

Niche segregation mechanisms in marine apex predators inhabiting dynamic environments

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Abstract

Aim: Understanding the mechanisms that allow the coexistence of species is key to preserve full ecosystem functioning. In dynamic environments, the study of ecological niches faces the complexity associated to the three dimensionality of the habitat and requires information that reflects such heterogeneity. Within this context, this study intends to identify the segregation mechanisms behind the co-occurrence of five phylogenetically related pelagic birds by applying a functional perspective based on seabirds' vertical ranges and prey availability features such as depth and body size.

Location: Bay of Biscay.

Methods: Based on the hypothesis that niche differentiation may occur in any of the three dimensions of the marine environment, we (a) identified the biologically meaningful vertical range affecting seabird species, (b) modelled their environmental and trophic niches, (c) estimated an environmental and trophic overlap index for each pairwise species, and (d) developed a conceptual framework with the most plausible segregation hypotheses.

Results: The application of the conceptual framework revealed that in this particular area, pelagic birds coexist through environmental and trophic niche partitioning and potentially through vertical segregation, based on the different biologically meaningful vertical ranges we identified for each species. Indeed, some species responded to prey and oceanographic conditions on the surface (10 m), while others responded to the conditions on deeper waters (above the depth of maximum temperature gradient). These different responses could be interpreted as an additional mechanism to reduce competition, although seabirds diving records would be needed to contrast this hypothesis.

Main conclusions: Niche differentiation was found to be primarily driven by trophic and environmental niche partitioning, although species were also influenced by conditions on the vertical dimension. Considering all the dimensions of the niche is essential to fully understand how diving seabirds coexist in dynamic systems and provides insights on species' 3D niches that may help advance into their management.

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KEYWORDS

3D environments, environmental niche, niche differentiation, pelagic birds, prey availability, trophic niche, vertical segregation

1 | INTRODUCTION

The niche concept has been a major theme in ecology, mostly influenced by the definition stated by Hutchinson (1957), who described it as a “n-dimensional hypervolume of environmental states within which a species is able to survive.” However, even the classical definition may create a dichotomy that affects the way in which the entire concept is approached (Chase & Leibold, 2003). In fact, much of the confusion surrounding the term results because no distinction is made between the responses of organisms to their environment and the effect of organisms on their environment (Chase & Leibold, 2003; Peterson et al., 2011). Under such circumstances, two different niches should be discerned: the Grinnellian and the Eltonian niches (Devictor et al., 2010; Soberon, 2007). The Grinnellian niche (Grinnell, 1917) describes the response of the species to a given set of non-interactive variables, while the Eltonian niche (Elton, 1927) describes the biotic interactions and resource–consumer dynamics through trophic variables. Despite the attempts at synthesis and unification (Chase & Leibold, 2003), the complementary concepts of the environmental niche (*sensu* Grinnell, 1917) and trophic niche (*sensu* Elton, 1927) serve as basis to assess the ecological and biogeographical dis-/similarities of species and contribute to the understanding of their distribution and diversity (Broennimann et al., 2011; Soberon, 2007). Indeed, some of the main segregation mechanisms driving species coexistence are known to occur either by means of trophic (MacArthur, 1968; Tilman, 1982) or environmental niche partitioning (Chesson, 2000). The split up of the niche provides, therefore, an excellent opportunity to advance in the identification of segregation mechanisms, which is specially poorly understood in complex and dynamic environments such as marine ecosystems.

The study of environmental niches in marine ecosystems, for instance, faces the difficulties inherent in understanding the three dimensionality of the habitat, where physical and ecological processes occurring below the surface layer, such as subsurface thermal structure or subsurface primary production, have been found to be highly important (Kuhn, 2010; Scott et al., 2013). On the other hand, trophic niche analyses require the consideration of complex predator–prey interactions, that result from the trade-off between the energetic cost of seeking prey and the foraging profitability obtained from successful events (MacArthur & Pianka, 1966; Pyke, 1984). Traditionally, predator–prey interactions have been studied using a predominantly taxonomic approach (species–species perspective), although functional characteristics related to the species' role, such as biological traits, have been proved to affect predator–prey interactions (Spitz et al., 2014). In 3D dynamic

environments, addressing community ecology from functional traits perspective may be specially relevant, since prey depth (i.e. the depth at which prey is available), together with body size or energy density, can be key to understand predators' prey preferences (Boyd et al., 2017; Lambert et al., 2018; Spitz et al., 2018; Waggitt et al., 2018). Similarly, predators' physiology and morphology may also play an essential role in the foraging process by defining the metabolic cost of living or the diving capabilities of species (Spitz et al., 2012, 2014).

Among marine top predators exploiting dynamic environments, seabirds are considered one of the most diverse taxa, with several evidences indicating niche differentiation among its members (Phillips et al., 2011). Most studies, however, have been conducted during the breeding season, when the competition for resources is particularly intense and segregation mechanisms are more likely to arise (Mancini et al., 2014; Navarro et al., 2013). As a result, limited knowledge exists about the potential segregation mechanisms outside the breeding season (Thiebot et al., 2012), despite being the period in which animals migrate or disperse to favourable foraging areas, aggregating in highly productive regions and coinciding with a high number of migratory species (Grecian et al., 2016). Investigating and explaining niche segregation outside the breeding season could help complement management strategies involving all life stages, and thus, bigger efforts should be made in studying the non-breeding areas of seabirds.

The Bay of Biscay (BoB hereafter) represents such an example, as numerous seabird species stopover there during their feeding migrations attracted by a highly diverse and abundant community of small pelagic fishes (Astarloa et al., 2019). It conforms, therefore, an exceptional biogeographical area to test segregation hypothesis and provides an incomparable opportunity to understand the mechanisms that allow the coexistence of protected species. In fact, many pelagic birds visiting the BoB are protected under different international agreements, such as the Bird Directive (Council Directive 2009/147/EC) and the Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR Convention), among others. Despite the conservation efforts, seabirds are still one of the most threatened groups, comprising rapid declining populations and critically endangered species (Croxall et al., 2012; Dias et al., 2019). Effective conservation and management measures require the identification of variables shaping species' niches (García-Barón et al., 2019, 2020) and that is why, understanding the role that prey and environment play in species distribution turns so necessary. Within that context, the present study focused on disentangling the assembly rules of pelagic birds by addressing the following research questions:

1. Does niche segregation occur among wide-ranging species during their feeding migrations?
2. Does this niche segregation occur in the environmental niche or in the trophic niche?
3. Do prey and environmental conditions on the vertical dimension influence the trophic and environmental niche of species?

To answer these questions, we modelled species environmental and trophic niches and developed a conceptual framework with the most plausible segregation hypotheses (Figure 1). This way, we aim to contribute to the understanding of protected and endangered species coexistence and provide insights on the 3D niches of species that may help advance into their management and conservation.

2 | METHODS

2.1 | Data collection: integrated monitoring schemes

Data on pelagic birds, prey species and environmental predictors were collected through the multidisciplinary oceanographic survey JUVENA, which takes place every September in the BoB by means of two different research vessels, *Ramon Margalef* and *Enma Bardan* (R/V RM and R/V EB, hereafter). Since 2013, different components of the pelagic environment (i.e. plankton, fish, megafauna, physical oceanography, marine litter) are monitored, although its main aim is to assess the population of juvenile European anchovy *Engraulis encrasicolus*. The sampling strategy is based on parallel transects perpendicularly arranged to the coast and spaced at 15 nautical miles, whose offshore and along-coast extension changes from year to year depending on the distribution of the European anchovy (see details in Boyra et al., 2013; Louzao et al., 2019). A schematic workflow of the entire analytical process is described in Figure 2.

