearwater, one of the most globally threatened seabird species, is regarded as an umbrella species that can benefit from top-down conservation approaches (Ronconi et al., 2012; Siddig et al., 2016; Crawford, Makhado & Oosthuizen, 2018). This and other seabird species are useful bio-indicators to assess disturbances in marine management (Furness & Camphuysen, 1997; Rajpar et al., 2018) and, in particular, the Balearic shearwater is a priority in European conservation plans, being legally protected across most of its distribution range in Europe. Its protected area covers waters off Spain, Portugal, France, and the UK (Arcos, 2011). The status of the species was recently re-evaluated and ratified as Critically Endangered by the IUCN Red List Committee because of the main threats remaining active (Genovart et al., 2016; IUCN, 2020). With regard to this, the identification and assessment of the environmental factors driving Balearic shearwater distribution is key to underpinning an effective conservation strategy (Oppel et al., 2012; Araújo et al., 2017; Pérez-Roda et al., 2017). Our findings demonstrate that spatial models of the Balearic shearwater and other seabirds based on primary production cannot be extrapolated to different regions because of the significant lag between this variable and processes more closely related to the distribution of the top predators, such as the presence of their prey (Fauchald, 2009). In this way, the general assumption of predicting the distribution of the endangered top predators based on primary productivity could skew the prediction, relative to the actual distribution of the species, and as a consequence mask the most appropriate area to be protected. In a recent article, it has been shown that the SPA in the GoC, designated in 2014, does not match the key habitat of the Balearic shearwater, thereby compromising its effective conservation (Arroyo, De la Cruz & Delgado, 2020). Our study adequately predicts the area with the highest probability of finding Balearic shearwaters in the GoC, which essentially coincides with the key area for the species described in Arroyo, De la Cruz & Delgado (2020). This discrepancy highlights the need to expand the limits of the current SPA in the GoC to ensure the

effective conservation of the species in one of the most important foraging areas during its migration.

To understand the mechanisms that drive the distribution of seabird species better, we must consider the complex oceanic processes and interspecific relationships that occur in the marine environment.

ACKNOWLEDGEMENTS

We are especially grateful to the Spanish Institute of Oceanography (IEO) for their collaboration each season and to all the birdwatchers that participated in the seabird counts on board IEO vessels throughout years. This research was partially supported by the Ministry of Science, Innovation and Universities through the MEGAN project (ref. CTM2013-49048-C2-1-R). The publication of this research has been partially funded by the ECOFISH project, with the collaboration of the Biodiversity Foundation from the Ministry for Ecological Transition, through the Pleamar Program, co-financed by the FEMP.

We also thank the University of Cádiz and the Coastal Wetland Conservation Research Team for their help with logistics. We thank Pep Arcos for useful comments and suggestions and thank Andy Paterson and Charles Wheaton for helping us to improve the English.

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest associated with this work.

ORCID

Andrés de la Cruz  <https://orcid.org/0000-0002-0363-2498>

Fernando Ramos  <https://orcid.org/0000-0001-9591-7214>

Gabriel Navarro  <https://orcid.org/0000-0002-8919-0060>

Andrés Cózar  <https://orcid.org/0000-0003-1370-9935>

Juan Bécars  <https://orcid.org/0000-0001-9402-3737>

Gonzalo Muñoz Arroyo  <https://orcid.org/0000-0002-1064-5342>

REFERENCES

- Afán, I., Chiaradia, A., Forero, M.G., Dann, P. & Ramírez, F. (2015). A novel spatio-temporal scale based on ocean currents unravels environmental drivers of reproductive timing in a marine predator. *Proceedings of the Royal Society B: Biological Sciences*, 282(1810), 20150721. <https://doi.org/10.1098/rspb.2015.0721>
- Akaike, H. (1973). Information theory and the maximum likelihood principle. In: B.N. Petrov, B.F. Csaki (Eds.), *Second International Symposium on Information Theory*. Budapest: Akadémiai Kiadó, pp. 267–281.
- Alves, F., Alessandrini, A., Servidio, A., Mendonça, A.S., Hartman, K.L., Prieto, R. et al. (2018). Complex biogeographical patterns support an ecological connectivity network of a large marine predator in the north-east Atlantic. *Diversity and Distributions*, 25(2), 269–284. <https://doi.org/10.1111/ddi.12848>
- Araújo, H., Bastos-Santos, J., Rodrigues, P.C., Ferreira, M., Pereira, A., Henriques, A.C. et al. (2017). The importance of Portuguese Continental Shelf Waters to Balearic Shearwaters revealed by aerial census. *Marine Biology*, 164(55), 1–14. <https://doi.org/10.1007/s00227-017-3089-x>

