ICES Journal of
Marine Science

ICES CIEM International Council for the Exploration of the Sea Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science (2021), https://doi.org/10.1093/icesjms/fsab256

Downloaded from https://academic.oup.com/icesjms/advance-article/doi/10.1093/icesjms/fsab256/6479775 by guest on 23 December 2021

Original Article

Seabird distribution is better predicted by abundance of prey than oceanography. A case study in the Gulf of Cadiz (SW, Iberian Peninsula)

Andrés de la Cruz [1,*], Fernando Ramos[2], Jorge Tornero[2], Margarita María Rincón[2], Mª Paz Jiménez[2], and Gonzalo Muñoz Arroyo[1]

[1] *Biology Department, Institute of Marine Research (INMAR), International Campus of Excellence in Marine Science (CEIMAR), University of Cadiz, Puerto Real, 11510 Cadiz, Spain*

[2] *Cadiz Oceanographic Centre, Spanish Institute of Oceanography (IEO-CSIC). Puerto Pesquero, Muelle de Levante, 11006 Cadiz, Spain*

[*] *Corresponding author: Tel: +34 606765186; e-mail: andres.delacruz@uca.es*

de la Cruz, A., Ramos, F., Tornero, J., Rincón, M. M., Jiménez, M. P., and Arroyo, G. M. Seabird distribution is better predicted by abundance of prey than oceanography. A case study in the Gulf of Cadiz (SW, Iberian Peninsula). – ICES Journal of Marine Science, 0: 1–14.

Received 24 December 2020; revised 2 December 2021; accepted 4 December 2021.

Quantifying factors that influence marine predator distributions is essential to understanding the current and future change in marine biodiversity. Here, we test whether marine predator distribution relates to prey, or is better predicted by other specific habitat features. We examine the correlation between spatial distribution of three seabird species and their prey, as well as environmental proxies (oceanographic characteristics) in the Gulf of Cadiz, NE Atlantic. We modeled the at-sea distribution of Cory's shearwater, Balearic shearwater and Northern gannet, based on: (i) pelagic fish abundance according to acoustic surveys, and (ii) a forecast-model of remotely sensed environmental variables (productivity, sea surface temperature, and salinity). In general, seabird distributions were better predicted by abundance of fish than by environmental variables at the habitat scale. We obtained consistent correlations between seabird presence and the abundance of medium-sized (10–20 cm) sardines, anchovies and Mediterranean horse mackerel, providing information on their preferred prey. Additionally, oceanographic productivity variables moderately contributed to seabird distribution models, with better predictive value for the critically endangered Balearic shearwater and Northern gannet in the summer, whilst the model for Cory's shearwater's produced poorer predictions. Predator–prey combined studies may represent essential tools for an efficient ecosystem-based management of marine environments.

Keywords: Gulf of Cadiz, marine top predators, oceanographic factors, overlapping distribution, predator–prey relationship, seabirds.

Introduction

There is increasing evidence that the biodiversity of marine ecosystems is changing as a result of climate change and human activity. Changes in the distribution of marine organisms are a consequence of changing climate conditions and human intervention (Canonico *et al.*, 2019). Recent studies have reported how in the coming decades, climate change may alter the overlapping of marine predators' habitat with that occupied by their prey population. This would lead to an overall decrease in the population of most predator–prey systems (Sadykova *et al.*, 2020).

Revealing the links between the marine environment, prey occurrence and predator distribution has key implications both for identification of critical marine habitat for Marine Protected Area selection, and for fisheries stock assessments and management (Sadykova *et al.*, 2020; Evans *et al.*, 2021). As sentinels of changes in the oceans, marine top predators offer a unique perspective into oceanic processes, since they can move across ocean basins and amplify trophic information across multiple spatiotemporal scales (Hazen *et al.*, 2019). Among these top predators, seabirds are conspicuous, their movements cover wide ranges of the ocean and they respond to changes in ecosystem structure and function

© The Author(s) 2021. Published by Oxford University Press on behalf of International Council for the Exploration of the Sea. All rights reserved. For permissions, please e-mail: journals.permissions@oup.com

that would otherwise be difficult to observe directly (Hazen *et al.*, 2019).

For several decades, acoustic technology in oceanographic campaigns has allowed us to combine surveys of spatial distribution and abundance of fish populations with simultaneous observation of predators, from the same vessel (Russell *et al.*, 1992). Generally, these studies have tried to relate the distribution of marine predators (mostly seabirds and cetaceans), their foraging behaviour and aggregation to increases in availability of prey (Fauchald *et al.*, 2000; Fauchald and Erikstad, 2002). However, many studies have not been able to establish a direct relationship between the distribution of apex predators and their prey (Phillips *et al.*, 2021). The wide heterogeneity and complexity of marine ecosystems and the spatial variability of prey abundance mean that models based on prey distribution do not always succeed at explaining that of predators (Torres *et al.*, 2008).

In the open ocean, resources distribution follows a hierarchical patchy structure, with dense aggregations of prey within patches of lower prey density, separated by areas where prey is scarce (Fauchald *et al.*, 2000). Predator distribution is therefore conditioned by foraging behavior and aggregate response to increased prey availability (Fauchald *et al.*, 2000; Fauchald and Erikstad, 2002). Prey availability relies on a combination of factors including abundance, accessibility and patchiness (Boyd *et al.*, 2017), school density (Enstipp *et al.*, 2007) and predator avoidance behaviour (Logerwell and Hargreaves, 1996), among others. Therefore, studies looking for relationships between marine predators and their prey, based on the abundance of the latter, may not find consistent associations if such abundance does not reflect actual availability.

The response of predators to the distribution of prey can change over a range of spatial scales, so that correlations at a given scale may be masked by those at both larger and smaller scales (Fauchald *et al.*, 2000). At a small scale, the dominant relationships are anti-predator responses and prey consumption, whilst at a large scale, predator aggregation is more pronounced (Rose and Leggett, 1990). Thus, fine-scale (<5 km) investigations have reported weak predator–prey associations, whereas studies conducted at larger scales have frequently documented stronger correlations (revised in Russell *et al.*, 1992). Therefore, it would be desirable that the "observational scale" (the resolution and extent at which processes are sampled) should be determined by the scale of the process to be investigated, although this is not always achievable, due to logistical and data limitations (Hunsicker *et al.*, 2011). In particular, most of these field measurements of marine predator–prey interactions over a broad range of scales are often derived from trawl and hydroacoustic surveys that require costly and logistically complex ship-time (trawling) and echo sounding equipment. This can lead to mismatches between field data and parameterization of functional response models, which should be handled by addressing the issues of scale (Hunsicker *et al.*, 2011).

On the other hand, the relationships between marine predators and their natural prey may also be masked by the appearance of alternative food sources, often derived from human activities, such as fishing discards, which have become a key food resource for many species as well as a subsidiary food source for a large number of seabirds (Bartumeus *et al.*, 2010).

At the same time, recent advances in remote sensing technology for oceans have provided novel predictive variables that facilitate the modeling of species distribution (Reisinger *et al.*, 2018). This has generated numerous studies that have linked the distribution of marine predators to specific oceanographic features at intermediate to broad spatial scales (Torres *et al.*, 2008). High concentrations of apical predators in oligotrophic open marine environments generally take place in highly productive areas, which are in turn associated with oceanographic processes such as upwellings or ocean fronts (Alves *et al.*, 2018). Several productivity-predicting variables have been linked to marine predator distribution, such as chlorophyll-*a* concentration, sea surface temperature and its gradients (Louzao *et al.*, 2012), salinity or the occurrence of fronts or eddies (Worm *et al.*, 2005). However, these variables may fail to explain the actual distribution of some marine predators in particularly dynamic environments, due to the spatio-temporal decoupling of processes along the food chain (de la Cruz *et al.*, 2021). For that reason, the use of more integrative forecasting models, integrating key dynamic oceanographic characteristics (such as temperature, primary productivity or salinity) at larger time scales, can achieve a better understanding of the drivers of distribution of highly mobile marine organisms (Franco *et al.*, 2020).

In this context, we examined the relationships in spatial distribution between predators (a group of species of seabirds) and their prey (pelagic fish) within a productive region, the Gulf of Cadiz (GoC hereinafter) to test whether seabird distribution can be better-predicted using prey distribution, oceanography, or a combination of both factors. The GoC produces high concentrations of chlorophyll-a and rich spawning areas for pelagic fish every year (Navarro and Ruiz, 2006), but its location and function are highly dynamic throughout the basin, influenced by meteorological factors, river runoff and prevailing winds (García Lafuente and Ruiz, 2007; Prieto *et al.*, 2009). This generates a high spatial heterogeneity within and between years (Navarro and Ruiz, 2006).

We hypothesize that in highly dynamic areas, the distribution of prey can be a more direct predictor of the distribution of predators than the oceanographic factors that indicate primary productivity. To test our hypothesis, we looked for spatial correlations between the occurrence of the three most frequent species of seabirds in the area (Cory's shearwater *Calonectris borealis*, Balearic shearwater *Puffinus mauretanicus* and Northern gannet *Morus bassanus*), the abundance of their potential prey (pelagic shoaling fish) and the dynamic oceanographic factors most closely related to primary productivity. At the same time, we assessed spatial overlap between seabirds and their main prey.

The results provide useful information and knowledge for ecosystem-based management of seabird populations and their habitats in the GoC, since future management measures within such key areas should take into account predator–prey relationships for a more realistic and effective approach.