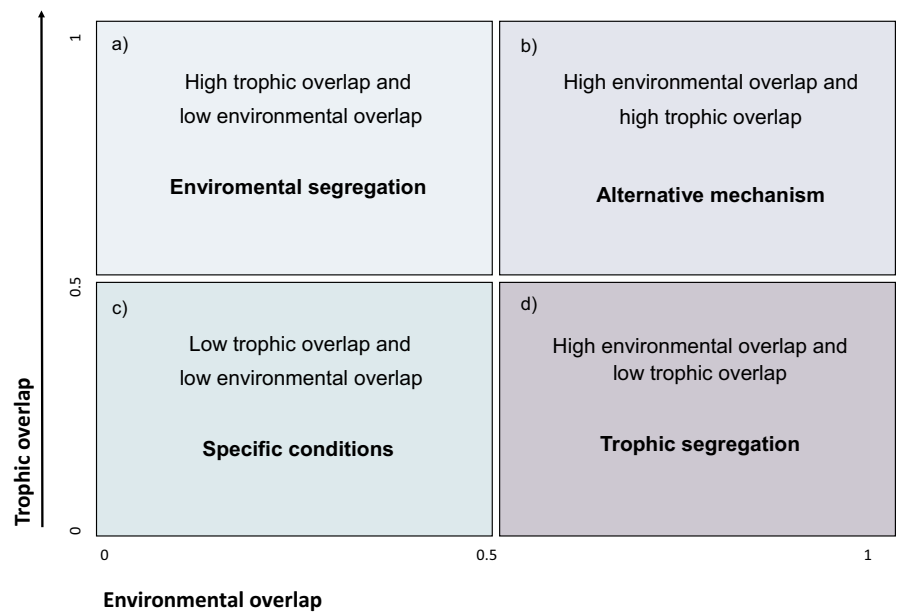
2.1.1 | Pelagic birds

Five phylogenetically related shearwaters were selected based on their conservation status and their high diversity and abundant records: the Cory's shearwater *Calonectris borealis*, the great shearwater *Ardenna gravis*, the near threatened sooty shearwater *A. grisea*, the Manx shearwater *Puffinus puffinus* and the critically endangered Balearic shearwater *P. mauretanicus*. Sightings of these species were recorded aboard R/V RM by a team of three experienced observers (2 at a time) that followed the line-transect methodology (Buckland et al., 2001). This methodology is conducted within the distance sampling framework to estimate seabirds' densities and requires the collection in the field of at least the radial distance of each observation (Heinemann, 1981), the angle of the cluster sighting with respect to the trackline (estimated with an angle meter), time of observation, species composition and group size. In addition, the behaviour of observed species (e.g. attraction) as well as environmental descriptors affecting the detectability of species (e.g. Beaufort sea-state, visibility, glare intensity or observation conditions) were collected in order to account for response bias (when animals react to the presence of the platform) and perception bias (when observer miss animals because their visibility is compromised), respectively. Sampling effort was performed during daytime, at a constant speed and under Beaufort sea-state conditions ≤ 6 and it was geographically located every minute with the vessel GPS (Figure 3).

2.1.2 | Pelagic prey

Acoustically based biomasses were included in the analysis only for those fish species that were considered, based on bibliography, part of the diet of the seabirds (see Appendix S1: Table S1.1): European anchovy (juveniles and adults were treated separately due to their different spatial distribution), European sardine *Sardina pilchardus*, European sprat *Sprattus sprattus*, Atlantic mackerel *Scomber*

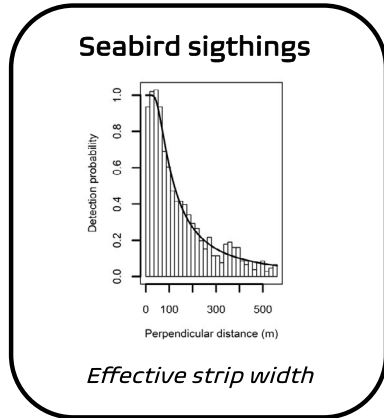
FIGURE 1 Conceptual framework displaying the plausible segregation hypotheses that arise from the pairwise comparison of environmental and trophic overlap. Main hypotheses comprise (a) environmental segregation, (b) alternative mechanisms, (c) specific conditions and (d) trophic segregation



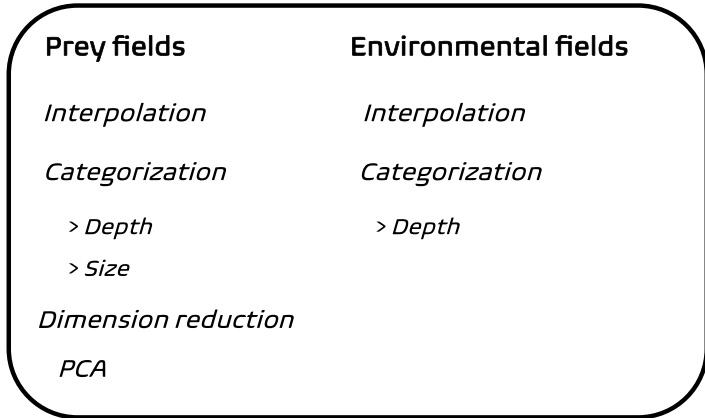
Step 1: Data collection



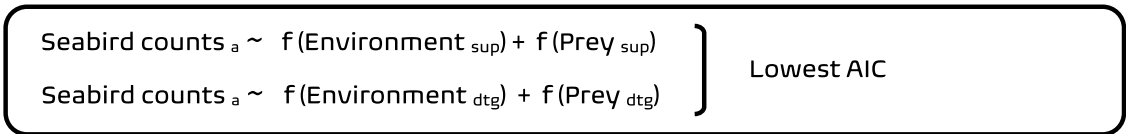
Step 2: Detection functions



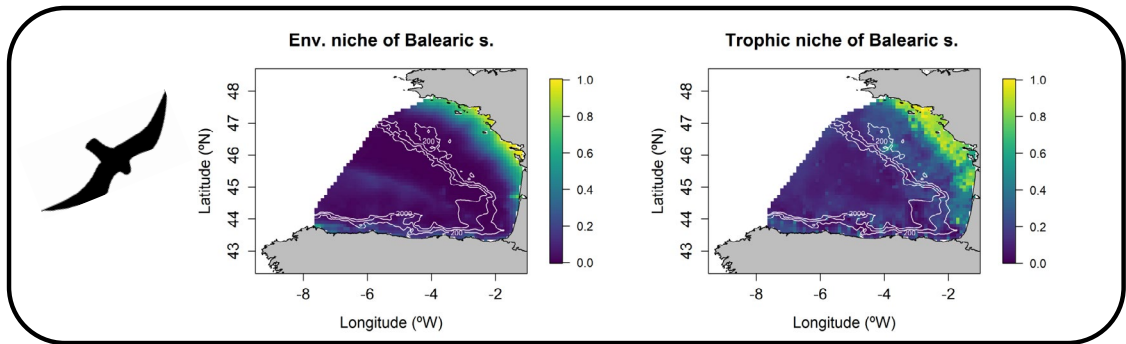
Step 3: Processing of explanatory variables



Step 4: Biologically meaningful vertical range (BMVR) selection



Step 5: Trophic and environmental niche modelling at each species BMVR



Step 6: High abundance areas and niche overlap between pair-wise species*

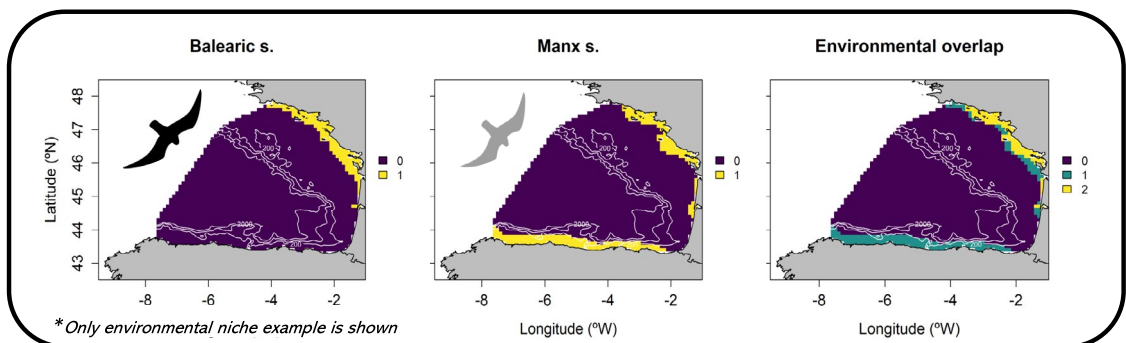


FIGURE 2 Schematic overview of the main steps conducted to identify segregation mechanisms in pelagic apex predators