- Araújo, M.B. & Guisan, A. (2006). Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, 33(10), 1677–1688. <https://doi.org/10.1111/j.1365-2699.2006.01584.x>
- Araújo, M.B. & New, M. (2007). Ensemble forecasting of species distributions. *Trends in Ecology & Evolution*, 22(1), 42–47. <https://doi.org/10.1016/j.tree.2006.09.010>
- Araújo, M.B. & Williams, P.H. (2000). Selecting areas for species persistence using occurrence data. *Biological Conservation*, 96(3), 331–345. [https://doi.org/10.1016/S0006-3207\(00\)00074-4](https://doi.org/10.1016/S0006-3207(00)00074-4)
- Arcos, J.M. (2011). *International species action plan for the Balearic shearwater, Puffinus mauretanicus*. Madrid: SEO/BirdLife & BirdLife International.
- Arcos, J.M., Bécarea, J., Rodríguez, B. & Ruiz, A. (2009). *Áreas importantes Para la conservación de las aves marinas en España*. Madrid, Spain: Sociedad Española de Ornitología (SEO/BirdLife).
- Arcos, J.M., Bécarea, J., Villero, D., Brotons, L., Rodríguez, B. & Ruiz, A. (2012). Assessing the location and stability of foraging hotspots for pelagic seabirds: An approach to identify marine Important Bird Areas (IBAs) in Spain. *Biological Conservation*, 156, 30–42. <https://doi.org/10.1016/j.biocon.2011.12.011>
- Arcos, J.M. & Oro, D. (2002). Significance of fisheries discards for a threatened Mediterranean seabird, the Balearic shearwater *Puffinus mauretanicus*. *Marine Ecology Progress Series*, 239, 209–220. <https://doi.org/10.3354/meps239209>
- Arroyo, G.M., De la Cruz, A. & Delgado, D. (2020). How adequately are the critically endangered Balearic Shearwaters protected by the Special Protection Areas (SPAs) for seabirds? A case study in the Gulf of Cadiz. *Global Ecology and Conservation*, 21, 1–10. <https://doi.org/10.1016/j.gecco.2019.e00861>
- Arroyo, G.M., Mateos, M., Muñoz, A.R., De la Cruz, A., Cuenca, D. & Onrubia, A. (2016). New population estimates of a critically endangered species, the Balearic Shearwater *Puffinus mauretanicus*, based on coastal migration counts. *Bird Conservation International*, 26(1), 87–99. <https://doi.org/10.1017/S095927091400032X>
- Baldó, F., García-Isarch, E., Jiménez, M.P., Romero, Z., Sánchez-Lamadrid, A. & Catalán, I.A. (2006). Spatial and temporal distribution of the early life stages of three commercial fish species in the northeastern shelf of the Gulf of Cádiz. *Deep Sea Research Part II: Topical Studies in Oceanography*, 53(11–13), 1391–1401. <https://doi.org/10.1016/j.dsr2.2006.04.004>
- Ballance, L.T., Pitman, R.L. & Fiedler, P.C. (2006). Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: A review. *Progress in Oceanography*, 69(2–4), 360–390. <https://doi.org/10.1016/j.pocean.2006.03.013>
- Birdlife International. (2020). *Species factsheet: Puffinus mauretanicus*. IUCN Red List for birds.
- Breen, P., Brown, S., Reid, D. & Rogan, E. (2016). Modelling cetacean distribution and mapping overlap with fisheries in the northeast Atlantic. *Ocean and Coastal Management*, 134, 140–149. <https://doi.org/10.1016/j.ocecoaman.2016.09.004>
- Brooks, T., Balmford, A., Burgess, N.D., Hansen, L.A., Moore, J.L., Rahbek, C. et al. (2001). Conservation priorities for birds and biodiversity: Do East African Important Bird Areas represent species diversity in other terrestrial vertebrate groups? *Ostrich*, 15, 3–12.
- Brotons, L., Herrando, S. & Pla, M. (2007). Updating bird species distribution at large spatial scales: Applications of habitat modelling to data from long-term monitoring programs. *Diversity and Distributions*, 13(3), 276–288. <https://doi.org/10.1111/j.1472-4642.2007.00339.x>
- Brotons, L., Thuiller, W., Araújo, M.B. & Hirzel, A.H. (2004). Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. *Ecography*, 27(4), 437–448. <https://doi.org/10.1111/j.0906-7590.2004.03764.x>