Methods

Study area

The South-Atlantic Spanish Region (Subdivision 9a South of the ICES) is part of the GoC, SW Iberian Peninsula. This is a very dynamic area that is influenced by complex oceanographic processes and holds a very rich biodiversity that is related with its continental platform and the influence of intense runoff from important rivers (Navarro and Ruiz, 2006). This runoff determines the input of chlorophyll and suspended material from estuary to coastal fringe, which is characterized by strong seasonality and high chlorophyll-*a* concentrations throughout the year (Navarro and Ruiz, 2006). The plume of nutrients fertilizing the GoC is displaced by the coastal currents as a function of the wind, with a prevalent eastward direction towards Cape Trafalgar and the Strait of Gibraltar due to the predominance of westerly winds in the summer (García La-

Downloaded from https://academic.oup.com/icesjms/advance-article/doi/10.1093/icesjms/fsab256/6479775 by guest on 23 December 2021

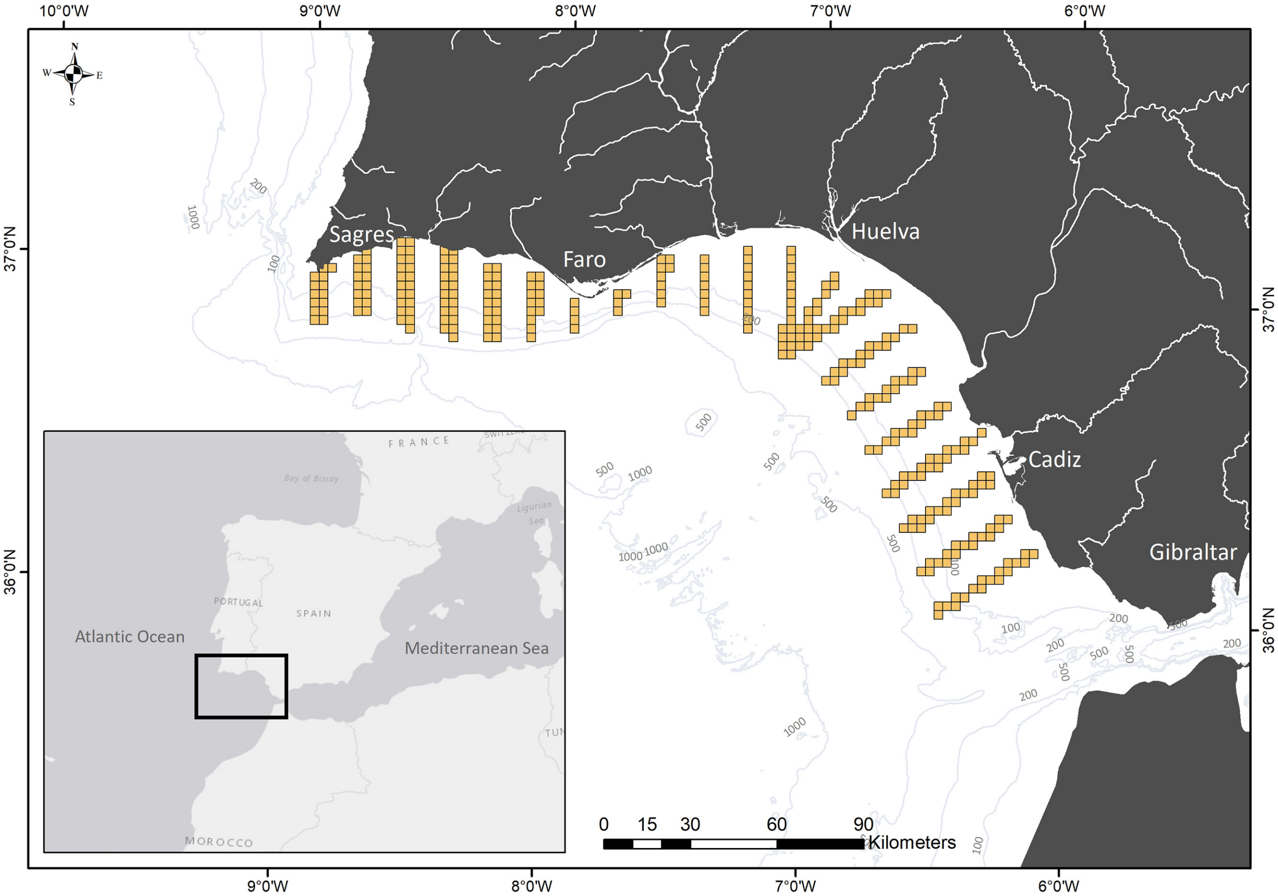

Figure 1. General map of the study area with an overview of the areas sampled during the ECOCADIZ surveys between the years 2015–2019. Isobaths of 100, 200, 500 and 1000 m are depicted. Seabird survey units (yellow squares), correspond to presence and absence of seabirds and models were applied on those particular areas.

fuente and Ruiz, 2007). These characteristics favor the upwelling of nutrients in the area and fisheries of different target species and with different fishing gear focus on the area. These important fishing grounds are exploited not only by the fishing industry, but also by many seabirds, for which it is a very important feeding area (Arroyo *et al.*, 2020) that comprises five Special Protected Areas for seabirds (marine SPAs) within the framework of the Natura 2000 network, with GoC as the most important one (ES0000500).

In this context, our study has been carried out within the framework of the annual ECOCADIZ acoustic-trawl surveys, conducted by the Spanish Institute of Oceanography (IEO) with the Research Vessel 'Miguel Oliver', between 2015 and 2019. This survey series was planned and conducted following the protocols and standards recommended by the ICES Working Group of Acoustic and Egg surveys for small pelagic fish in NE Atlantic (WGACEGG; Doray *et al.*, 2021). The survey series took place every summer (late July until mid-August), from Cape Trafalgar (36.15°N, −6.02°W) in Spain to Cape St. Vincent (36.97°N, −8.95°W) in Portugal. The total surveyed area spanned almost 8000 km^2 (Figure 1).

Seabird sightings

Seabirds were counted from one or two sides at the bow of the vessel by one experienced observer, using strip-transect techniques which assumes that all animals within the strip (300 m in our study) were detected (Tasker *et al.*, 1984). The observer searched for seabirds ahead of the vessel, within an angle of 180° from a platform located at 11 m above sea level.

This study focuses on three representative species of GoC seabirds: Cory's shearwater, Balearic shearwater and Northern gannet. These species are found in the GoC at the end of the summer, in different statuses: non-breeding and breeding adult birds in the postnuptial period, and juvenile or immature birds that have not bred that year. All these birds use the GoC as a feeding ground or migratory transit area, so they are not conditioned to return to their breeding colonies at that time. As a large percentage of seabirds sightings corresponded to flying birds (86% of Cory's shearwater; 82.2% of Northern gannet; 83.6% of Balearic shearwater), snap-shot methodology was applied in order to avoid re-count bias in relation to flying birds (Tasker *et al.*, 1984).

It is well known that weather conditions may substantially affect the detectability of seabirds (Buckland *et al.*, 2001). However, our seabird counts in the GoC were carried out in July-August, when weather conditions are mostly sunny and calm, as is typical of southern Spanish summers. All birds were recorded during favourable weather conditions (wind speed less than 6 Beaufort scale; sea state less than 4 Douglas scale; visibility range more than 1000 m; no fog, no rain). However, the wind regime in this area is notably variable, with intense easterly winds on some days. Although no observations were made during a wind speed above level

Downloaded from https://academic.oup.com/icesjms/advance-article/doi/10.1093/icesjms/fsab256/6479775 by guest on 23 December 2021

6 Beaufort, wind intensity might affect the probability of detecting some species, because of taller waves and a shorter visibility range. However, the probability of detecting shearwaters could also increase under strong winds conditions, when dynamic soaring flight becomes more prominent. We then tested the potential effect of wind intensity on the occurrence probability of the different seabird species, by using Generalized Lineal Models (GzLM, fitted with a binomial error distribution and logit link function). Wind data were obtained from the REDEXT data series (http://www.puertos.es) for the Gulf of Cadiz (2342) through the buoy located at 36.49°N 6.96°W. Variation due to the distance travelled at constant speed by the vessel during the 10 min survey series was negligible.

Fish abundance estimates

Acoustic Data Sampling

Abundance of pelagic fish species (potential seabird prey) was estimated following the protocol established by the ECOCADIZ survey design, which consists of parallel line transects, perpendicular to the isobaths and regularly spaced 8 nautical miles apart, from Cape Trafalgar to Cape St. Vincent and from the coast (20 m depth) to the 200 m isobath (Figure 1). The acoustic data were recorded en route during the daytime, while steaming at 10 knots along transects and at multiple frequencies (18, 38, 70, 120, and 200 kHz), using a Simrad EK60 hull-mounted split-beam echosounder (Kongsberg Simrad AS, Kongsberg, Norway), calibrated for each survey using the standard method described by Demer *et al.* (2015). The raw acoustic data were post-processed using the Echoview software package (Echoview Software Pty. Ltd.).

Species identification by trawling

Pelagic trawl hauls were performed adaptively during daytime at a towing speed of 4–4.5 knots, to collect information on relative species composition and particular biological parameters (length, weight, age, etc.) of fish echo traces. Thus, trawl hauls were performed at the positions where fish echo traces that were considered to be representative had been observed. Trawl catches do not allow the identification of single schools but an ensemble of schools over several nautical miles, which means that groups of schools or even of species assemblages would be identified. The trawl gear used for the ECOCADIZ acoustic-trawl survey was a 63.5/51 pelagic trawl, with a theoretical vertical opening of about 20–22 m that does not exceed 10–15 m in practice.