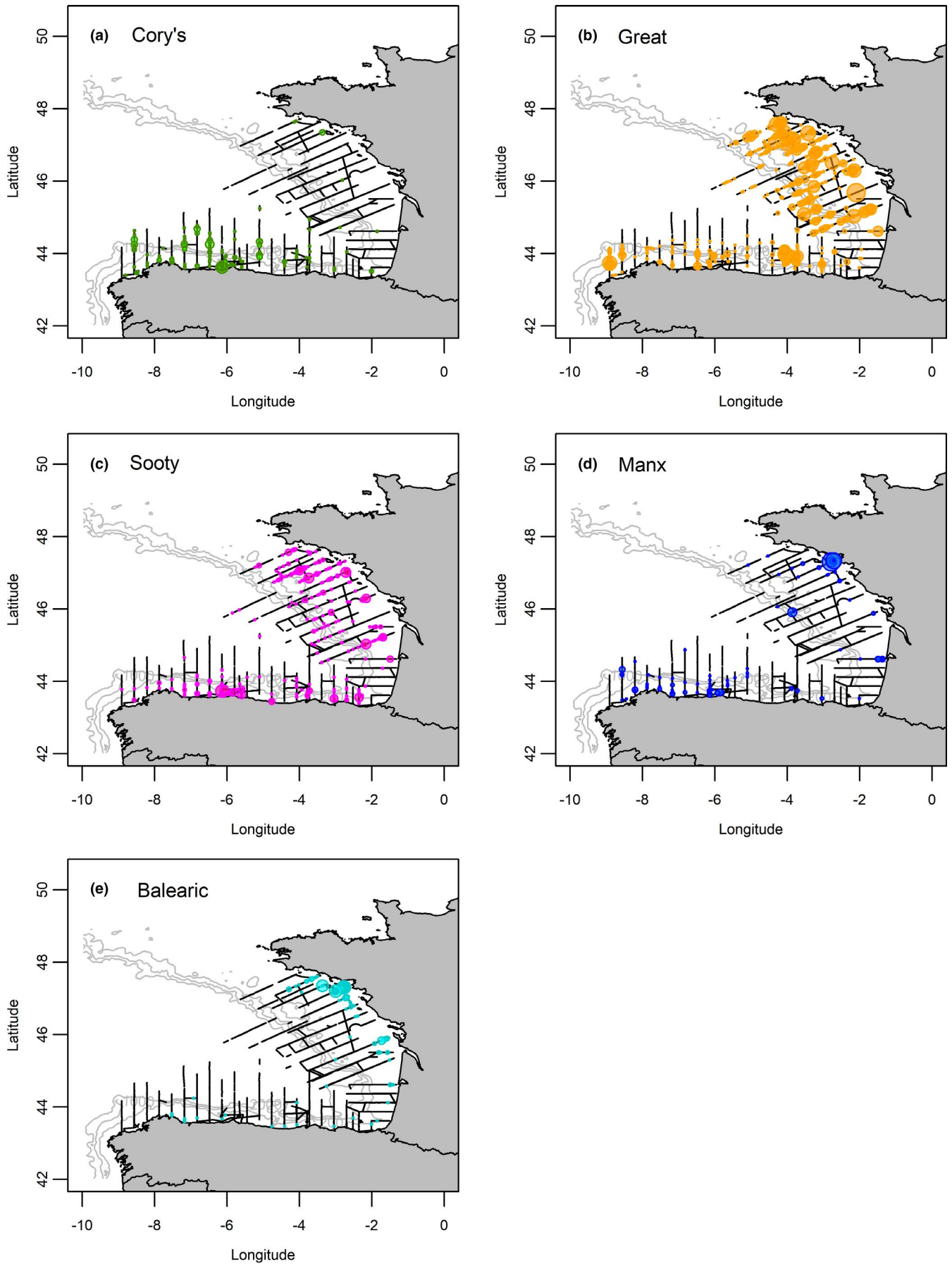


FIGURE 3 Overview of the study area accompanied by the sightings of the five pelagic birds (a–e). Circle sizes are proportional to group size. Isobaths of 200 m, 1,000 m and 2,000 m are indicated

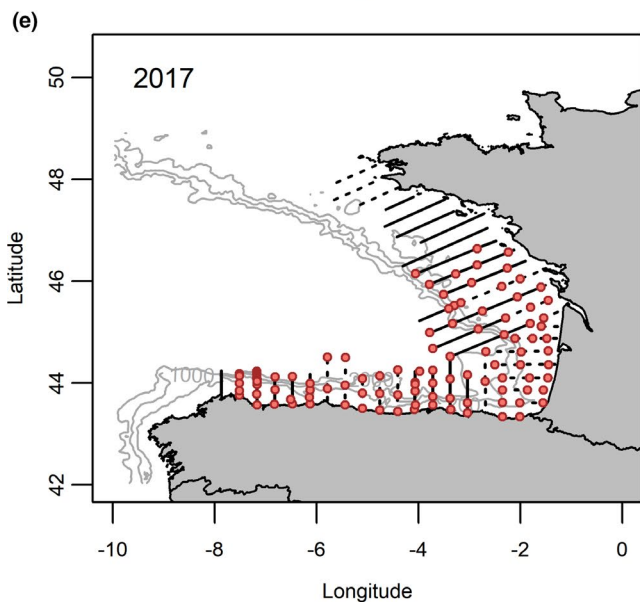
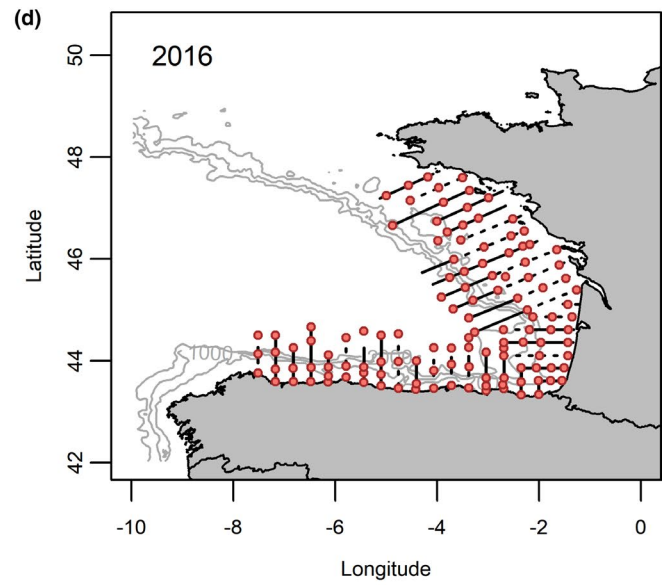
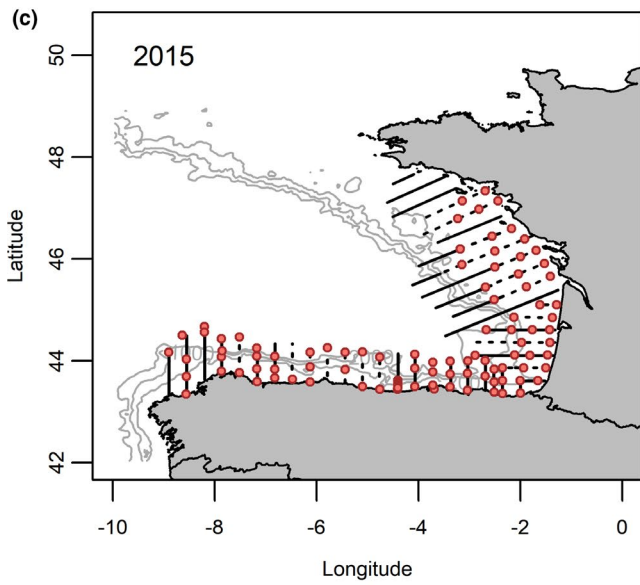
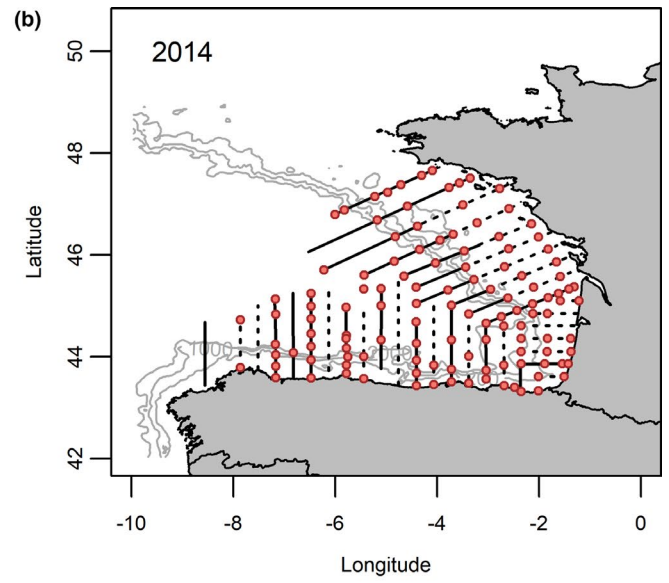
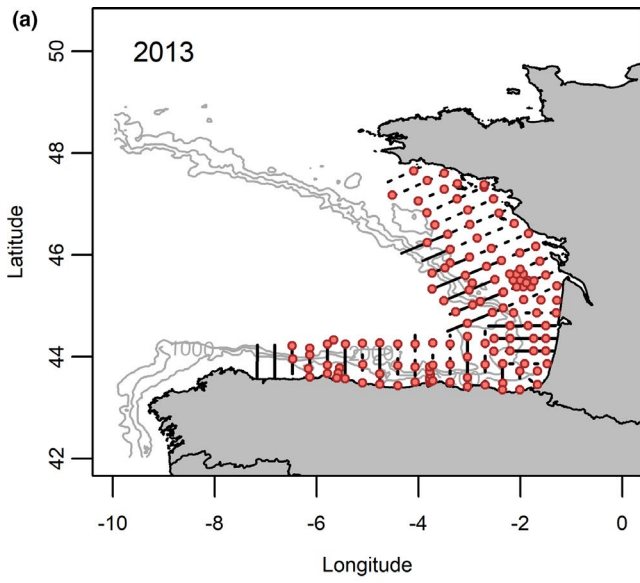