- Burnham, K. & Anderson, D. (2002). *Model selection and multimodel inference. A practical information-theoretic approach*, 2nd edition. New York: Springer.
- Caballero, I., Morris, E.P., Prieto, L. & Navarro, G. (2014). The influence of the Guadalquivir river on spatio-temporal variability in the pelagic ecosystem of the eastern Gulf of Cádiz. *Mediterranean Marine Science*, 15(4), 721–738. <https://doi.org/10.12681/mms844>
- Camphuysen, K. & Garthe, S. (2004). Foraging Associations. *Atlantic Seabirds*, 6(1), 1–32.
- Catalán, I.A., Jiménez, M.T., Alconchel, J.I., Prieto, L. & Muñoz, J.L. (2006). Spatial and temporal changes of coastal demersal assemblages in the Gulf of Cadiz (SW Spain) in relation to environmental conditions. *Deep Sea Research Part II: Topical Studies in Oceanography*, 53(11–13), 1402–1419. <https://doi.org/10.1016/j.dsr2.2006.04.005>
- Chudzińska, M.E., van Beest, F.M., Madsen, J. & Nabe-Nielsen, J. (2015). Using habitat selection theories to predict the spatiotemporal distribution of migratory birds during stopover - a case study of pink-footed geese *Anser brachyrhynchus*. *Oikos*, 124(7), 851–860. <https://doi.org/10.1111/oik.01881>
- Crawford, R.J.M., Makhado, A.B. & Oosthuizen, W.H. (2018). Bottom-up and top-down control of the Benguela ecosystem's seabirds. *Journal of Marine Systems*, 188, 133–141. <https://doi.org/10.1016/j.jmarsys.2017.04.004>
- Croll, D., Marinovic, B., Benson, S., Chavez, F., Black, N., Ternullo, R. et al. (2005). From wind to whales: Trophic links in a coastal upwelling system. *Marine Ecology Progress Series*, 289, 117–130. <https://doi.org/10.3354/meps289117>
- Dale, M.R.T. & Fortin, M.-J. (2002). Spatial autocorrelation and statistical tests in ecology. *Ecoscience*, 9(2), 162–167. <https://doi.org/10.1080/11956860.2002.11682702>
- Davidson, L.N.K. & Dulvy, N.K. (2017). Global marine protected areas to prevent extinctions. *Nature Ecology and Evolution*, 1(2), 1–6. <https://doi.org/10.1038/s41559-016-0040>
- Dias, M.P., Martin, R., Pearmain, E.J., Burfield, I.J., Small, C., Phillips, R.A. et al. (2019). Threats to seabirds: A global assessment. *Biological Conservation*, 525–537. <https://doi.org/10.1016/j.biocon.2019.06.033>
- Dormann, C., McPherson, J., Araújo, M., Bivand, R., Bolliger, J., Carl, G. et al. (2007). Methods to account for spatial autocorrelation in the analysis of species distributional data: A review. *Ecography*, 30(5), 609–628. <https://doi.org/10.1111/j.2007.0906-7590.05171.x>
- Edrén, S.M.C., Wisz, M.S., Teilmann, J., Dietz, R. & Söderkvist, J. (2010). Modelling spatial patterns in harbour porpoise satellite telemetry data using maximum entropy. *Ecography*, 33(4), 698–708. <https://doi.org/10.1111/j.1600-0587.2009.05901.x>
- Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A. et al. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29(2), 129–151. <https://doi.org/10.1111/j.2006.0906-7590.04596.x>
- Elith, J. & Leathwick, J.R. (2009). Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annual Review of Ecology, Evolution, and Systematics*, 40(1), 677–697. <https://doi.org/10.1146/annurev.ecolsys.110308.120159>
- Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y. & Yates, C.J. (2011). A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, 17(1), 43–57. <https://doi.org/10.1111/j.1472-4642.2010.00725.x>
- Engler, R., Guisan, A. & Rechsteiner, L. (2004). An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. *Journal of Applied Ecology*, 41(2), 263–274. <https://doi.org/10.1111/j.0021-8901.2004.00881.x>
- Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J. et al. (2011). Trophic Downgrading of Planet Earth. *Science*, 333(6040), 301–306. <https://doi.org/10.1126/science.1205106>
- European Commission. (2009). *Directive 2009/147/EC of the European Parliament and of the council on the conservation of wild birds*. Brussels: Official Journal of the European Union.