Echogram scrutiny and echo-integration

Fish acoustic densities were echo-integrated within one nautical mile (nm) long Elementary Distance Sampling Units (EDSU) along transects. Before their echo-integration, virtual echograms of 38 kHz frequency (i.e. the frequency used for biomass estimation) were generated based on multi-frequency algorithms (templates) in order to separate fish echo traces from other echoes (e.g. plankton, sound scattering layers). The regions containing the fish echo traces were delineated along each one of the EDSU in the echogram and allocated either to a single fish species (direct allocation based on expert judgment) or, more commonly, to multispecies aggregations, whose composition was given by the species composition of fishing hauls performed on similar echo traces in the area of interest (Nakken and Dommasnes, 1977). The resulting data after their echo-integration were Nautical Area Backscattering Coefficients (NASC) (Maclennan, 2002) by species, according to the EDSU along the transects.

Acoustic abundance and biomass estimates

After performing echo-integration of the EDSU data, each species' spatial distribution was analysed according to both its NASC values and the length frequency distribution (LFD) of positive hauls. This would result in homogeneous assessment polygons (i.e. coherent post-strata). The differences in the LFDs within each polygon were tested by means of the Kolmogorov–Smirnoff (K–S) test. LFDs without any significant differences were grouped together to obtain homogeneous LFD-based post-strata. Finally, the species-specific NASC values within each post-stratum were further converted to abundance and biomass per species values, based on the target strength and the mean weight by 0.5-cm size class of the species in the catch (Simmonds and Maclennan, 2005). This procedure allows us to estimate abundance (in thousands of fish) and biomass (tonnes) by size class per species, for every EDSU along transects (more details can be found in Doray *et al.*, 2021).

The value of each fish abundance estimate in the nearest EDSU after the acoustic evaluation was assigned to each seabird survey unit.

Fish species and size selection

In order to avoid problems related to sample size, only the species that were present in at least 10% of the EDSUs (1 nm) were considered for our models. Thus, the following species were incorporated: European anchovy *Engraulis encrasicolus* (ANE), European pilchard (sardine) *Sardina pilchardus* (PIL), Atlantic mackerel *Scomber scombrus* (MAC), Chub mackerel *Scomber colias* (VAM), Atlantic horse mackerel *Trachurus trachurus* (HOM), Mediterranean horse mackerel *Trachurus mediterraneus* (HMM), Blue jack mackerel *Trachurus picturatus* (JAA) and Bogue *Boops boops* (BOG). Since seabird distribution can be determined not only by prey species availability but also by size of prey items (Tucker *et al.*, 2016), the different species were classified according to three size-range categories following Arcos (2001): small size (0–99 mm), medium size (100–199 mm) and large size (≥ 200 mm).

Description of the environmental variables

We selected a set of environmental oceanographic variables that might condition both seabird and prey distribution, based on existing knowledge of their preferred habitat (Louzao *et al.*, 2012). We used an oceanographic forecast-model for the entire study period, rather than contemporary values of the oceanographic variables from each year. These data were obtained from the Copernicus Marine Environment Monitoring Service (CMEMS) at: https://resources.marine.copernicus.eu/with a spatial resolution of 0.028 degrees for the period of study (2015–2019). They included the following parameters:

Sea Surface Temperature (SST, °C) as a proxy of water mass; chlorophyll-*a* concentration (CHL, mg/m^3) and net primary production of biomass expressed as carbon per sea water volume unit (PROD, $mg/m^3{\cdot}day$) as a proxy of primary productivity; and salinity (SAL, practical salinity unit ≈ gr/l) characterizing different water masses and the influence from the estuaries' freshwater flows. These variables were extracted using the 'Extract Values to Point' tool, Ar-

Downloaded from https://academic.oup.com/icesjms/advance-article/doi/10.1093/icesjms/fsab256/6479775 by guest on 23 December 2021

cGis 10.6, particular to the sampled area (seabird survey unit) data layer.

Construction of the species distribution model

Prior to the construction of the model, all the continuous variables were standardized, i.e. the scales were converted to z-score in order to avoid convergence problems and allow the comparison of the different outputs. In order to determine colinearity between all the potential predictors, a matrix comprising pairwise correlations of prey species and oceanographic variables was compiled using Spearman-rank correlation. When the pairs of predictor variables were strongly correlated ($|rs| > 0.65$, Table S2), the redundant variable with the greatest explanatory power was maintained and incorporated in the next analysis. This was determined by comparing AIC criteria values of GzLM univariate models (fitted with a binomial error distribution and logit link function) (Zuur *et al.*, 2009). The variables that were finally selected are included in Table S3.

The exact number of seabirds detected in each sighting was recorded, but most of the observations (82% ±0.39 for the three species) correspond to individuals or small groups. In particular, 72% ±0.11 of Cory's shearwater sightings correspond to groups of 1–5 individuals; 12% ±0.03 to groups of 6–10 individuals; 8% ±0.05 to groups of 11–20 individuals; and 8% ±0.06 to groups of over 20 individuals. Regarding the Balearic shearwater, 80% ±0.19 of yearly sightings correspond to groups of 1–5 individuals; 9% ±0.06 to groups of 6–10 individuals; 5% ±0.05 to groups of 11–20 individuals; and 7% ±0.10 to groups of more than 20 individuals. Finally, with respect to the Northern gannet, 1–5 individuals comprised 93% ±0.09, and more than six birds together were only seen in 7% ±0.09 of the survey units. In addition, greater concentrations of individuals corresponded to rafts of resting birds. Therefore, presence/absence data were considered the dependent variable (response) in the models rather than bird abundance, as this latter concept would bias (skew) the results towards the occurrence of these rafts. Generalized Linear Models (GzLM) were applied using a binomial distribution and logit link function to establish simple correlations between seabird occurrence and explanatory variables (year, oceanographic variables and prey abundance) (Tremblay *et al.*, 2009). When the variable *year* reached a significant value in the GzLM, we ran a *year* variable as a random factor using a Generalized Linear Mixed Model (GzLMM) to control for any possible temporal pseudo-replication. Both model types, GzLM and GzLMM are widely used to identify species distribution and the correlation between such distribution and the best explanatory variables (Tremblay *et al.*, 2009). Such variables were incorporated in the model following a stepwise forward procedure, according to their explanatory capacity, and ranked by AIC (Akaike, 1973; Burnham and Anderson, 2004). As a final check, we implemented a backwards step in the final model, where each variable was separately dropped out of the model to verify if a lower AIC was obtained. The best models attained for each species are depicted in Table 3.

Verification of the spatial autocorrelations displayed by the models

Most of the species distribution data are spatially autocorrelated and it is known that modeling of this type of data may invalidate the common assumption that observations are independent, which would result in the depiction of artificial or spurious relationships (Dormann *et al.*, 2007). In order to settle this issue, we applied Moran's I coefficient to determine the spatial autocorrelation patterns in residuals of the best models. This index ranges from −1 (perfect dispersion) to +1 (perfect correlation), where zero values indicate random spatial patterns.

Since a positive, albeit weak, significant spatial autocorrelation was found in all the residuals models except for the one corresponding to Cory's shearwaters, we included a spatial autocorrelation structure in the models. After applying such spatial structure, some results still indicated a positive spatial autocorrelation. Nevertheless, the value of the Moran index became almost zero after including the spatial autocorrelation structure in the models, denoting random spatial patterns, and therefore no more biased spatial autocorrelations were expected to appear in the models (Table 3).

Model evaluation

Finally, to evaluate the predictive capacity of the best model, we used the area under the Receiver Operating Characteristic Curve (AUC). AUC has been extensively used in the species' distribution modeling literature to evaluate logistic regression models and assess the ability of a model to successfully discriminate between sites where a particular species is present, versus those where it is absent (Russell *et al.*, 2015). AUC is a threshold-independent summary statistic that ranges from zero to one. An AUC of 0.5 indicates an unsuccessful model performance that would equal that of a random prediction, whereas predictive performance values from 0.5 to 1 would classify as follows: 0.9 excellent, 0.9–0.8 good, 0.8–0.7 reasonable, 0.7–0.6 poor (Engler *et al.*, 2004).

Spatial distribution overlapping

In order to estimate the home range of all the species in the study (both seabirds and fish), we calculated their utilization distribution contours at 50% (key area) and 95% (home range) (UDC 50, UDC 95), based on their presence according to a Kernel Density Estimation (KDE) analysis. Then, we determined the overlapping degree of predator and prey distributions based on the Volume of Intersection Index (VI) (Seidel, 1992) as a statistical measurement of distribution overlap, following Fieberg (2014). The VI index generates values from zero to one, where zero means no overlap and one means total overlap or identical distribution.

Implementation method

All the analyses were performed using R software (R Development Core Team, 2020). The GzLM-type models were run using the glm R function from the 'stats' package (R Development Core Team, 2020) and the GzLMM type models were run using the glmer R function from the 'lme4' package (Bates et al., 2015). Home ranges (UDC Contours) were calculated using the kernel density estimation feature in the adehabitatHR R package (Calenge, 2006). Since the selection of the smoothing factor (h) is very important in determining the level of detail of the kernel density estimation (small h values will highlight small details and larger values will evidence only prominent features (Kappes *et al.*, 2011), we performed kernel estimations using the *ad-hoc* option of the *kernelUD* function, which provides the optimal h-value for each species analysis. After evaluating all smoothing factor values, we opted for a conservative and reasonable value of 0.07 for all species (fish and seabirds) in or-

Downloaded from https://academic.oup.com/icesjms/advance-article/doi/10.1093/icesjms/fsab256/6479775 by guest on 23 December 2021

Table 1. Fish species considered in this study to exceed 10% of the annual abundance. General distribution pattern in the GoC. Frequency of presence and average abundance (x1000) per evaluated mile. SD: Standard deviation (x1000). SMA: small size (<99 mm), MED: medium size (100–199 mm) and LAR: large size (>200 mm).