FIGURE 4 Overview of the annual acoustic sampling accompanied by the CTD casts collected along the transects. The dash lines correspond to R/V EB, while the solid lines refer to R/V RM, which usually cover the inner and the outer section of the transects, respectively. The red circles correspond to the locations of the CTD casts. Isobaths of 200 m, 1,000 m and 2,000 m are indicated

TABLE 1 Summary of the environmental variables used in the study

Variables	Acronym	Type	Dimension
Temperature (°C)	T	Dynamic	3D
Salinity (psu)	SAL	Dynamic	3D
Geostrophic velocity (m/s)	GV	Dynamic	3D
Depth of maximum temperature gradient (m)	DTG	Dynamic	2D
Maximum temperature gradient (°C/m)	MTG	Dynamic	2D
Sea surface temperature gradient	SSTG	Dynamic	2D
Depth (m)	DEP	Static	2D
Depth gradient	DEPG	Static	2D
Distance to coast (km)	DCO	Static	2D
Distance to shelf break (km)	DSHEL	Static	2D

Note: Dynamic variables were estimated from oceanographic data collected on board, whereas static variables were extracted from NOAA (ETOPO1 database).

scombrus, Atlantic horse mackerel *Trachurus trachurus* and Mueller's pearlside *Maurolicus muelleri*. Acoustic data were collected on RM and EB research vessels (Figure 4) by means of Simrad EK60 split-beam echosounders (Kongsberg Simrad AS, Kongsberg, Norway), that sampled the water column during daytime from the surface (5 m) to depths that ranged from 200 to 400 m depending on the year (Appendix S1: Table S1.2). The collected acoustic data by both vessels were processed in the positive strata by layer echo integration using an ESDU (Echo integration Sampling Distance Unit) of 0.1 nmi and categorized into ten layers of varying depths according to the year (Appendix S1: Table S1.2). In parallel, mid-water trawls were performed to assign the eco-traces to species (identification purposes) and to obtain the necessary biological data (length, weight and age) to convert the acoustic back-scattered energy to fish abundance. Finally, abundance in number of individuals was multiplied by the mean weight, obtaining biomass estimates (tonnes) per age, length and depth interval (Boyra et al., 2013).

2.1.3 | Oceanographic and geographic environment

Oceanographic data were collected in both vessels using a CTD profiler. For each transect, a minimum of three profiles were performed

(coastal, continental shelf and oceanic waters) measuring the water column from the surface (10 m, first available data) up to 200 m depth (Figure 4). Temperature (T), salinity (SAL) and density data were directly inferred from CTD casts. Horizontal fields of these three variables were estimated every 5 db from the vertical profiles using optimal statistical interpolation scheme (Gomis et al., 2001) on a spatial grid with regular node distances of $0.15 \times 0.15^\circ$ latitude-longitude covering all the study area (see details in Appendix S2). Then, geostrophic velocities (GV) were derived from the interpolated density fields following Rubio et al. (2009). Secondly, the depth of the maximum temperature gradient (DTG, as a proxy of ocean mixed layer depth and water column stability indicator), the maximum temperature gradient (MTG, as a proxy of the strength of the water column stratification) and the sea surface temperature gradient (SSTG, as an important predictor for seabirds distributions) were estimated from temperature fields as described in Louzao et al. (2019).

In order to characterize the geographic environment, depth (DEP) was extracted from NOAA at a resolution of 0.016° (map package, Pante & Simon-Bouhet, 2013) and used to calculate the distance to the coast (DCO) and the distance to the shelf break (DSHEL), defined by the isobath of 200 m. The spatial gradient in depth (DEPG) was also estimated (Table 1); in fact, areas of strong spatial gradient may correspond to areas where internal waves generate, which can promote an increase in primary production and small preys' availability according to Scott et al. (2010). For that, a spatial moving window of 3×3 cells was used in which the spatial differences in bathymetric values were calculated and scaled to the maximum value [(maximum value - minimum value)/maximum value] following the approach in Louzao et al. (2019).

2.2 | Detection functions of seabirds' sightings

In line transects, it is assumed that the likelihood of detecting animals becomes smaller as the distance to the observer increases. To account for that bias, distance sampling analyses were applied, which mainly consist on fitting a detection function to the observed distances in order to estimate the proportion of animals missed by the observer (Thomas et al., 2002). To do so, sightings of seabirds were first filtered (by removing sightings with attraction behaviour) to avoid the response bias generated when animals react to the presence of the platform; in fact, fisheries discards can attract large feeding flocks and lead to misunderstand the distribution and abundance of seabirds (Valeiras, 2003). Due to the low number of sightings per year of some species (Buckland et al., 2001), small (Balearic and Manx shearwaters) and large species (Cory's, great and sooty shearwaters) were grouped together based on their size (see Appendix S3). Once we defined the groups, the 5% of the sightings

Species categories	Scientific name	Size (cm)	Depth categories	Depth layers
Anchovy adult	<i>Engraulis encrasicolus</i>	10–20	2	Surface and deep
Anchovy juvenile	<i>Engraulis encrasicolus</i>	0–10	2	Surface and deep
Anchovy juvenile	<i>Engraulis encrasicolus</i>	10–20	2	Surface and deep
Sardine	<i>Sardina pilchardus</i>	10–20	2	Surface and deep
Horse mackerel	<i>Trachurus trachurus</i>	0–10	2	Surface and deep
Horse mackerel	<i>Trachurus trachurus</i>	10–20	2	Surface and deep
Mackerel	<i>Scomber scombrus</i>	10–20	2	Surface and deep
Mackerel	<i>Scomber scombrus</i>	20–30	2	Surface and deep
Sprat	<i>Sprattus sprattus</i>	0–10	2	Surface and deep
Mueller's pearlside	<i>Maurolicus muelleri</i>	0–10	1	Surface-200 m

Note: The biomasses of all prey species categories, excepting the Mueller's pearlside, were split into surface (~10 m) and deep layers (above the depth of maximum temperature gradient).

detected at the largest distances were truncated to delete outliers (i.e. by setting the truncation distance, w) (Buckland et al., 2001) and analysed using multiple covariate distance sampling (Marques & Buckland, 2004). Hazard rate and half normal functions with no adjustments were then fitted in each of the groups using the ds function from the *Distance* package (Miller, 2020). As covariates, only those descriptors related to the effort were considered, that is Beaufort sea-state, visibility, cloudiness, glare intensity, observation conditions and year (see details in Appendix S4: Table S4.1), which were introduced in the detection function as factor and selected by means of forward selection (Appendix S4: Table S4.2) until the lowest Akaike information criterion (AIC hereafter) was obtained (Guisan & Zimmermann, 2000; Sakamoto et al., 1986). From here, the probability of detecting an animal (P_a) was estimated, which multiplied by the truncation distance (w) provided the effective strip half width ($ESW = P_a * w$). ESW can be defined as the perpendicular distance in which the missing detections equal the recorded detections and serves to estimate the area effectively covered, when considering both observation sides and transect length ($A = ESW * 2 * L$). In such estimations, seabirds' behaviour (on flight versus. on water) can be an important aspect to be considered, since flying individuals can lead to overestimate densities when they move faster than the observation platform (Buckland et al., 2001). In our case, most seabirds were recorded on flight (90%–95% of individuals in all species), and hence, little bias was expected between areas with flying and sitting individuals; overall overestimation, on the other hand, was considered negligible, since obtaining absolute abundances was out of our scope.