- Fauchald, P. (2009). Spatial interaction between seabirds and prey: Review and synthesis. *Marine Ecology Progress Series*, 391, 139–151. <https://doi.org/10.3354/meps07818>
- Fernandes, R.F., Honrado, J.P., Guisan, A., Roxo, A., Alves, P., Martins, J. et al. (2019). Species distribution models support the need of international cooperation towards successful management of plant invasions. *Journal for Nature Conservation*, 49, 85–94. <https://doi.org/10.1016/j.jnc.2019.04.001>
- Fielding, A. & Bell, R.J. (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, 24(1), 38–49. <https://doi.org/10.1017/S0376892997000088>
- Franklin, J. (2010). *Mapping species distribution: Spatial inference and prediction*. San Diego State University: Cambridge University Press.
- Furness, R.W. & Camphuysen, K.C.J. (1997). Seabirds as monitors of the marine environment. *ICES Journal of Marine Science*, 54(4), 726–737. <https://doi.org/10.1006/jmsc.1997.0243>
- Game, E.T., Grantham, H.S., Hobday, A.J., Pressey, R.L., Lombard, A.T., Beckley, L.E. et al. (2009). Pelagic protected areas: The missing dimension in ocean conservation. *Trends in Ecology & Evolution*, 24(7), 360–369. <https://doi.org/10.1016/j.tree.2009.01.011>
- García Lafuente, J. & Ruiz, J. (2007). The Gulf of Cádiz pelagic ecosystem: A review. *Progress in Oceanography*, 74(2–3), 228–251. <https://doi.org/10.1016/j.pocean.2007.04.001>
- García-Barón, I., Authier, M., Caballero, A., Vázquez, J.A., Santos, M.B., Murcia, J.L. et al. (2019). Modelling the spatial abundance of a migratory predator: A call for transboundary marine protected areas. *Diversity and Distributions*, 25(3), 346–360. <https://doi.org/10.1111/ddi.12877>
- Genovart, M., Arcos, J.M., Álvarez, D., McMinn, M., Meier, R., Wynn, R.B. et al. (2016). Demography of the critically endangered Balearic shearwater: The impact of fisheries and time to extinction. *Journal of Applied Ecology*, 53(4), 1158–1168. <https://doi.org/10.1111/1365-2664.12622>
- Gill, P.C., Morrice, M.G., Brad, P., Rebecca, P., Levings, A.H. & Michael, C. (2011). Blue whale habitat selection and within-season distribution in a regional upwelling system off southern Australia. *Marine Ecology Progress Series*, 421, 243–263. <https://doi.org/10.3354/meps08914>
- Gladics, A.J., Suryan, R.M., Parrish, J.K., Horton, C.A., Daly, E.A. & Peterson, W.T. (2015). Environmental drivers and reproductive consequences of variation in the diet of a marine predator. *Journal of Marine Systems*, 146, 72–81. <https://doi.org/10.1016/j.jmarsys.2014.06.015>
- Gomiz-Pascual, J. (2017). *Conexión de procesos hidrológicos e hidrodinámicos entre el Golfo de Cádiz y el mar de Alborán*. Puerto Real: Universidad de Cádiz.
- Grémillet, D., Lewis, S., Drapeau, L., Van Der Lingen, C.D., Huggett, J.A., Coetzee, J.C. et al. (2008). Spatial match-mismatch in the Benguela upwelling zone: Should we expect chlorophyll and sea-surface temperature to predict marine predator distributions? *Journal of Applied Ecology*, 45(2), 610–621. <https://doi.org/10.1111/j.1365-2664.2007.01447.x>
- Guerra, A.S. (2019). Wolves of the Sea: Managing human-wildlife conflict in an increasingly tense ocean. *Marine Policy*, 99, 369–373. <https://doi.org/10.1016/j.marpol.2018.11.002>
- Guilford, T., Wynn, R., McMinn, M., Rodríguez, A., Fayet, A., Maurice, L. et al. (2012). Geolocators reveal migration and pre-breeding behaviour of the critically endangered balearic shearwater *Puffinus mauretanicus*. *PLoS ONE*, 7(3), e33753. <https://doi.org/10.1371/journal.pone.0033753>
- Guisan, A. & Thuiller, W. (2005). Predicting species distribution: Offering more than simple habitat models. *Ecology Letters*, 8(9), 993–1009. <https://doi.org/10.1111/j.1461-0248.2005.00792.x>
- Handley, J.M., Pearmain, E.J., Opper, S., Carneiro, A.P.B., Hazin, C., Phillips, R.A. et al. (2020). Evaluating the effectiveness of a large multi-use MPA in protecting Key Biodiversity Areas for marine predators. *Diversity and Distributions*, 26(6), 715–729. <https://doi.org/10.1111/ddi.13041>