Fish species and size	Occurrence percentage	Mean abundance (x1000)	SD (x1000)
European pilchard (sardine) _MED	64.39%	1297.94	9460.3
European anchovy _MED	66.81%	1107.53	4041.1
European anchovy _SMA	19.74%	234.07	1680
Chub mackerel _MED	60.42%	143.95	1017
Chub mackerel _LAR	71.00%	84.68	556.63
Atlantic horse mackerel _LAR	41.57%	17.98	128.7
Atlantic mackerel _MED	14.77%	15.03	214.1
European pilchard (sardine) _SMA	22.49%	14.47	144.07
Mediterranean horse mackerel_LAR	24.48%	13.97	77.49
European pilchard (sardine) _LAR	17.75%	11.4	147.57
Blue jack mackerel _MED	28.00%	9.52	98.36
Atlantic horse mackerel _MED	41.57%	9.08	57.58
Blue jack mackerel _LAR	21.50%	8.24	99.96
Bogue_LAR	51.38%	4.51	29.4
Atlantic mackerel _LAR	45.09%	3.04	21.78
Atlantic horse mackerel _SMA	10.47%	0.19	2.47
Bogue_MED	28.22%	0.16	1.28
Mediterranean horse mackerel_MED	3.75%	0.01	0.15

der to compare home range and key areas of all species (Haug *et al.*, 2015). Before computing kernel density estimation analysis, all geographical coordinates were projected using the proj4string tool of library raster (Hijmans and van Etten, 2012).

Volume of Intersection Index was calculated based on the Home range overlap indices obtained by means of the KernSmooth package (Wand and Ripley, 2015). The Models' performances were evaluated according to the AUC of the Receiver Operating Characteristic curve. Moran's I coefficient was calculated using the Moran's I R function from the 'ape' library (Paradis *et al.*, 2004).

Results

Fish species composition and distribution

Fifteen different fish species were recorded during the fishing operations. Eight of them were selected as they each accounted for more than 10% of the total catches. Sardines and anchovies were the two most abundant species, with an average of more than one million individuals in each sample unit. Chub mackerel also showed relatively high abundance during the surveys, with more than two hundred thousand individuals per sample unit, on average. It was also the most widely distributed species, occurring in more than 70% of the sample units, followed by sardines, anchovies and bogues, all of them occurring in more than half the total number of sample units (Table 1).

All the fish species considered in the study were found to be distributed throughout the entire study area (UDC 95) with the exception of the Blue jack mackerel, which was only found in the western sector, as well as the Mediterranean horse mackerel, which was only present in the eastern zone of the GoC (Figure 2). Moreover, most of the small and large-sized species showed a similar key area (UDC 50) pattern except for anchovies, sardines, and Mediterranean horse mackerel (Figure 2). Both small-sized anchovies and sardines concentrated their home ranges in the areas in front of the main estuaries (Guadiana and Guadalquivir), while medium-sized anchovies and sardines were located in a more western area (Figures 2, A and B). On the other hand, small-sized and large-sized Mediterranean horse mackerel exhibited a patchy home range (Figure 2, G).

Seabird distribution patterns

We conducted 907 seabird count survey units between 2015 and 2019. Overall, Cory's shearwater was the most abundant seabird species, with occurrence in 58.99% of the survey units. Northern gannet and Balearic shearwater were detected in 32.52% and 22.05% of the survey units, respectively (Table 2).

Cory's shearwater and Northern gannet were widely distributed and occupied almost the entire study area (Figure 3C and B). The Balearic shearwater's UDC 50 was located in the central area of the GoC, i.e. between the Spanish–Portuguese border and the Bay of Cadiz (Figure 3A).

Since we did not find any significant differences between presence and absence when these data were correlated with wind intensity to investigate possible biases due to detectability (Table S1), we assume that occurrence is a good response variable to determine the distribution of seabirds in the study area.

Modelling occurrence probability

Chlorophyll-*a* concentration (CHL) showed a high to very high collinearity with productivity (PROD, 0.97), salinity (SAL, −0.69) and sea surface temperature (SST, −0.77). Sea surface temperature showed high collinearity values with productivity (PROD, −0.70) and salinity (SAL, 0.86). Regarding fish species, medium and large-sized bogue, Atlantic horse mackerel, blue jack mackerel and chub mackerel showed also high collinearity values (0.70–0.78). No relationship higher than 0.48 was found between any of the species of fish or seabirds with any oceanographic forecast model (CHL, PROD, SAL, SST) (Table S2). Likewise, no species of seabirds showed high collinearity between them (max. 0.09).

The best fitting models, according to AUC, are included in Table 3. All these models included prey (fish) species as predictors, with

Downloaded from https://academic.oup.com/icesjms/advance-article/doi/10.1093/icesjms/fsab256/6479775 by guest on 23 December 2021

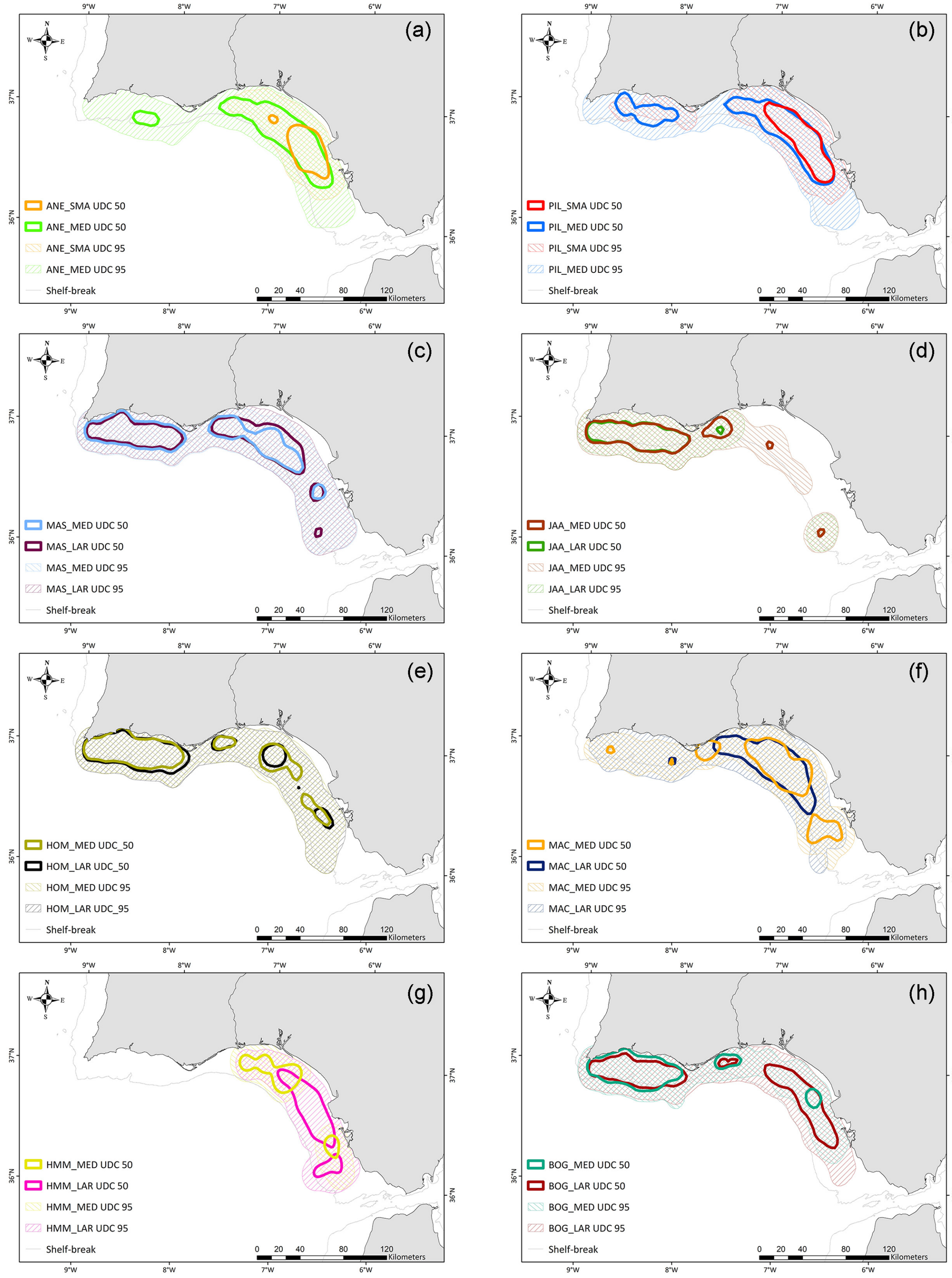

Figure 2. Distribution of fish species considered in this study. UDC 95 shows home range and UDC 50 shows home range or core area. SMA: small size (<99 mm), MED: medium size (100–199 mm) and LAR: large size (>200 mm). ANE: European anchovy Engraulis encrasicolus; PIL: European pilchard Sardina pilchardus; MAC: Atlantic mackerel Scomber scombrus; MAS: Chub mackerel Scomber colias; HOM: Atlantic horse mackerel Trachurus trachurus; HMM: Mediterranean horse mackerel Trachurus mediterraneus; JAA: Blue jack mackerel Trachurus picturatus; BOG: Bogue Boops boops.

Downloaded from https://academic.oup.com/icesjms/advance-article/doi/10.1093/icesjms/fsab256/6479775 by guest on 23 December 2021

Table 2. Seabird occurrence, general distribution pattern in the GoC and number of survey units where the different species of seabirds considered in this work appear each year.

Species	2015	2016	2017	2018	2019
Cory's shearwater	98	47	149	124	117
Balearic shearwater	42	17	86	27	28
Northern gannet	47	13	92	71	72
Total survey units	152	138	246	165	206

positive relationships and relative higher coefficient estimates, except in the case of Northern gannet. In general, the fish species distribution variables were incorporated before the oceanographic variables in the step-forward procedure and they accounted for a higher explanatory capacity, according to changes in the deviance and AIC (Table 3).