2.3 | Processing of explanatory variables

In order to understand the ecological niches of seabirds in the BoB, environmental and trophic relationships were modelled. However, the differences in the sampling coverage of seabirds, prey and environmental data did not allow for a homogenous prediction. To solve

TABLE 2 Prey species categorized by size and depth

that, prey and environmental data were first processed to obtain continuous fields of explanatory variables covering the study area and then categorized by depth and size to address the multidimensionality and functionality of the environmental and trophic niches (Figure 2; step 3).

2.3.1 | Prey fields

Since prey selection may be also conditioned by other factors related to prey availability such as body size or depth at which prey is available, the original biomasses (tonnes) of the seven prey species were categorized using 10 cm length classes (Lambert et al., 2018): <10 cm, 10–20 cm and 20–30 cm. The resulting biomass categories were then log-transformed and interpolated using universal kriging (Appendix S2) over a standard grid covering the study area (latitudinal range: 43.2–48°N; longitudinal range: 1–8°W) with a cell size of 0.1° spatial resolution. Secondly, all species biomasses but Mueller's pearlside (see below) were split into two main vertical layers (Appendix S5) following Louzao et al. (2019): 1) the surface layer and 2) the deep layer, limited by the depth of the maximum temperature gradient (DTG), a dynamic feature that approximates the depth of the ocean mixed layer and that usually comprises the first 40 m of the water column (for the interannual variability of DTG, see Appendix S6). For the surface layer, the biomasses of each prey species and each size class comprised in the shallowest depth layer were selected (between 5 and 15 m); for the deep layer, the same was done but summing the biomasses from the surface up to the DTG. As a result, we obtained the biomasses for a total of 18 prey categories (Table 2), that were afterwards introduced in a PCA (principal component analysis) to disentangle how prey fields were spatially and functionally structured.

In the case of the mesopelagic Mueller's pearlside, it was not classified into two layers, as it spends the daytime between ~50 and 200 m (Kaarvedt et al., 1998; Sobradillo et al., 2019); that is, in greater depths than the ones considered in this study (i.e. surface

and above the DTG). It is known, however, that it is an important resource among procellariids (Watanuki & Thiebot, 2018), so in order to test its relevance in our seabird community, we included as predictor the biomass of the Mueller's pearlside comprised between the surface and 200 m depth (Table 2). Although seabirds are not able to dive so deep, this estimation was used as a proxy of the biomass available at dusk and dawn, that it is when the pearlside migrates close to the surface and aggregates at about 20–40 m (Kaarvedt et al., 1998), becoming available to seabirds.

2.3.2 | Environmental fields

As with prey fields, those environmental variables collected at different depths (i.e. T, SAL and GV) were also vertically analysed and classified into surface and deep layers (Louzao et al., 2019). For the surface layer, the shallowest values were selected (10 m); for the deep layer, in contrast, the median values between surface and the DTG were estimated. Remaining environmental variables (DTG, MTG, SSTG, DEP, DEPG, DCO, DSHEL) were 2D variables (Table 1), so no vertical analysis was performed with them. Finally, all variables were resampled with the *raster* package (Hijmans et al., 2017) to match with the standard grid of prey (latitudinal range: 43.2–48°N; longitudinal range: 1–8°W, 0.1° spatial resolution).

2.4 | Biologically meaningful vertical range selection

Since pelagic birds show different diving abilities, the vertical range they exploit may also differ. Without obtaining in situ diving records, we cannot test that hypothesis, but we can determine the vertical range that best explains seabirds' density patterns (biologically meaningful vertical range, hereafter). For that, two models per species were fitted: one using the conditions given by the environmental and prey variables in the surface layer, and the other using the conditions given by the same variables but in the deep layer (Figure 2, step 4). Since this step required 3D data, the environmental variables comprised T, SAL and GV (Table 1), while the prey data included the first three axes of the PCA (explaining the 70% of the variability; Appendix S7). In all cases, individual density surface models were fitted from the previous detection function analyses using the *dsm* package (Miller et al., 2019). The number of individuals per unit effort was fitted by means of generalized additive models (GAM), assuming a negative binomial distribution with a probit link function (after testing with tweedy and quasipoisson families). Degrees of smoothness were limited to fit unimodal response curves and restricted to three (Brugge et al., 2016) to avoid overfitting (Burnham & Anderson, 2003). All variables were standardized to have a mean of zero and a standard deviation of one (Zuur et al., 2007) to make the comparison of effect sizes easier. The most plausible model was selected based on the lowest AIC (Guisan & Zimmermann, 2000; Sakamoto et al., 1986).

In addition, a literature survey was conducted to contrast the obtained results. For that, we focused on published biogging studies

providing the average diving depth reached by the species, as it refers to the vertical range more regularly exploited (Appendix S8: Table S8.1). This way, obtained results could be compared with expected results based on the average diving depths measured for each of the target species by different time dive recorders.

2.5 | Identification of segregation mechanisms

To identify niche differentiation mechanisms within the pelagic bird community, we modelled separately the environmental and trophic niche of species by integrating the data at their biologically meaningful vertical range (Figure 2, step 5), estimated an environmental and trophic overlap index for each pairwise species (Figure 2, step 6) and developed a conceptual framework with the most plausible segregation hypotheses (Figure 1).

2.5.1 | Environmental and trophic niche modelling

For the environmental niche, models combining environmental variables (both 3D and 2D, Table 1) were fitted in the biologically meaningful vertical range of each species, according to the results obtained in the previous section. For the trophic niche, the first three axes of the PCA (explaining the 70% of the variability; Appendix S7) and the biomass of the Mueller's pearlside were used.

In both cases, individual density surface models were fitted from the previous detection function analyses using the *dsm* package (Miller et al., 2019). For each species, the number of individuals per unit effort was fitted by means of generalized additive models (GAM), assuming a negative binomial distribution with a probit link function (after testing with tweedy and quasipoisson families). Degrees of smoothness were limited to fit unimodal response curves and restricted to three (Brugge et al., 2016) to avoid overfitting (Burnham & Anderson, 2003). All variables were standardized to have a mean of zero and a standard deviation of one (Zuur et al., 2007) and subsequently analysed by means of Spearman's rank correlation coefficient to identify highly correlated ($|r| \geq .6$) pairwise predictors (Thiers et al., 2014). The most plausible model was selected based on the lowest AIC (Guisan & Zimmermann, 2000; Sakamoto et al., 1986). When models differed in 2 units of AIC ($\Delta AIC < 2$), they were considered statistically equivalent and the one with a smaller number of variables was chosen following the parsimony principle (Arnold, 2010). Once the most plausible "environmental" and "trophic" niche models were defined, seabirds' densities were predicted per year over the standard grid (latitudinal range: 43.2–48°N; longitudinal range: 1–8°W, 0.1° spatial resolution) (Figure 5a,b).