- Hazen, E.L., Abrahms, B., Brodie, S., Carroll, G., Jacox, M.G., Savoca, M.S. et al. (2019). Marine top predators as climate and ecosystem sentinels. *Frontiers in Ecology and the Environment*, 17(10), 565–574. <https://doi.org/10.1002/fee.2125>
- Hunt, G. & Schneider, D. (1987). Scale-dependent processes in the physical and biological environment of marine birds. *Seabirds: feeding biology and role in marine ecosystems*. Cambridge: Cambridge University Press, pp. 7–41.
- Hyrenbach, K.D., Forney, K.A. & Dayton, P.K. (2000). Marine protected areas and ocean basin management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 10(6), 437–458. [https://doi.org/10.1002/1099-0755\(200011/12\)10:6<437::AID-AQC425>3.3.CO;2-H](https://doi.org/10.1002/1099-0755(200011/12)10:6<437::AID-AQC425>3.3.CO;2-H)
- IUCN. (2020). *Balearic Shearwater (Puffinus mauretanicus): request for information to resolve conservation status assessment*. BirdLife's globally threatened bird forums. Available at: <https://globally-threatened-bird-forums.birdlife.org/2020/03/balearic-shearwater-puffinus-mauretanicus-request-for-information-to-resolve-conservation-status-assessment/>
- Jamil, T., Ozinga, W.A., Kleyer, M. & ter Braak, C.J.F. (2013). Selecting traits that explain species-environment relationships: A generalized linear mixed model approach. *Journal of Vegetation Science*, 24(6), 988–1000. <https://doi.org/10.1111/j.1654-1103.2012.12036.x>
- Jenkins, C.N. & Van Houtan, K.S. (2016). Global and regional priorities for marine biodiversity protection. *Biological Conservation*, 204, 333–339. <https://doi.org/10.1016/j.biocon.2016.10.005>
- Jiménez, M., Sobrino, I. & Ramos, F. (2004). Objective methods for defining mixed-species trawl fisheries in Spanish waters of the Gulf of Cádiz. *Fisheries Research*, 67(2), 195–206. <https://doi.org/10.1016/j.fishres.2003.09.048>
- Käkelä, R., Käkelä, A., Martínez-Abraín, A., Sarzo, B., Louzao, M., Gerique, C. et al. (2010). Fatty acid signature analysis confirms foraging resources of a globally endangered Mediterranean seabird species: Calibration test and application to the wild. *Marine Ecology Progress Series*, 398, 245–258. <https://doi.org/10.3354/meps08291>
- Lascelles, B.G., Taylor, P.R., Miller, M.G.R., Dias, M.P., Opper, S., Torres, L. et al. (2016). Applying global criteria to tracking data to define important areas for marine conservation. *Diversity and Distributions*, 22(4), 422–431. <https://doi.org/10.1111/ddi.12411>
- Le Fèvre, J. (1987). Aspects of the Biology of Frontal Systems. *Advances in marine biology*, 23, 163–299. [https://doi.org/10.1016/S0065-2881\(08\)60109-1](https://doi.org/10.1016/S0065-2881(08)60109-1)
- Legendre, P. (1993). Spatial autocorrelation: trouble or new paradigm? *Ecology*, 74(6), 1659–1673. <https://doi.org/10.2307/1939924>
- Legendre, P., Dale, M.R.T., Fortin, M.J., Gurevitch, J., Hohn, M. & Myers, D. (2002). The consequences of spatial structure for the design and analysis of ecological field surveys. *Ecography*, 25(5), 601–615. <https://doi.org/10.1034/j.1600-0587.2002.250508.x>
- Lescroël, A., Mathevet, R., Péron, C., Authier, M., Provost, P., Takahashi, A. et al. (2016). Seeing the ocean through the eyes of seabirds: A new path for marine conservation? *Marine Policy*, 68, 212–220. <https://doi.org/10.1016/j.marpol.2016.02.015>
- Louzao, M., Arcos, J.M., Guijarro, B., Valls, M. & Oro, D. (2011a). Seabird-trawling interactions: Factors affecting species-specific to regional community utilisation of fisheries waste. *Fisheries Oceanography*, 20(4), 263–277. <https://doi.org/10.1111/j.1365-2419.2011.00579.x>
- Louzao, M., Delord, K., García, D., Boué, A. & Weimerskirch, H. (2012). Protecting Persistent Dynamic Oceanographic Features: Transboundary Conservation Efforts Are Needed for the Critically Endangered Balearic Shearwater. *PLoS ONE*, 7(5), e35728. <https://doi.org/10.1371/journal.pone.0035728>
- Louzao, M., Hyrenbach, K., Arcos, J.M., Abelló, P., De Sola, L. & Oro, D. (2006a). Oceanographic habitat of an endangered Mediterranean