With respect to Balearic shearwater, the best models indicated a higher probability of occurrence where medium-sized sardines were abundant (Table 3, Figure 3, A). Productivity is the second factor accounting for higher deviance, showing a positive effect on Balearic shearwater occurrence. Thus, medium-sized Mediter-

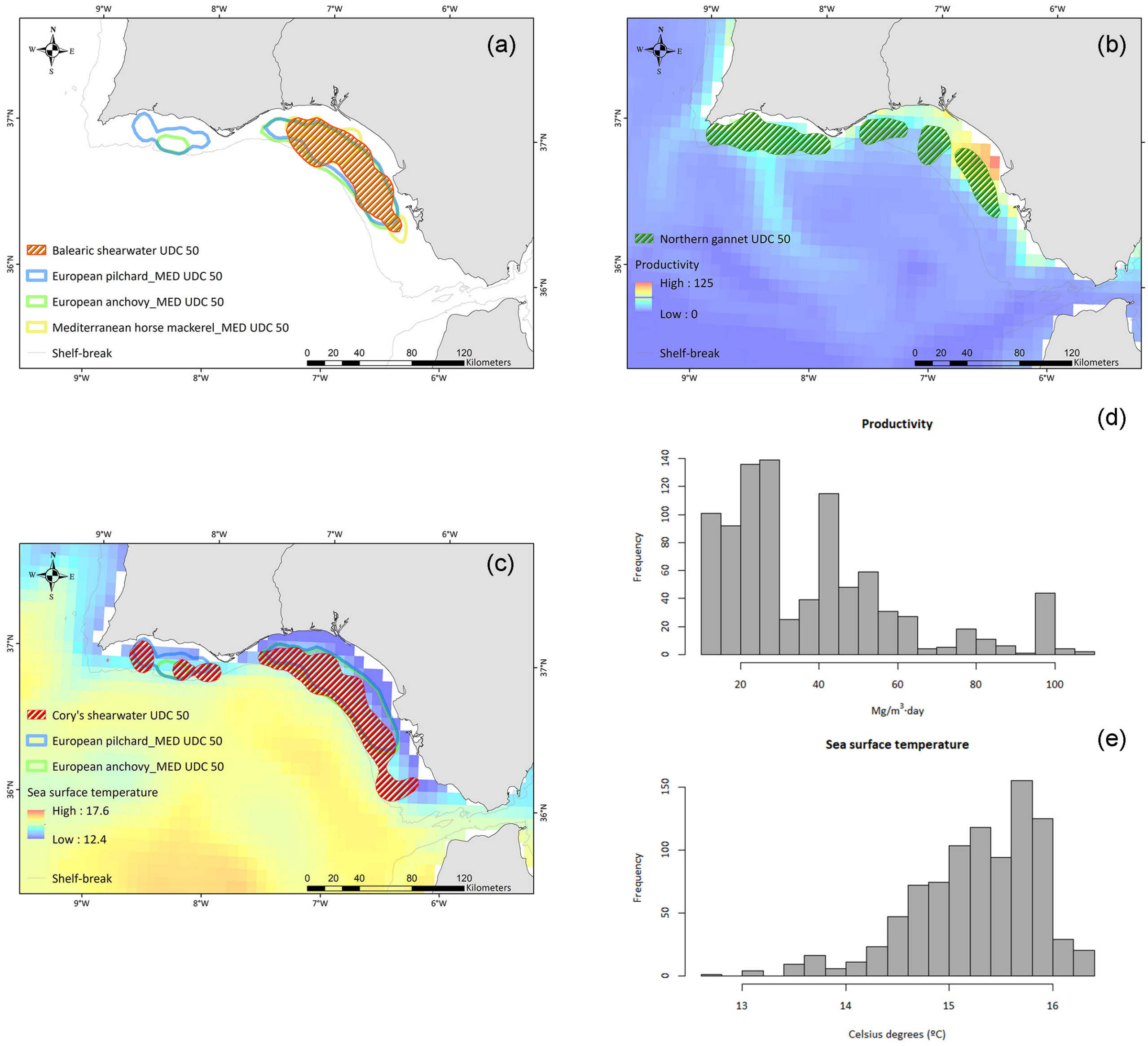

Figure 3. Key area (UDC 50) of the seabird and fish species considered and the forecast-model based on sea surface temperature (°C) and productivity (mg/m3·day) that show positive and relevant relationships in the models analysed within the period considered (2015–2019). (A) Balearic shearwater key area and its distribution better proxies: medium size of European pilchard, European anchovy and Mediterranean horse mackerel. (B) Northern gannet key area and its distribution better proxies: medium sized European pilchard and ocean. productivity. (C) Cory's shearwater key area and its distribution better proxies: medium size European pilchard, European anchovy and sea surface temperature. (D) Frequency distribution of productivity values on the seabird unit surveys (sampled area). (E) Frequency distribution of sea surface temperature values on the seabird unit surveys (sampled area).

Downloaded from https://academic.oup.com/icesjms/advance-article/doi/10.1093/icesjms/fsab256/6479775 by guest on 23 December 2021

Table 3. Best explanatory models obtained to study the distribution of the different species of seabirds considered in this study. Only models with significant variables have been included in the table, ordered by AIC (Akaike's Information Criterion) value. The best models have been shaded. GLzMM-PQL applied when spatial structure is applied in order to minimize autocorrelation bias. ANE: European anchovy *Engraulis encrasicolus*; PIL: European pilchard *Sardina pilchardus*; HMM: Mediterranean horse mackerel *Trachurus mediterraneus*; BOG: Bogue *Boops boops*. ∗_M means medium-sized fish. PROD indicates productivity in mg/m3·day; SST indicates sea surface temperature in °C. Moran I indicates the degree of data over-dispersion or aggregation; *p* Moran I indicates its statistical significance; Df.resid: Residuals degrees of freedom; AUC; area under the curve.

							Random effects							
Seabird's species		**Predictor**	**Estimate**	**Strd. Error**	**z value**	**Pr(>|z|)**	**Variance**	**Std. Dev**	**Moran I**	**p Moran I**	**AIC**	**Deviance**	**Df. Resid**	**AUC**
Balearic shearwater GzLMM-PQL	nullmodel										930.6	926.6		
	step#1	PIL_MED	0.522	0.145	3.608	<0.005	0.31	0.557	0.054	<0.005	914.2	908.2	904	0.691
	step#2	PIL_MED	0.466	0.146	3.184	<0.005	0.295	0.543	0.048	<0.005	902.9	894.9	903	0.703
		PROD	0.289	0.078	3.685	<0.005								
	step#3	PIL_MED	0.448	0.145	3.092	<0.005	0.259	0.509	0.046	<0.005	896.5	886.5	902	0.707
		PROD	0.29	0.079	3.692	<0.005								
		HMM_MED	0.356	0.175	2.031	0.042								
	step#3	PIL_MED	0.346	0.151	2.297	0.022	0.31	0.557	0.045	<0.005	900.3	890.3	902	0.705
		PROD_M	0.301	0.079	3.825	0								
		ANE_MED	0.177	0.084	2.117	0.034								
Northern gannet GzLMM-PQL	nullmodel										1110.4	1110.4		
	step#1	PROD	0.456	0.074	6.191	<0.005	0.459	0.678	0.037	<0.005	1076.5	1070.5	904	0.702
	step#2	PROD	0.436	0.074	5.873	<0.005	0.44	0.663	0.036	<0.005	1070.2	1062.2	903	0.713
		PIL_MED	0.381	0.167	2.287	0.022								
Cory's shearwater GzLMM	nullmodel										1191.7	1187.7	905	
	step#1	BOG_MED	− 0.322	0.126	− 2.568	0.01	0.34	0.583	0.014	0.024	1185.95	1162.59	904	0.648
	step#2	BOG_MED	− 0.313	0.124	− 2.529	0.011	0.339	0.582	0.009	0.097	1176.67	1150.77	903	0.657
		SST	0.206	0.07	2.953	0.003								
	step#3	BOG_MED	− 0.307	0.123	− 2.496	0.013	0.318	0.564	0.011	0.079	1171.94	1144.39	902	0.658
		SST	0.233	0.071	3.259	0.001								
		PIL_MED	0.474	0.239	1.98	0.048								
	step#3	BOG_MED	− 0.304	0.123	− 2.471	0.014	0.342	0.585	0.009	0.109	1171.75	1143.85	902	0.665
		SST	0.197	0.07	2.814	0.005								
		ANE_MED	0.265	0.124	2.133	0.033								

Downloaded from https://academic.oup.com/icesjms/advance-article/doi/10.1093/icesjms/fsab256/6479775 by guest on 23 December 2021

Table 4. Volume of Intersection Index (VI) as percentage overlap of the different seabird species' home range and fish distribution, with a relevant relationship in their best models. The column 'Relationship' indicates when the applied model shows a positive or negative relationship.

Seabird species	Fish species	VI 50%UDC	Relationship
Balearic shearwaters	European pilchard _MED	0.652	+
	Mediterranean horse mackerel_MED	0.472	+
	European anchovy _MED	0.710	+
Northern gannet	European pilchard _MED	0.626	+
Cory's shearwater	Bogue_MED	0.300	–
	European pilchard _MED	0.648	+
	European anchovy _MED	0.666	+

ranean horse mackerel and medium-sized anchovy abundance were also positively related to this bird species.

The Northern gannet models output indicated that their occurrence was positively correlated with a higher productivity, but also with the abundance of medium-sized sardines (Table 3, Figure 3B).