2.5.2 | Environmental and trophic niche overlap

In order to assess the degree of environmental and trophic niche segregation, an overlap index was calculated between pairwise species

based on Ballard et al. (2012). In the case of environmental niche overlap, we first estimated the mean density for the 2013–2017 period based on the predictions obtained from the environmental niche modelling and selected only those cells containing the highest 95% of the mean density in order to avoid very low values (Figure 5c,d). After that, we assessed the degree of environmental overlap (Figure 5e) by dividing the number of cells where both species were present (i.e.

cells containing both species) by the total number of cells where either species was present (i.e. cells containing one species or both) (Ballard et al., 2012). This led to a total number of 10 overlap values, derived from the pairwise combination of 5 species ($C_{5,2} = \binom{5}{2}$), that were posteriorly standardized so that values ranged between 0 and 1.

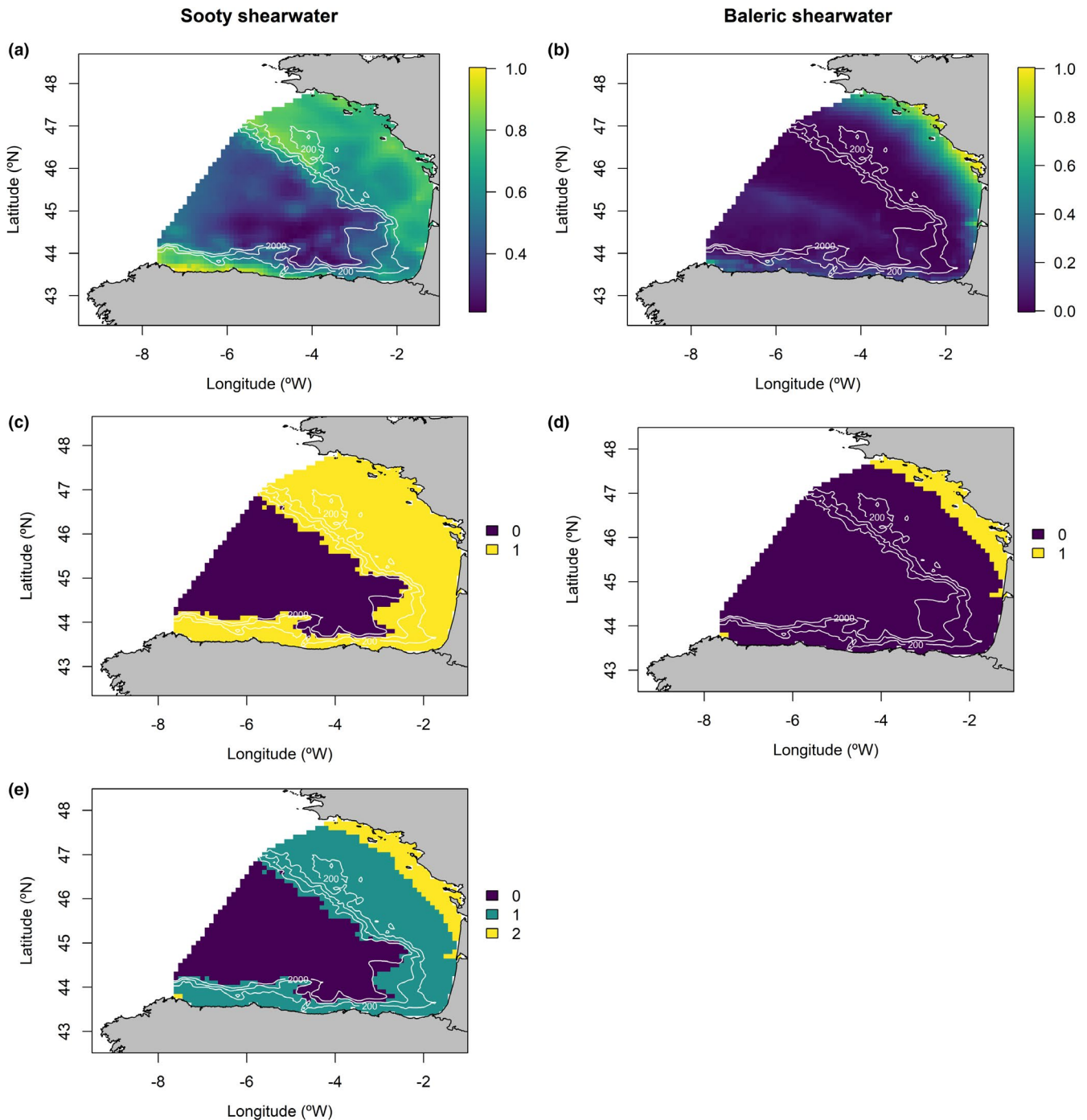


FIGURE 5 Example of how environmental overlap was estimated, showing the environmental niche (standardized densities) of sooty (a) and Balearic (b) shearwaters, followed by their respective (c, d) abundant areas (after keeping only the highest 95% of mean densities) and their environmental overlap (e)

TABLE 3 Summary of the features used in the detection function of each group of shearwaters

	Truncation distance (m)	Number of sightings	Detection function	Selected covariates	Average detection probability	Goodness-of-fit (Cramer von Miss)
Balearic and Manx shearwaters	362	227	Half normal	Year Beaufort General conditions	0.44	$p > .05$
Cory's and great shearwaters	561	1,053	Hazard rate	Year	0.31	$p > .05$
Sooty shearwater	479	278	Half normal	Year	0.39	$p > .05$

Note: Number of sightings refers to the final number obtained after having removed the 5% of the data detected at the largest distances.

TABLE 4 Summary of the vertical segregation test conducted for each shearwater species using conditions in the surface (first row) and conditions in the deep layer (second row)

Species	Models	AIC	Δ AIC
Cory's shearwater	T_{S+}, SAL_{S+}, GV_{S+}, $PCA1_{S+}$, $PCA2_{S+}$, $PCA3_{S+}$	1,419.71	0
	T_{D+} , SAL_{D+} , GV_{D+} , $PCA1_{D+}$, $PCA2_{D+}$, $PCA3_{D+}$	1,440.11	20.4
Great shearwater	T_{S+} , SAL_{S+} , GV_{S+} , $PCA1_{S+}$, $PCA2_{S+}$, $PCA3_{S+}$	6,764.13	0
	T_{D+} , SAL_{D+} , GV_{D+} , $PCA1_{D+}$, $PCA2_{D+}$, $PCA3_{D+}$	6,846.45	82.32
Sooty shearwater	T_{S+} , SAL_{S+} , GV_{S+} , $PCA1_{S+}$, $PCA2_{S+}$, $PCA3_{S+}$	2,928.49	3.19
	T_{D+} , SAL_{D+} , GV_{D+} , $PCA1_{D+}$, $PCA2_{D+}$, $PCA3_{D+}$	2,925.30	0
Balearic shearwater	$T_{S_{UP+}}$, SAL_{S+} , GV_{S+} , $PCA1_{S+}$, $PCA2_{S+}$, $PCA3_{S+}$	1,348.09	52.26
	T_{D+} , SAL_{D+} , GV_{D+} , $PCA1_{D+}$, $PCA2_{D+}$, $PCA3_{D+}$	1,292.83	0
Manx shearwater	T_{S+} , $SAL_{S_{UP+}}$, GV_{S+} , $PCA1_{S+}$, $PCA2_{S+}$, $PCA3_{S+}$	1,187.58	0
	T_{D+} , SAL_{D+} , GV_{D+} , $PCA1_{D+}$, $PCA2_{D+}$, $PCA3_{D+}$	1,190.32	2.73

Note: Biologically meaningful vertical range is shown in bold.

To estimate the degree of trophic niche overlap, the same procedure was followed based on trophic niche modelling results.

Finally, the conceptual framework displayed in Figure 1 was developed, which describes the plausible hypotheses that may arise from the pairwise comparison of environmental and trophic overlap indexes. These main hypotheses comprise two clear segregation mechanisms, defined as environmental segregation (high trophic overlap but low environmental overlap) and trophic segregation (high environmental overlap but low trophic overlap), and two additional situations described as specific conditions (low trophic and low environmental overlap) and alternative mechanisms (high trophic and high environmental overlap). Specific conditions would refer to any situation explaining why the pairwise species found in that section do not overlap (e.g. isolation, breeding, specialization), whereas alternative mechanism hypothesis would try to find out how those species can coexist in a situation of both high trophic and environmental overlap.