- procellariiform: Implications for marine protected areas. *Ecological Applications*, 16(5), 1683–1695. [https://doi.org/10.1890/1051-0761\(2006\)016\[1683:OHOAEM\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016[1683:OHOAEM]2.0.CO;2)
- Louzao, M., Igual, J.M., McMinn, M., Aguilar, J.S., Triay, R. & Oro, D. (2006b). Small pelagic fish, trawling discards and breeding performance of the critically endangered Balearic shearwater: Improving conservation diagnosis. *Marine Ecology Progress Series*, 318, 247–254. <https://doi.org/10.3354/meps318247>
- Louzao, M., Navarro, J., Forero, M.G., Igual, J.M., Genovart, M., Hobson, K. A. et al. (2011b). Exploiting the closest productive area: Geographical segregation of foraging grounds in a critically endangered seabird. *Marine Ecology Progress Series*, 429, 291–301. <https://doi.org/10.3354/meps09126>
- Luypaert, T., Hagan, J.G., McCarthy, M.L. & Poti, M. (2019). Status of Marine Biodiversity in the Anthropocene. In: S. Jungblut, V. Liebich, M. Bode-Dalby (Eds.) *The Oceans: Our Research, Our Future*. YOUNMARES 9. Cham: Springer, pp. 57–82.
- Maiorano, L., Chiaverini, L., Falco, M. & Ciucci, P. (2019). Combining multi-state species distribution models, mortality estimates, and landscape connectivity to model potential species distribution for endangered species in human dominated landscapes. *Biological Conservation*, 237, 19–27. <https://doi.org/10.1016/j.biocon.2019.06.014>
- Malakoff, D. (2004). New Tools Reveal Treasures at Ocean Hot Spots. *Science*, 304(5674), 1104–1105. <https://doi.org/10.1126/science.304.5674.1104>
- Marine Information Service. (2016). *EMODnet digital bathymetry (DTM)*. EMODnet Bathymetry. Marine Information Service. Available at: <http://sextant.ifremer.fr/record/c7b53704-999d-4721-b1a3-04ec60c87238/> [Accessed 30 March 2018]
- Marshall, K.N., Stier, A.C., Samhoury, J.F., Kelly, R.P. & Ward, E.J. (2016). Conservation Challenges of Predator Recovery. *Conservation Letters*, 9(1), 70–78. <https://doi.org/10.1111/conl.12186>
- Massé, J., Uriarte, A., Angélico, M.M. & Carrera, P. (2018). Pelagic survey series for sardine and anchovy in ICES Subareas 8 and 9 (WGACEG) – Towards an ecosystem approach. ICES Cooperative Research Report.
- Mateos, M. & Arroyo, G.M. (2011). Ocean surface winds drive local-scale movements within long-distance migrations of seabirds. *Marine Biology*, 158(2), 329–339. <https://doi.org/10.1007/s00227-010-1561-y>
- Mateos, M., Arroyo, G.M., Rodríguez, A., Cuenca, D. & De la Cruz, A. (2010). Calibration of visually estimated distances to migrating seabirds with radar measurements. *Journal of Field Ornithology*, 81(3), 302–309. <https://doi.org/10.1111/j.1557-9263.2010.00286.x>
- Maxwell, S.M., Hazen, E.L., Bograd, S.J., Halpern, B.S., Breed, G.A., Nickel, B. et al. (2013). Cumulative human impacts on marine predators. *Nature Communications*, 4, 1–9. <https://doi.org/10.1038/ncomms3688>
- Maxwell, S.M., Hazen, E.L., Lewison, R.L., Dunn, D.C., Bailey, H., Bograd, S.J. et al. (2015). Dynamic ocean management: Defining and conceptualizing real-time management of the ocean. *Marine Policy*, 58, 42–50. <https://doi.org/10.1016/j.marpol.2015.03.014>
- Meier, R.E., Wynn, R.B., Votier, S.C., McMinn Grivé, M., Rodríguez, A., Maurice, L. et al. (2015). Consistent foraging areas and commuting corridors of the critically endangered Balearic shearwater *Puffinus mauretanicus* in the northwestern Mediterranean. *Biological Conservation*, 190, 87–97. <https://doi.org/10.1016/j.biocon.2015.05.012>
- Meynard, C.N., Leroy, B. & Kaplan, D.M. (2019). Testing methods in species distribution modelling using virtual species: What have we learnt and what are we missing? *Ecography*, 42, 2021–2036. <https://doi.org/10.1111/ecog.04385>
- Ministerio de Agricultura Alimentación y Medio ambiente. (2014). *Orden AAA/1260/2014, de 9 de julio, por la que se declaran Zonas de Especial Protección para las Aves en aguas marinas españolas*. BOE 173. Spain. Available at: https://www.boe.es/boe_catalan/dias/2002/12/02/pdfs/A03057-03062.pdf