In the case of Cory's shearwater, the best models showed a moderate predictive performance, with an average AUC value of 0.656 ± 0.001. In any case, its distribution seemed to be inversely correlated with medium-sized bogue abundance, and positively with sea surface temperature. However, its occurrence models improved notably when the distribution of either medium-sized anchovies or sardines was included (Table 3, Figure 3A).

Predator and prey distribution overlapping

The VI analyses showed that the distributions of predators and their main prey species (based on the models outcome) overlapped highly, with positive relationships always exceeding 47% (Table 4). Balearic shearwater showed the best overlap index with medium-sized anchovy, sharing 71% of their home range distribution, and 65% with medium-sized sardine, whereas Northern gannet overlapped 62.6% with medium-sized sardine. Cory's shearwater showed an overlap index of its home range with medium-sized sardine of more than 64% (Table 4).

Discussion

Seabird distribution overlap with that of their prey

Marine top predators are known to concentrate their foraging areas in specific locations where prey are abundant (Green *et al.*, 2020). However, the task of revealing correlations between predator and prey is not an easy one (Fauchald, 2009).

According to the results obtained, the distribution of the main species of seabirds in the GoC correlated and overlapped with that of their main prey, i.e. pelagic fish. Most of the distribution models revealed that prey fish species were among the main predictors, and spatial analysis showed a high degree of overlap in the distribution of seabirds with their prey. This direct correlation between fish abundance and the presence of their predators is not such a general rule as might be expected. In fact, numerous studies have reported a frequent lack of correlation between the distributions of predator and prey (e.g. Logerwell and Hargreaves, 1996; Evans *et al.*, 2021).

Multiple environmental and behavioral processes that operate at different scales (Hunsicker *et al.*, 2011) influence interactions between predators and prey. Moreover, the spatial scale at which predators respond to prey is conditioned by species-specific foraging behaviour (White *et al.*, 2010). In our study, the relationships are not equally strong in all species. For Balearic shearwater, models produced a reasonably good fit that was linked to the distribution of medium-sized sardines and Mediterranean horse mackerel, as well as primary productivity. Moreover, its spatial distribution tightly overlapped with that of medium-sized anchovies. Balearic shearwaters in the GoC concentrate in shallow areas of the continental shelf (de la Cruz *et al.*, 2021), in an area of enhanced productivity due to the effect of the nearby Guadalquivir River (Ruiz *et al.*, 2017) where potential prey (cupleids) also tend to aggregate. Such shallow waters near the coastline have the potential to concentrate predators and prey on the shelf, which would lead to higher co-occurrence (Yen *et al.*, 2004). Balearic shearwaters are known to have a restricted range of movement when foraging (ca. 200 km; Louzao *et al.*, 2011), they undertake their movements relatively close to the coast (Mateos *et al.*, 2010) and other authors have identified the GoC as Important Atlantic Areas for the species during its non-breeding period (Pérez-Roda *et al.*, 2017). Therefore, the scale of our study (280 linear km between Trafalgar and Cape Saint Vincent) adequately covered their range of movements when foraging in our area.

The Northern gannet showed reasonable correlation and spatial overlap with medium-sized sardines. This species can feed on a wide range of prey and is known for its dietary flexibility and adaptable foraging behavior (Pettex *et al.*, 2012). It should also be noted that a large number of gannets, the majority immature birds, are found in our study area in the summer months, far-away from their breeding colonies. These immatures gannets have been shown to have a much wider foraging distribution, lower foraging site fidelity and lower foraging efficiency than breeding adults (Grecian *et al.*, 2018).

Cory's shearwater distribution models did not produce sufficient discriminant power to reveal consistent relationships. This is the most abundant seabird species in GoC and it can be seen practically anywhere in the study area, concentrating to feed in large numbers during their migratory periods (pers. obs.). Cory's shearwaters are typical gliding seabirds with a wide foraging range (circa 500 km; Navarro *et al.*, 2009). In addition, during the summer, both *Calonectris* species (i.e. Cory's shearwater (*C. borealis)* and the Mediterranean Scopoli's shearwater *C. diomedea*, which are difficult to distinguish at a distance), coincide in the GoC (pers. obs.) and this co-occurrence may represent an additional difficulty, since they have been shown to differ in foraging strategies (Navarro *et al.*, 2009).

Our results have also revealed both prey and size selectivity at regional scales for some species**.** Medium-sized (11–20 cm) sardines, Mediterranean horse mackerel and anchovies were the best predictors of distribution of Balearic shearwaters and Northern gannets,

Downloaded from https://academic.oup.com/icesjms/advance-article/doi/10.1093/icesjms/fsab256/6479775 by guest on 23 December 2021

showing high spatial overlap. These seabirds may capture larger individuals of fusiform fish if they are easier to capture or nutritionally profitable, as has been demonstrated in discard experiments (Arcos, 2001). However, in natural conditions, larger-size prey may require more time to be captured and swallowed (Cansse *et al.*, 2020), which would reduce efficiency and profitability. Sardines and anchovies have been documented as the main food source for Balearic shearwater in the Mediterranean Sea (Arcos and Oro, 2002), and the medium-sized cohort of this species represents the most abundant and widely available resource in the GoC, according to the acoustic evaluation results. Therefore, the association of seabirds with these species likely represents maximum gains for minimum costs whilst foraging.

Although our study reveals consistent spatial relationships between seabird species and their main prey at the regional level, the ability of the models to explain variability in distribution is limited. Here, it should be noted that prey accessibility may be a more reliable predictor of predators' distributions than prey abundance itself (Sydeman *et al.*, 2017). For flying predators such as seabirds, prey accessibility is constrained by depth distribution, depending on the diving capacity of the predator (Fauchald, 2009; Boyd *et al.*, 2017). Although seabirds can generally dive to a considerable depth, they mostly exploit prey that is available at relatively close to the surface (Chimienti *et al.*, 2017). In our study, the fish abundance data analysed integrated fish density values throughout the entire water column and therefore, no information on fish vertical distribution was considered. In the GoC, seabirds and their prey tend to concentrate in certain shallow areas of the continental shelf (De la Cruz et al. 2021)), where the aggregation of a large biomass of prey translates to high prey availability.

The occurrence of alternative food sources, such as that provided by the fisheries through discard, might modify the natural way in which seabirds explore the seascape whilst searching for prey (Bartumeus *et al.*, 2010), potentially masking the relationship between seabirds and their natural prey. Discarding is a common practice in the multispecies trawl fleet in the GoC, with an average estimate of about 3500 T discarded annually (Gamaza-Márquez *et al.*, 2020). Moreover, all the seabird species considered in this study have been documented attending trawlers in some parts of their range (Arcos and Oro, 2002; Martínez-Abraín *et al.*, 2002; Depestele *et al.*, 2016). The use of discard by seabirds might be limiting the ability of our models to explain the distribution of some of these species. However, trawl fishery in this area targets a wide range of demersal species. Therefore, the relationship with mid-size pelagic fish (such as clupeids) is unlikely to be connected to fishery discards, as these species are mostly targeted by purse seiners, which hardly produce discards in the area.

The role of environmental variables in predicting seabird distribution

In our study, environmental parameters related to primary productivity have showed poorer predictive capacity than prey variables, contrasting with previous evidence. Primary productivity has been postulated as one of the main environmental drivers associated with macro-scale distribution of marine predators (Alves *et al.*, 2018; Kane *et al.*, 2020). Thus, several studies using contemporary data on the concentration of chlorophyll-*a* as a proxy of primary productivity have revealed positive relationships between the distribution of seabirds species and highly productive areas (Louzao *et al.*, 2012; Arroyo *et al.*, 2020). However, in areas with narrow-shelves, such as the GoC, primary productivity is usually concentrated along the coastline, with upwelling and riverine input as the cause for the constant high concentrations of chlorophyll-*a* along the coastal fringe throughout the year (Navarro and Ruiz, 2006). In a recent study, we failed to find a relationship in the distribution of the Balearic shearwater with contemporary values of chlorophyll-a concentration in the GoC (de la Cruz *et al.*, 2021). However, oceanographic forecast models based on the integration of primary productivity values throughout the whole study period have revealed positive relationships between some seabird species and areas of persistent high primary productivity in our region. Predictability of oceanographic features in time and space is known to strongly influence the selection of foraging areas by seabirds, in such a way that they respond to favorable conditions that persist over time rather than to contemporary but more ephemeral ones (Scales *et al.*, 2014). Therefore, some migratory seabirds may be attracted to previously productive foraging sites that do not necessarily provide favorable foraging opportunities on every visit (Regular *et al.*, 2013). In this sense, our study supports the notion that forecast models for oceanographic parameters that integrate variability throughout a specific time period may be better at predicting predator distribution than contemporary measurements of these parameters, particularly when dealing with dynamic marine environments where variable factors act at different time scales (Franco *et al.*, 2020).

The collinearity analyses did not show any correlation between the distribution of any of the fish species with any of the environmental parameters considered (Table S2). This finding supports that, in dynamic marine ecosystems, spatio-temporal decoupling of translation processes across different trophic links may break up these spatial relationships (de la Cruz *et al.*, 2021).

Due to the limited size of the study area at a regional scale and the wide distribution of the species studied, the models show a moderate-reasonable prediction capacity, although not excellent. However, the general results show how the distribution and abundance of prey correlate better with the distribution of predators than the oceanographic variables tested.

Since the main question addressed in this study is limited to a particular region and season, it would be interesting to test whether these results translate to larger areas and longer periods.