3 | RESULTS

3.1 | Sightings and detectability of seabirds

The most frequently observed species was the great shearwater (944 sightings), followed by the sooty (293 sightings), the Cory's (165 sightings), the Balearic (124 sightings) and the Manx shearwater (115 sightings). These sightings were relatively equally distributed over the BoB for great, sooty and in a lesser extent, for Manx shearwaters (Figure 3b-d), while sightings of Cory's and Balearic shearwaters were mainly recorded in the Spanish and French side of the study area, respectively (Figure 3a,e). When grouping these species, detection functions showed that same detectability could be assumed for Balearic and Manx shearwaters (i.e. small shearwaters) and for Cory's and great shearwaters (Appendix S3). Sooty shearwater turned out to be the most different species in terms of detectability, so it was analysed separately (Appendix S3), resulting in three

different detection functions (Table 3 and Appendix S9: Figure S9.1). In the case of small shearwaters, the function with the lowest AIC was a half normal function, with year, Beaufort and general conditions as covariates (Table 3, Appendix S9). For Cory's and great shearwaters, the best function was a hazard rate with year as covariate, while in the case of the sooty shearwater, the best function was a half normal with year as covariate (Table 3, Appendix S9).

3.2 | Biologically meaningful vertical range

According to the test conducted to identify each species' biologically meaningful vertical range, we found that the density patterns of Cory's, great and Manx shearwaters were better explained by the explanatory variables of the surface layer (10 m), while the density patterns of sooty and Balearic shearwaters were better explained by the explanatory variables integrated over the deep layer (above DTG) (Table 4). Obtained results were in agreement with the results expected from the literature review (Appendix S8: Table S8.2), in which the average diving depth records indicated a surface diving behaviour for Cory's, great and Manx shearwaters (with an average depth of 1.7, 3.2 and 5.7 m, respectively) and a subsurface diving performance for sooty shearwater (average depth 12.3 m). The only exception was the Balearic shearwater, as the average diving depth found in the literature did not agree with the obtained results from the modelling of the biologically meaningful vertical range (Appendix S8: Table S8.2).

3.3 | Environmental and trophic drivers

Trophic niche models showed a high preference for PCA1 (small-medium fish species) in Balearic and Manx, for PCA3 (big fish species) in Cory's and for the Mueller's pearlside in great and sooty shearwaters, highlighting three main groups (Figure 6). Environmental models, although more diverse, showed a more homogenous pattern in terms of variables' importance, suggesting a more balanced contribution of the environmental variables (Figure 6). Nevertheless, some similarities could be found too; large shearwaters (Cory's, great and sooty), for instance, were found to rely moderately on salinity (SAL) and depth (DEP), whereas small shearwaters preferred those variables linked to land or shelf-break closeness (DCO and DSHEL). Temperature (T), although present in most of the models, was found to be of low importance for all the species (Figure 6). In general, environmental niche models provided higher percentages of deviance explained, that ranged between 15% and 71%, while trophic niche models showed a deviance explained between 5% and 59% (see Appendix S10).

3.4 | Niche differentiation mechanisms

Overlap indexes obtained from previous environmental and trophic niche models were displayed following Figure 1 in order to assign the main four segregation hypotheses to each pairwise species (Figure 7). In this way, the pairs composed by Balearic-great,

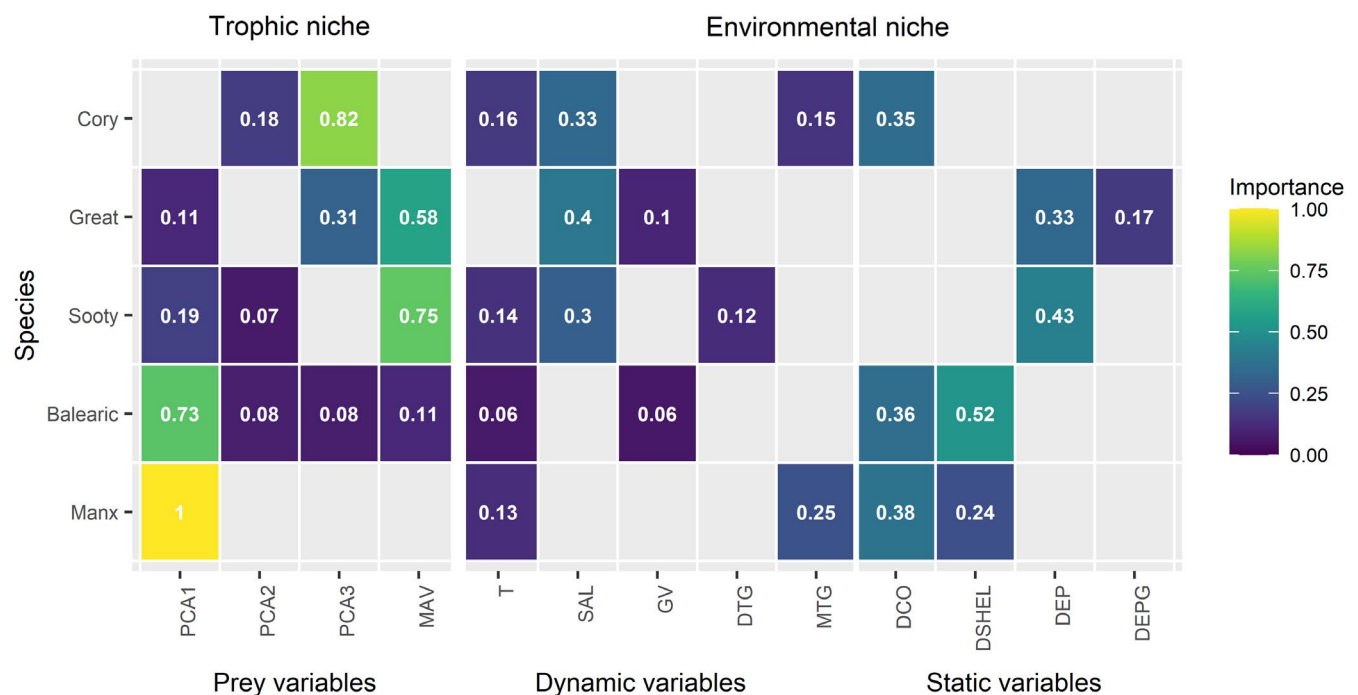


FIGURE 6 Relative importance of the variables included in the environmental and prey-based models, integrated at the biologically meaningful vertical range of each species. Prey variables: the main three axes of the PCA (PCA1, PCA2 and PCA3) plus Mueller's pearlside (MAV). Environmental variables: temperature (T), salinity (SAL), geostrophic velocity (GV), depth of the maximum temperature gradient (DTG), maximum temperature gradient (MTG), distance to coast (DCO), distance to shelf break (DSHEL), depth (DEP) and depth gradient (DEPG)

Manx–great and Balearic–sooty were assumed to segregate environmentally (Figures 7a and 1a), while Manx–Cory's shearwaters were presumed to segregate through trophic niche partitioning (Figures 7d and 1d). The category classified as specific conditions (Figure 1c) was assigned to the Cory's shearwater, as it was present in all pairwise combinations showing low trophic and low environmental overlap, including Cory's–Balearic, Cory's–sooty and Cory's–great pairs (Figure 7c). On the other hand, Manx–Balearic, Manx–sooty and sooty–great pairs showed the opposite pattern, suggesting that these pairwise species coexist through an alternative mechanism in conditions of high environmental and high trophic overlap (Figures 7b and 1b).

4 | DISCUSSION

Unlike other marine predators, air breathing seabirds are limited in prey accessibility due to their anatomy and their diving capabilities. Thus, considering the processes that concentrate prey close to the surface, prey size or depth at which seabirds can fish is essential. In this study, the incorporation of such elements has enabled us to conclude that (a) wide-ranging species coexist through environmental and trophic niche partitioning, (b) species respond differently to prey and oceanographic conditions on the vertical dimension (potential vertical segregation) and (c) phylogenetically and morphologically closer species (e.g. sooty–great or Manx–Balearic) show more similarities in their trophic and environmental niches.