- Moran, P. (1950). Notes on continuous stochastic phenomena. *Biometrika*, 37(1–2), 17–23. <https://doi.org/10.1093/biomet/37.1-2.17>
- Navarro, G. & Ruiz, J. (2006). Spatial and temporal variability of phytoplankton in the Gulf of Cádiz through remote sensing images. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 53(11–13), 1241–1260. <https://doi.org/10.1016/j.dsr2.2006.04.014>
- Novianto, D. & Susilo, E. (2016). Role of Sub Surface Temperature, Salinity and Chlorophyll To Albacore Tuna Abundance in Indian Ocean. *Indonesian Fisheries Research Journal*, 22(1), 17. <https://doi.org/10.15578/ifrj.22.1.2016.17-26>
- Oppel, S., Meirinho, A., Ramírez, I., Gardner, B., O'Connell, A.F., Miller, P.I. et al. (2012). Comparison of five modelling techniques to predict the spatial distribution and abundance of seabirds. *Biological Conservation*, 156, 94–104. <https://doi.org/10.1016/j.biocon.2011.11.013>
- Oro, D., Aguilar, J.S., Igual, J.M. & Louzao, M. (2004). Modelling demography and extinction risk in the endangered Balearic shearwater. *Biological Conservation*, 116(1), 93–102. [https://doi.org/10.1016/S0006-3207\(03\)00180-0](https://doi.org/10.1016/S0006-3207(03)00180-0)
- O'Toole, M., Guinet, C., Lea, M. & Hindell, M. (2017). Marine predators and phytoplankton: How elephant seals use the recurrent Kerguelen plume. *Marine Ecology Progress Series*, 581, 215–227. <https://doi.org/10.3354/meps12312>
- Paleczny, M., Hammill, E., Karpouzi, V. & Pauly, D. (2015). Population Trend of the World's Monitored Seabirds, 1950–2010. *PLoS ONE*, 10(6), e0129342. <https://doi.org/10.1371/journal.pone.0129342>
- Panigada, S., Zanardelli, M., MacKenzie, M., Donovan, C., Mélin, F. & Hammond, P.S. (2008). Modelling habitat preferences for fin whales and striped dolphins in the Pelagos Sanctuary (Western Mediterranean Sea) with physiographic and remote sensing variables. *Remote Sensing of Environment*, 112(8), 3400–3412. <https://doi.org/10.1016/j.rse.2007.11.017>
- Paradis, E., Claude, J. & Strimmer, K. (2004). APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, 20(2), 289–290. <https://doi.org/10.1093/bioinformatics/btg412>
- Peres-Neto, P.R. & Legendre, P. (2010). Estimating and controlling for spatial structure in the study of ecological communities. *Global Ecology and Biogeography*, 19(2), 174–184. <https://doi.org/10.1111/j.1466-8238.2009.00506.x>
- Pérez-Roda, A., Delord, K., Boué, A., Arcos, J.M., García, D., Micol, T. et al. (2017). Identifying Important Atlantic Areas for the conservation of Balearic shearwaters: Spatial overlap with conservation areas. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 141(November 2016), 285–293. <https://doi.org/10.1016/j.dsr2.2016.11.011>
- Peterson, A.T., Sobrerón, J., Pearson, R.G., Anderson, R., Martínez-Meyer, E., Nakamura, M. et al. (2011). *Ecological niches and geographic distributions*. Princeton: University Press.
- Phillips, S. (2017). A Brief Tutorial on Maxent. Available at: http://biodiversityinformatics.amnh.org/open_source/maxent/ [Accessed 08 January 2019].
- Piatt, I. & Sydeman, W. (2007). Seabirds as indicators of marine ecosystems. *Marine Ecology Progress Series*, 352, 199–204. <https://doi.org/10.3354/meps07070>
- Pirotta, E., Matthiopoulos, J., MacKenzie, M., Scott-Hayward, L. & Rendell, L. (2011). Modelling sperm whale habitat preference: A novel approach combining transect and follow data. *Marine Ecology Progress Series*, 436, 257–272. <https://doi.org/10.3354/meps09236>
- Polovina, J.J., Balazs, G.H., Howell, E.A., Parker, D.M., Seki, M.P. & Dutton, P.H. (2004). Forage and migration habitat of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific Ocean. *Fisheries Oceanography*, 13(1), 36–51. <https://doi.org/10.1046/j.1365-2419.2003.00270.x>
- Prieto, L., Navarro, G., Rodríguez-Gálvez, S., Huertas, I.E., Naranjo, J.M. & Ruiz, J. (2009). Oceanographic and meteorological forcing of the