Effect of management and conservation strategies on fishing grounds

Unraveling when and where species are expected to be found and what specific drivers will determine their occurrence is essential in order to gain a real understanding of the functioning of a particular ecosystem. This study has shown the existence of consistent correlations and distribution range overlaps between the most abundant species of seabirds in the GoC and their prey at a habitat-scale (10–100km). Although this may seem an obvious statement, many previous studies failed to disentangle these relationships (Torres *et al.*, 2008). For this reason, incorporating food resource distribution to predictive models should notably improve their prediction capacity (Kane *et al.*, 2020).

This finding is particularly relevant when applied to critically endangered species, such as the Balearic shearwater. The GoC is a key foraging area for this species during the post-breeding period (Arroyo *et al.*, 2020). Although the distribution of this species has been described in terms of environmental parameters related to primary

Downloaded from https://academic.oup.com/icesjms/advance-article/doi/10.1093/icesjms/fsab256/6479775 by guest on 23 December 2021

productivity in other areas of its range (Louzao *et al.*, 2012), its occurrence in the GoC has been revealed to be associated with the presence of shoals of mid-sized pelagic fish.

Our study has revealed that medium-sized pelagic fish such as sardines, anchovies and Mediterranean horse mackerel are the main prey of fish-eating seabirds in the GoC. However, fish stocks are currently suffering due to highly intense exploitation and biomass is alarmingly below biologically viable thresholds (FAO, 2020). In our study area, sardine catches have radically decreased over the last 40 years and the current assessment of the sardine stock is close to the endangered threshold (ICES, 2020a). Similarly, European anchovy stock in the GoC (southern zone of the 9th division ICES) has shown a negative trend in the last decade (ICES, 2020b). Recent predictive models for the GoC show that the current management system that establishes the fixed total allowable catch (TAC) of pelagic fish puts the sustainability of these fisheries at risk (Ruiz *et al.*, 2017). The close association in distribution of the seabirds we studied and their prey further reinforces the notion that a decrease in pelagic fish populations in our study area can be expected to have a negative impact at higher trophic levels, which may jeopardize populations or even the survival of species that depend on this resource.

Data Availability Statement

The data underlying this article will be shared on reasonable request to the corresponding author.

Supplementary Data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Conflicts of interest

The authors declare no conflicts of interest.

Acknowledgments

We are especially grateful to the Spanish Institute of Oceanography for their valuable collaboration whilst onboard their oceanographic vessels and to all the birdwatchers that have participated in seabird counts throughout these years. This research was partially supported by the Ministry for Ecological Transition and Demographic Challenge, through the MEGAN project (Ref. CTM2013-49048-C2-1-R) and the ECOFISH project, with the collaboration of the Biodiversity Foundation, the Ministry for Ecological Transition and Demographic Challenge, through the Pleamar Program, co-financed by the FEMP.

Thanks to the University of Cadiz and the Coastal Wetland Conservation Research Team for their help with logistics. Thanks also to José Luis Oviedo Pro for his valuable comments and suggestions, and to Chris Mills and Keith Bensusan for helping to improve the English version of this manuscript.

References

Akaike, H. 1973. Information theory and the maximum likelihood principle. *In* Second International Symposium on Information Theory, pp. 267–281. Ed. by Petrov, B. N., and Csaki, B. F.

Alves, F., Alessandrini, A., Servidio, A., Mendonça, A. S., Hartman, K. L., Prieto, R., Berrow, S. *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: 269–284.

Arcos, J. M. 2001. Attendance to trawlers and consumption of discards by seabirds in two NW Mediterranean areas (Barcelona and Ebro Delta) throughout the year. Universitat de Barcelona. 125 pp.

Arcos, J. M., and Oro, D. 2002. Significance of fisheries discards for a threatened Mediterranean seabird, the Balearic shearwater Puffinus mauretanicus. Marine Ecology Progress Series, 239: 209–220.

Arroyo, G. M., De la Cruz, A., and 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.

Bartumeus, F., Giuggioli, L., Louzao, M., Bretagnolle, V., Oro, D., and Levin, S. A. 2010. Fishery Discards Impact on Seabird Movement Patterns at Regional Scales. Current Biology 20: 215–222.

Bates, D., Mächler, M., Bolker, B., and Walker, S. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67: 1–51.

Boyd, C., Grünbaum, D., Hunt, G., Punt, A. E., Weimerskirch, H., and Bertrand, S. 2017. Effects of variation in the abundance and distribution of prey on the foraging success of central place foragers. Journal of Applied Ecology, 54: 1362–1372.

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L., and Thomas, L. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, Oxford. 432 pp.

Burnham, K., and Anderson, D. 2004. Model Selection and Multimodel Inference. Springer New York, New York, NY. 514 pp.

Calenge, C. 2006. The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. Ecological Modelling, 197: 516–519.

Canonico, G., Buttigieg, P. L., Montes, E., Muller-Karger, F. E., Stepien, C., Wright, D., Benson, A. *et al.* 2019. Global observational needs and resources for marine biodiversity. Frontiers in Marine Science, 6: 1–20.

Cansse, T., Fauchet, L., Wells, M., and Arnould, J. 2020. Factors influencing prey capture success and profitability in Australasian gannets (Morus serrator). Biology Open, 9: 1–9.

Chimienti, M., Cornulier, T., Owen, E., Bolton, M., Davies, I. M., Travis, J. M. J., and Scott, B. E. 2017. Taking movement data to new depths: Inferring prey availability and patch profitability from seabird foraging behavior. Ecology and Evolution, 7: 10252–10265.

de la Cruz, A., Ramos, F., Navarro, G., Cózar, A., Bécares, J., and Arroyo, G. M. 2021. Drivers for spatial modelling of a critically endangered seabird on a dynamic ocean area: Balearic shearwaters are non-vegetarian. Aquatic Conservation: Marine and Freshwater Ecosystems, 31: 1700–1714.

Demer, D. A., Berger, L., Bernasconi, M., Bethke, E., Boswell, K. M., Chu, D., Domokos, R. *et al.* 2015. Calibration of acoustic instruments. ICES Cooperative Research Report No. 326. 133 pp.

Depestele, J., Rochet, M.-J., Dorémus, G., Laffargue, P., and Stienen, E. W. M. 2016. Favorites and leftovers on the menu of scavenging seabirds: modelling spatiotemporal variation in discard consumption. Canadian Journal of Fisheries and Aquatic Sciences, 73: 1446–1459.

Doray, M., Boyra, G., and van der Kooij, J. 2021. ICES Survey Protocols – Manual for Acoustic Surveys Coordinated under the ICES Working Group on Acoustic and Egg Surveys for Small Pelagic Fish (WGACEGG). *In* ICES Techniques in Marine Environmental Sciences, 1st Editio, p. 100. Ed. by Doray, M., Boyra, G., and van der Kooij, J..

Dormann, C., McPherson, J., Araújo, M., Bivand, R., Bolliger, J., Carl, G., Davies, R. *et al.* 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: A review. Ecography, 30: 609–628.

Engler, R., Guisan, A., and Rechsteiner, L. 2004. An improved approach for predicting the distribution of rare and endangered species from

Downloaded from https://academic.oup.com/icesjms/advance-article/doi/10.1093/icesjms/fsab256/6479775 by guest on 23 December 2021

occurrence and pseudo-absence data. Journal of Applied Ecology, 41: 263–274.

Enstipp, M. R., Grémillet, D., and Jones, D. R. 2007. Investigating the functional link between prey abundance and seabird predatory performance. Marine Ecology Progress Series, 331: 267–279.

Evans, R., Lea, M., and Hindell, M. A. 2021. Predicting the distribution of foraging seabirds during a period of heightened environmental variability. Ecological Applications, 0: 1–20.

FAO. 2020. The State of World Fisheries and Aquaculture 2020. FAO. 200pp.

Fauchald, P., Erikstad, K. E., and Skarsfjord, H. 2000. Scale-dependent predator-prey interactions: The hierarchical spatial distribution of seabirds and prey. Ecology, 81: 773–783.

Fauchald, P., and Erikstad, K. E. 2002. Scale-dependent predator-prey interactions: The aggregative response of seabirds to prey under variable prey abundance and patchiness. Marine Ecology Progress Series, 231: 279–291.

Fauchald, P. 2009. Spatial interaction between seabirds and prey: Review and synthesis. Marine Ecology Progress Series, 391: 139–151.

Fieberg, J. 2014. Home range overlap indices implemented using kernel density estimators with plug-in smoothing parameters and Program R [Dataset]. Retrieved from the Data Repository for the University of Minnesota.

Franco, B. C., Combes, V., and González Carman, V. 2020. Subsurface Ocean Warming Hotspots and Potential Impacts on Marine Species: The Southwest South Atlantic Ocean Case Study. Frontiers in Marine Science, 7: 1–13.

Gamaza-Márquez, M. A., Pennino, M. G., Torres, M. A., Acosta, J. J., Erzini, K., and Sobrino, I. 2020. Discard practices in the gulf of Cadiz multispecies trawl fishery. Implications for the EU 'landing obligation'. Marine Policy, 118: 1–11.

García Lafuente, J., and Ruiz, J. 2007. The Gulf of Cádiz pelagic ecosystem: A review. Progress in Oceanography, 74: 228–251.

Grecian, W. J., Lane, J. V., Michelot, T., Wade, H. M., and Hamer, K. C. 2018. Understanding the ontogeny of foraging behaviour: insights from combining marine predator bio-logging with satellite-derived oceanography in hidden Markov models. Journal of The Royal Society Interface, 15: 1–9.

Green, D. B., Bestley, S., Trebilco, R., Corney, S. P., Lehodey, P., McMahon, C. R., Guinet, C. *et al.* 2020. Modelled mid-trophic pelagic prey fields improve understanding of marine predator foraging behaviour. Ecography, 43: 1014–1026.

Haug, F. D., Paiva, V. H., Werner, A. C., and Ramos, J. A. 2015. Foraging by experienced and inexperienced Cory's shearwater along a 3-year period of ameliorating foraging conditions. Marine Biology, 162: 649–660.