These major findings were mainly extracted from the conceptual diagram, resulting from the modelling of environmental and

trophic niches. Previous co-occurrence analyses conducted in the area already described some of the results found here, such as the environmental overlap between Manx–sooty or the environmental dissimilarity in Cory's–Balearic shearwaters (Astarloa et al., 2019). However, the way in which this approach was addressed (i.e. by considering both environmental and trophic niches, prey depth and size, conditions on the vertical dimension) provided more detailed information on species assemblage and revealed four different scenarios resulting from niche overlap patterns that could not have been identified otherwise.

The two clearest scenarios were the environmental and trophic segregation (Figures 1a, 7a and Figures 1d, 7d, respectively). The former, detected in Balearic–great, Manx–great and Balearic–sooty pairs, can be understood with the spatial distribution described for these species. In fact, Balearic and Manx shearwaters are known to occupy primarily coastal waters (Authier et al., 2018), whereas sooty and great shearwaters show preference for shelf and oceanic waters, respectively (Louzao et al., 2019). When they stopover in the BoB, Balearic and Manx stay closer to the coast, while great and sooty shearwaters exploit offshore areas, leading to a non-overlap pattern in their environmental niche.

On the other hand, trophic segregation was only identified in the case of Manx–Cory's pairwise species. This segregation mechanism can be explained by the results given by diet-based studies, that suggest that Cory's shearwater feeds on Atlantic mackerel and horse mackerel (Paiva et al., 2010), while the Manx shearwater mainly relies on clupeids (e.g. herring, sprat) (Thompson, 1987). This single association also indicated that overall, the community of pelagic birds in the BoB was characterized by a low trophic segregation, which can be due to the generalist behaviour of most species, known to

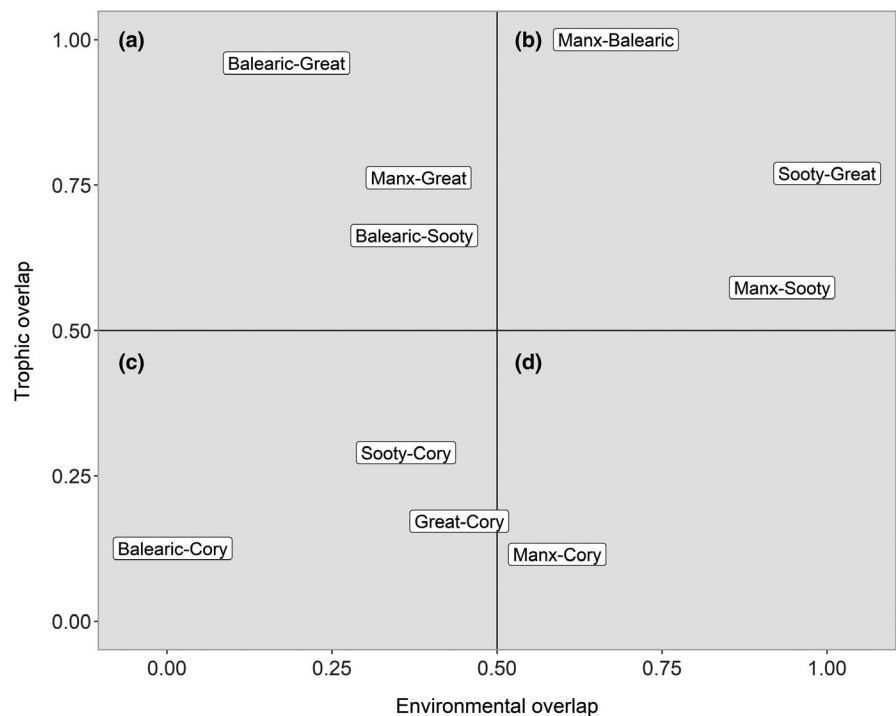


FIGURE 7 Comparison of trophic versus environmental overlap indexes that display pairwise species in sections of (a) high trophic overlap but low environmental overlap, (b) high trophic and high environmental overlap, (c) low trophic and low environmental overlap and (d) high environmental overlap but low trophic overlap. The most plausible segregation hypothesis explaining each section can be found in Figure 1

take advantage of available pelagic feeding resources (Bicknell et al., 2013). In fact, even the critically endangered Balearic shearwater, with a potentially more restricted foraging range compared to the remaining wide-ranging pelagic birds, feeds on the main pelagic resources of the BoB (e.g. mackerel, horse mackerel, anchovy, sardine) (Meier et al., 2017). However, it must be mentioned that, despite not having found strong evidence of trophic segregation in the conceptual diagram, the modelling of trophic niches already revealed some differences in the seabird community. Indeed, great and sooty shearwaters were associated to Mueller's pearlside, Balearic and Manx shearwaters to small-medium fish species (PCA1), and Cory's shearwaters to big fish species (PCA3), meaning that clustering prey species based on functional characteristics can help uncover subtle differences on the trophic preferences of species (Lambert et al., 2018).

The remaining two scenarios (Figure 1b,c) could not be explained by environmental and trophic requirements and instead, further information on the biology of the species was required to be untangled. Low patterns of both trophic and environmental overlap, for instance, were related to the reproductive behaviour of the Cory's shearwater (involved in all associations with low overlap). In fact, it was the only species that was breeding (they breed in the north west of the Iberian Peninsula) at the time the study was conducted (Munilla et al., 2016). During this period, seabirds act as central place foragers (Orians & Pearson, 1979), which means they have to make a balance between selecting productive areas (to obtain enough food supplies for their chicks and themselves) and performing not too long trips (to come back to the colony to feed the chicks). The limited foraging trips of the species, as a result of its reproductive status, could therefore be responsible of such different pattern.

High environmental and trophic overlap patterns, in contrast, were hypothesized to be linked to a potential vertical segregation, as all the pairs showing highly overlapped patterns had opposite biologically meaningful vertical ranges: Manx-Balearic (surface vs. deep), Manx-sooty (surface vs. deep) and sooty-great (deep vs. surface). If so, this could mean that vertical segregation occurs when species share similar environmental and trophic requirements and would agree with previous studies conducted with sympatric species in which vertical segregation has been found (Mori & Boyd, 2004; Navarro et al., 2013). In addition, our results also seem to indicate that vertical segregation mainly occurs between closely related species, such as the sooty and great shearwaters (*Ardenna* genus) or the Manx and Balearic shearwaters (*Puffinus* genus). Phylogenetically related species are expected to be ecologically similar (Losos, 2008), so we could additionally suggest that under very similar niche conditions, segregating in the vertical dimension is the only way to reduce competition. Indeed, the similarities in the niche of these species did not only arise in niche overlap analysis but also when identifying environmental and trophic drivers.

Vertical segregation hypothesis, however, cannot be confirmed without diving depth records, although it seems plausible based

on the high agreement found between the biologically meaningful vertical ranges defined here and the average depths recorded by data loggers (see Appendix S8). Indeed, the only exception in which the average depth recorded in previous studies was not in agreement with our results was the case of the Balearic shearwater (see Appendix S8). This may be due to the low sample size (only diving data from one individual was obtained in Aguilar et al. (2003), but see Meier et al. (2015)) or due to the contrasting oceanographic and prey conditions between the Mediterranean Sea and the Atlantic Ocean (i.e. oligotrophic versus eutrophic conditions, respectively). However, with the available data, no significant conclusion can be made, and we can only acknowledge that further research is needed to elucidate the diving behaviour and the vertical range of the Balearic shearwater.

Advancing in the understanding of endangered, threatened and protected (ETP) species is critical. The pelagic bird community of the BoB, characterized by a highly migratory behaviour, is protected under multiple international agreements. By combining data collected from integrated ecosystem surveys and habitat modelling, we have proved that studying seabirds outside their breeding areas can also provide useful results about their ecological niches. Indeed, we have contributed to understand the underlying environmental and trophic drivers of both environmental and trophic niches, needed to identify critical feeding grounds and high biodiversity areas in the context of marine spatial planning. Assessing the degree of overlap between such areas and anthropogenic pressures (e.g. fishing by-catch) could be, for instance, a potentially useful step to conduct in the near future that will undoubtedly help advance in the conservation of these species.

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

Any request for survey data should be addressed to their owners.

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BIOSKETCH

Amaia Astarloa is a PhD student focused on understanding the role that prey and environment play in driving marine predators' distribution and abundance and its implications for fishing, conservation and climate change management.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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