- pelagic ecosystem on the Gulf of Cadiz shelf (SW Iberian Peninsula). *Continental Shelf Research*, 29(17), 2122–2137. <https://doi.org/10.1016/j.csr.2009.08.007>
- Provencher, J.F., Borrelle, S., Sherley, R.B., Avery-Gomm, S., Hodum, P., Bond, A. et al. (2019). Seabirds. In: *World seas: an environmental evaluation*, 2nd edition. Elsevier, pp. 133–162. <https://doi.org/10.1016/B978-0-12-805052-1.00007-3>
- R Development Core Team. (2020). R: a language and environment for statistical computing. Vienna, Austria: R Foundation for statistical computing. Available at: <http://www.r-project.org>
- Rajpar, M.N., Ozdemir, I., Zakaria, M., Sheryar, S. & Rab, A. (2018). Seabirds as Bioindicators of Marine Ecosystems. In: *Seabirds*. London: InTech, p. 13. <https://doi.org/10.5772/intechopen.75458>
- Reisinger, R.R., Raymond, B., Hindell, M.A., Bester, M.N., Crawford, R.J.M., Davies, D. et al. (2018). Habitat modelling of tracking data from multiple marine predators identifies important areas in the Southern Indian Ocean. *Diversity and Distributions*, 24(4), 535–550. <https://doi.org/10.1111/ddi.12702>
- Renault, L., Deutsch, C., McWilliams, J.C., Frenzel, H., Liang, J.-H. & Colas, F. (2016). Partial decoupling of primary productivity from upwelling in the California Current system. *Nature Geoscience*, 9(7), 505–508. <https://doi.org/10.1038/ngeo2722>
- Ronconi, R.A., Lascelles, B.G., Langham, G.M., Reid, J.B. & Oro, D. (2012). The role of seabirds in Marine Protected Area identification, delineation, and monitoring: Introduction and synthesis. *Biological Conservation*, 156, 1–4. <https://doi.org/10.1016/j.biocon.2012.02.016>
- Ruiz, J., Garcia-Isarch, E., Emma Huertas, I., Prieto, L., Juárez, A., Muñoz, J. L. et al. (2006). Meteorological and oceanographic factors influencing *Engraulis encrasicolus* early life stages and catches in the Gulf of Cádiz. *Deep Sea Research Part II: Topical Studies in Oceanography*, 53(11–13), 1363–1376. <https://doi.org/10.1016/j.dsr2.2006.04.007>
- Ruiz, J., Gonzalez-Quirós, R., Prieto, L. & Navarro, G. (2009). A Bayesian model for anchovy (*Engraulis encrasicolus*): The combined forcing of man and environment. *Fisheries Oceanography*, 18(1), 62–76. <https://doi.org/10.1111/j.1365-2419.2008.00497.x>
- Ruiz, J., Macías, D. & Navarro, G. (2017). Natural forcings on a transformed territory overshoot thresholds of primary productivity in the Guadalquivir estuary. *Continental Shelf Research*, 148, 199–207. <https://doi.org/10.1016/j.csr.2017.09.002>
- Sánchez-Carnero, N., Rodríguez-Pérez, D., Couñago, E., Le Barzik, F. & Freire, J. (2016). Species distribution models and local ecological knowledge in marine protected areas: The case of Os Miñarzos (Spain). *Ocean and Coastal Management*, 124, 66–77. <https://doi.org/10.1016/j.ocecoaman.2016.02.008>
- Schank, C.J., Cove, M.V., Kelly, M.J., Nielsen, C.K., O'Farrill, G., Meyer, N. et al. (2019). A Sensitivity Analysis of the Application of Integrated Species Distribution Models to Mobile Species: A Case Study with the Endangered Baird's Tapir. *Environmental Conservation*, 46(3), 184–192. <https://doi.org/10.1017/S0376892919000055>
- Segurado, P., Araújo, M.B. & Kunin, W.E. (2006). Consequences of spatial autocorrelation for niche-based models. *Journal of Applied Ecology*, 43(3), 433–444. <https://doi.org/10.1111/j.1365-2664.2006.01162.x>
- Siddiq, A.A.H., Ellison, A.M., Ochs, A., Villar-Leeman, C. & Lau, M.K. (2016). How do ecologists select and use indicator species to monitor ecological change? Insights from 14 years of publication in Ecological Indicators. *Ecological Indicators*, 60, 223–230. <https://doi.org/10.1016/j.ecolind.2015.06.036>
- Soulé, M.E., Estes, J.A., Miller, B. & Honnold, D.L. (2005). Strongly Interacting Species: Conservation Policy, Management, and Ethics. *Bioscience*, 55(2), 168. [https://doi.org/10.1641/0006-3568\(2005\)055\[0168:siscpm\]2.0.co;2](https://doi.org/10.1641/0006-3568(2005)055[0168:siscpm]2.0.co;2)
- Springer, A.M., Estes, J.A., van Vliet, G.B., Williams, T.M., Doak, D.F., Danner, E.M. et al. (2003). Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? *Proceedings of the National Academy of Sciences of the United States of America*, 100(21), 12223–12228. <https://doi.org/10.1073/pnas.1635156100>
- Tasker, M., Jones, P.H., Dixon, T. & Blake, B.F. (1984). Counting seabirds at sea from ships: A review of methods employed and a suggestion for a standardized approach. *The Auk*, 101(3), 567–577. <https://doi.org/10.2307/4086610>
- Torres, M.Á., Coll, M., Heymans, J.J., Christensen, V. & Sobrino, I. (2013). Food-web structure of and fishing impacts on the Gulf of Cadiz ecosystem (South-western Spain). *Ecological Modelling*, 265, 26–44. <https://doi.org/10.1016/j.ecolmodel.2013.05.019>
- Trew, B.T., Grantham, H.S., Barrientos, C., Collins, T., Doherty, P.D., Formia, A. et al. (2019). Using Cumulative Impact Mapping to Prioritize Marine Conservation Efforts in Equatorial Guinea. *Frontiers in Marine Science*, 6, 1–17. <https://doi.org/10.3389/fmars.2019.00717>
- Tummon, F., Hassler, B., Harris, N.R.P., Staehelin, J., Steinbrecht, W., Anderson, J. et al. (2015). Intercomparison of vertically resolved merged satellite ozone data sets: Interannual variability and long-term trends. *Atmospheric Chemistry and Physics*, 15(6), 3021–3043. <https://doi.org/10.5194/acp-15-3021-2015>
- Weimerskirch, H., Le Corre, M., Jaquemet, S. & Marsac, F. (2005). Foraging strategy of a tropical seabird, the red-footed booby, in a dynamic marine environment. *Marine Ecology Progress Series*, 288, 251–261. <https://doi.org/10.3354/meps288251>
- Worm, B., Sandow, M., Oschlies, A., Lotze, H.K. & Myers, R.A. (2005). Global Patterns of Predator Diversity in the Open Oceans. *Science*, 309(5739), 1365–1369. <https://doi.org/10.1126/science.1113399>
- Zainuddin, M., Farhum, A., Safruddin, S., Selamat, M.B., Sudirman, S., Nurdin, N. et al. (2017). Detection of pelagic habitat hotspots for skipjack tuna in the Gulf of Bone-Flores Sea, southwestern Coral Triangle tuna, Indonesia. *PLoS ONE*, 12(10), e0185601. <https://doi.org/10.1371/journal.pone.0185601>
- Zuur, A., Ieno, E., Walker, N., Saveliev, A. & Smith, G. (2009). *Mixed effects models and extensions in ecology with R*. New York: Springer Science & Business Media.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

How to cite this article: de la Cruz A, Ramos F, Navarro G, Cózar A, Bécares J, Arroyo GM. Drivers for spatial modelling of a critically endangered seabird on a dynamic ocean area: Balearic shearwaters are non-vegetarian. *Aquatic Conserv: Mar Freshw Ecosyst*. 2021;1–15. <https://doi.org/10.1002/aqc.3542>