Hazen, E. L., Abrahms, B., Brodie, S., Carroll, G., Jacox, M. G., Savoca, M. S., Scales, K. L. *et al.* 2019. Marine top predators as climate and ecosystem sentinels. Frontiers in Ecology and the Environment, 17: 565–574.

Hijmans, R. J., and van Etten, J. 2012. raster: Geographic analysis and modeling with raster data.

Hunsicker, M. E., Ciannelli, L., Bailey, K. M., Buckel, J. A., Wilson White, J., Link, J. S., Essington, T. E. *et al.* 2011. Functional responses and scaling in predator-prey interactions of marine fishes: contemporary issues and emerging concepts. Ecology Letters, 14: 1288–1299.

ICES. 2020a. Sardine (Sardina pilchardus) in divisions 8.c and 9.a (Cantabrian Sea and Atlantic Iberian waters). *In* Report of the ICES Advisory Committee, 2020, pp. 1–8.

ICES. 2020b. Anchovy (Engraulis encrasicolus) in Division 9.a (Atlantic Iberian waters). *In* Report of the ICES Advisory Committee, 2020, pp. 1–7.

Kane, A., Pirotta, E., Wischnewski, S., Critchley, E., Bennison, A., Jessopp, M., and Quinn, J. 2020. Spatio-temporal patterns of foraging behaviour in a wide-ranging seabird reveal the role of primary productivity in locating prey. Marine Ecology Progress Series, 646: 175–188.

Kappes, M. A., Weimerskirch, H., Pinaud, D., and Le Corre, M. 2011. Variability of resource partitioning in sympatric tropical boobies. Marine Ecology Progress Series, 441: 281–294.

Logerwell, E. A., and Hargreaves, N. B. 1996. The distribution of sea birds relative to their fish prey off Vancouver Island: Opposing results at large and small spatial scales. Fisheries Oceanography, 5: 163–175.

Louzao, M., Navarro, J., Forero, M. G., Igual, J. M., Genovart, M., Hobson, K. A., and Oro, D. 2011. Exploiting the closest productive area: Geographical segregation of foraging grounds in a critically endangered seabird. Marine Ecology Progress Series, 429: 291–301.

Louzao, M., Delord, K., García, D., Boué, A., and Weimerskirch, H. 2012. Protecting Persistent Dynamic Oceanographic Features: Transboundary Conservation Efforts Are Needed for the Critically Endangered Balearic Shearwater. Plos One, 7: 1–12.

Maclennan, D. 2002. A consistent approach to definitions and symbols in fisheries acoustics. ICES Journal of Marine Science, 59: 365–369.

Martínez-Abraín, A., Maestre, R., and Oro, D. 2002. Demersal trawling waste as a food source for Western Mediterranean seabirds during the summer. ICES Journal of Marine Science, 59: 529–537.

Mateos, M., Arroyo, G. M., Rodríguez, A., Cuenca, D., and De la Cruz, A. 2010. Calibration of visually estimated distances to migrating seabirds with radar measurements. Journal of Field Ornithology, 81: 302–309.

Nakken, O., and Dommasnes, A. 1977. Acoustic estimates of the Barents Sea capelin stock 1971–1976. 1–10 pp.

Navarro, G., and 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: 1241–1260.

Navarro, J., Forero, M. G., González-Solís, J., Igual, J. M., Bécares, J., and Hobson, K. A. 2009. Foraging segregation between two closely related shearwaters breeding in sympatry. Biology Letters, 5: 545–548.

Paradis, E., Claude, J., and Strimmer, K. 2004. APE: Analyses of phylogenetics and evolution in R language. Bioinformatics, 20: 289–290.

Pérez-Roda, A., Delord, K., Boué, A., Arcos, J. M., García, D., Micol, T., Weimerskirch, H. *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: 285–293.

Pettex, E., Lorentsen, S.-H., Grémillet, D., Gimenez, O., Barrett, R. T., Pons, J.-B., Bohec, C. *et al.* 2012. Multi-scale foraging variability in Northern gannet (Morus bassanus) fuels potential foraging plasticity. Marine Biology, 159: 2743–2756.

Phillips, J. A., Banks, A. N., Bolton, M., Brereton, T., Cazenave, P., Gillies, N., Padget, O. *et al.* 2021. Consistent concentrations of critically endangered Balearic shearwaters in UK waters revealed by at-sea surveys. Ecology and Evolution, 11: 1544–1557.

Prieto, L., Navarro, G., Rodríguez-Gálvez, S., Huertas, I. E., Naranjo, J. M., and Ruiz, J. 2009. Oceanographic and meteorological forcing of the pelagic ecosystem on the Gulf of Cadiz shelf (SW Iberian Peninsula). Continental Shelf Research, 29: 2122–2137.

R Development Core Team. 2020. R: A language and environment for statistical computing. Viena, Austria.

Regular, P. M., Hedd, A., and Montevecchi, W. A. 2013. Must marine predators always follow scaling laws? Memory guides the foraging decisions of a pursuit-diving seabird. Animal Behaviour, 86: 545–552.

Reisinger, R. R., Raymond, B., Hindell, M. A., Bester, M. N., Crawford, R. J. M., Davies, D., de Bruyn, P. J. N. *et al.* 2018. Habitat modelling of tracking data from multiple marine predators identifies important areas in the Southern Indian Ocean. Diversity and Distributions, 24: 535–550.

Rose, G. A., and Leggett, W. C. 1990. The importance of scale to predator-prey spatial correlations: an example of Atlantic fishes. Ecology, 71: 33–43.

Downloaded from https://academic.oup.com/icesjms/advance-article/doi/10.1093/icesjms/fsab256/6479775 by guest on 23 December 2021

Ruiz, J., Rincón, M. M., Castilla, D., Ramos, F., and del Hoyo, J. J. G. 2017. Biological and economic vulnerabilities of fixed TACs in small pelagics: An analysis of the European anchovy (Engraulis encrasicolus) in the Gulf ofCádiz. Marine Policy, 78: 171–180.

Russell, D. J. F., Wanless, S., Collingham, Y. C., Anderson, B. J., Beale, C., Reid, J. B., Huntley, B. *et al.* 2015. Beyond climate envelopes: Bioclimate modelling accords with observed 25-year changes in seabird populations of the British Isles. Diversity and Distributions, 21: 211–222.

Russell, R. W., Hunt, G., Coyle, K. O., and Cooney, R. T. 1992. Foraging in a fractal environment: Spatial patterns in a marine predator-prey system. Landscape Ecology, 7: 195–209.

Sadykova, D., Scott, B. E., De Dominicis, M., Wakelin, S. L., Wolf, J., and Sadykov, A. 2020. Ecological costs of climate change on marine predator–prey population distributions by 2050. Ecology and Evolution, 10: 1069–1086.

Scales, K. L., Miller, P. I., Embling, C. B., Ingram, S. N., Pirotta, E., and Votier, S. C. 2014. Mesoscale fronts as foraging habitats: Composite front mapping reveals oceanographic drivers of habitat use for a pelagic seabird. Journal of the Royal Society Interface, 11: 1–9.

Seidel, K. 1992. Statistical properties and application of a new measure of joint space use for wildlife. University of Washington.

Simmonds, J. E., and Maclennan, D. N. 2005. Fisheries acoustics - Theory and practice. Blackwell Publishing, London.

Sydeman, W. J., Thompson, S. A., Anker-Nilssen, T., Arimitsu, M., Bennison, A., Bertrand, S., Boersch-Supan, P. *et al.* 2017. Best practices for assessing forage fish fisheries-seabird resource competition. Fisheries Research, 194: 209–221.

Tasker, M., Jones, P. H., Dixon, T., and Blake, B. F. 1984. Counting seabirds at sea from ships: A review of methods employed and a suggestion for a standardized aproach. The Auk, 101: 567–577.

Torres, L. G., Read, A. J., and Halpin, P. 2008. Fine-scale habitat modeling of a top marine predator: Do prey data improve predictive capacity? Ecological Applications, 18: 1702–1717.

Tremblay, Y., Bertrand, S., Henry, R. W., Kappes, M. A., Costa, D. P., and Shaffer, S. A. 2009. Analytical approaches to investigating seabird-environment interactions: A review. Marine Ecology Progress Series, 391: 153–163.

Tucker, S., Hipfner, J. M., and Trudel, M. 2016. Size- and condition-dependent predation: A seabird disproportionately targets substandard individual juvenile salmon. Ecology, 97: 461–471.

Wand, M., and Ripley, B. 2015. KernSmooth. Functions for Kernel Smoothing Supporting Wand & Jones (1995). R package version.

White, J., Samhouri, J., Stier, A., Wormald, C., Hamilton, S., and Sandin, S. 2010. Synthesizing mechanisms of density dependence in reef fishes: behavior, habitat configuration, and observation scale. Ecology: 100319061621033.

Worm, B., Sandow, M., Oschlies, A., Lotze, H. K., and Myers, R. A. 2005. Ecology: Global patterns of predator diversity in the open oceans. Science:309, 1365–1369.

Yen, P. P. W., Sydeman, W. J., and Hyrenbach, K. D. 2004. Marine bird and cetacean associations with bathymetric habitats and shallow-water topographies: implications for trophic transfer and conservation. Journal of Marine Systems, 50: 79–99.

Zuur, A., Ieno, E., Walker, N., Saveliev, A., and Smith, G. 2009. Mixed effects models and extensions in ecology with R, Springer, New York.

Handling Editor: Howard Browman

Downloaded from https://academic.oup.com/icesjms/advance-article/doi/10.1093/icesjms/fsab256/6479775 by guest on 23 December 2021