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Marine megafauna niche coexistence and hotspot areas in a temperate ecosystem

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31 ABSTRACT

32 In the last few decades, there has been a remarkable development of niche models to
33 help understand the ecological response of species to current rapid environmental
34 changes. In the present study, we applied niche modelling to the megafauna community
35 of shelf waters of the northwestern (NW) and northern Iberian Peninsula in order to
36 analyse the coexistence of different species taking into consideration their niche
37 preferences. The Spanish Institute of Oceanography conducts the PELACUS
38 multidisciplinary survey annually, to assess pelagic fish stocks and collect information
39 on the status of other ecosystem components such as oceanographic conditions,
40 phytoplankton, zooplankton and marine megafauna. Using data collected from these
41 surveys, we developed niche models for 14 marine megafauna taxa (3 cetaceans, 10
42 seabirds and 1 fish) incorporating multi-trophic ecological descriptors collected
43 simultaneously during the surveys alongside the more commonly used oceanographic
44 variables (e.g. chlorophyll *a* and sea surface temperature). Megafauna niche models
45 were developed by pooling observations from 2007 to 2013 and were found to be driven
46 by mean fish biomass and its variability, in addition to sea surface temperature.
47 Hierarchical clustering identified four distinct megafauna assemblages, the first
48 comprising of wide-ranging species and the other three associated with shelf-slope
49 waters in Galicia, coastal/shelf waters in Galicia, and the eastern Cantabrian Sea,
50 respectively. Community-level hotspot areas were found in shelf and shelf-break sectors
51 of Galicia, along with small diversity spots scattered throughout the Cantabrian coastal
52 area. Our results showed that synoptically collected survey-based ecological descriptors,
53 especially acoustic-based preyscapes, were among the most important variables
54 explaining megafauna niche preference. These findings highlight the advantage of using

55 integrated ecosystem surveys to collect simultaneous information on a suite of
56 ecosystem components for spatial assessments.

57

58 *Keywords:* niche coexistence; marine megafauna; preyscapes; species distribution
59 models; integrated ecosystem surveys;

1. Introduction

The concept of ecological niche has been widely used for characterizing the environmental space (in relation to both abiotic and biotic factors) in which a species can occur (Holt, 2009). In recent decades, there has been a remarkable development of niche modelling algorithms resulting from an increased interest in characterising species' niches to improve understanding of their ecological response to rapid environmental changes (Franklin, 2013). This approach associates the geographical distribution of species with a set of environmental variables that can explain their distribution with the ultimate aim of obtaining predictions of future distributions (Guisan and Zimmermann, 2000). Even though there are certain limitations associated with the use of niche models, and other approaches could be considered more appropriate (e.g. mechanistic process-based models), they are a valuable starting point for understanding a species' niche (Holt, 2009). When this approach is applied to the individual species of a community, it is possible to assess their coexistence and evaluate multispecies niche preferences (Ballard et al., 2012).

Marine megafauna species have been proposed as indicators of the status of the marine environment (e.g. MAPAMA, 2012; Santos and Pierce, 2015). To aid in the management of megafauna, we need to identify those ecological descriptors that best explain species distribution. By obtaining spatial predictions for multiple species, ecologically meaningful areas could be defined to inform conservation efforts (Arcos et al., 2012). In the marine environment, niche models have been traditionally developed based on ecological descriptors such as chlorophyll *a* and sea surface temperature (e.g. Arrizabalaga et al., 2014; Louzao et al., 2013; McGowan et al., 2013; Pérez-Jorge et al., 2015; Redfern et al., 2006) since megafauna species may use oceanographic variables as cues for locating prey as well as responding directly to oceanographic conditions, for

example due to thermal niche constraints (see MacLeod, 2009). It has been hypothesised that the functional relationship between marine megafauna distribution and environmental cues might be influenced by the trophic connections between predator and prey distributions (Lambert et al., 2018), with a degree of spatial overlap that can vary across multiple scales (Fauchald, 2009).

Multidisciplinary oceanographic surveys provide a suitable monitoring platform to gather simultaneously oceanographic and biological information on the distribution and abundance of different trophic levels, from plankton to marine megafauna (Doray et al., 2017). The biological information recorded includes estimates of the biomass of species such as pelagic fishes, which are important prey for several marine megafauna species (e.g. Astarloa et al., 2019; Certain et al., 2011; Mèndez-Fernandez et al., 2012; Santos et al., 2014, 2013; Spitz et al., 2014). The PELACUS spring surveys of the Spanish Institute of Oceanography (IEO) have been conducted annually since the late 1980s to inform the assessment of pelagic fish stocks in the northern and northwestern Atlantic continental shelf of the Iberian Peninsula using acoustic methods (Santos et al., 2013). Ancillary oceanographic and biological data (i.e. phytoplankton and zooplankton biomass) are collected to help characterise the structure, functioning and dynamics of the pelagic ecosystem. Since 2007, sightings of marine megafauna (e.g. marine mammals and seabirds) have been routinely collected by dedicated observers (Saavedra et al., 2018), in addition to the collection of information on the presence, type and abundance of different indicators of human pressures (e.g., fishing vessels, marine debris). Recently, marine litter sampling was also implemented within these surveys (Gago et al., 2015).

We applied a niche modelling approach to the data on the marine megafauna community of this temperate region in southern Atlantic European waters. This area

includes many megafauna species (Authier et al., 2018; García-Barón et al., 2019; Lambert et al., 2017; Pettex et al., 2017; Sims et al., 2009, 2003; Virgili et al., 2017). It represents an important migration flyway for European seabirds, thousands of which cross this biogeographic area (Arcos et al., 2009; Fort et al., 2012; Louzao et al., 2015). The study area also offers suitable habitats for a range of cetacean species, with a diverse physiographic environment that combines narrow and wide shelves indented with several canyon systems, seamounts and an extensive oceanic realm (Kiszka et al., 2007). In addition, there are multiple interacting oceanographic processes, such as slope currents, upwelling-downwelling processes, river plumes and various types of eddy-like structures (e.g. Charria et al., 2017; González-Pola et al., 2012; Kersalé et al., 2016; Koutsikopoulos and Le Cann, 1996).

Here, we developed megafauna niche models, based on the PELACUS megafauna database, explicitly incorporating multi-trophic ecological descriptors (e.g. phytoplankton, zooplankton and pelagic fish), in addition to traditional dynamic and static environmental variables. We developed niche models for the 2007-2013 period, pooling observations from all years to increase the number of megafauna taxa that could be included. We hypothesised that the contribution of survey-based ecological descriptors describing spatial patterns of prey biomass (preyscapes hereafter) should contribute to explain marine megafauna distribution more effectively than is possible using traditional oceanographic variables, the effects of which on megafauna distribution are likely to be indirect (e.g. as proxies for high prey abundance). In addition, we identified megafauna assemblages sharing similar niche preferences to assess community-level niche coexistence and marine megafauna hotspots in the northwestern and northern Iberian Peninsula.

2. Methods

2.1. Data collection

Sightings of marine megafauna were collected during the IEO's annual spring PELACUS acoustic surveys (March-April) on board R/V Thalassa (2007-2012) and R/V Miguel Oliver (2013). The sampling grid consists of parallel equidistant transects perpendicular to the coast, separated by 8 nm, over the entire continental shelf between the 30 and 200 m isobaths (2007-2012), from the Portuguese to the French borders (Fig. 1). The sampling grid extended to the 500 m isobath in 2013 (Fig. 1). Information on the spatial distribution and biomass of different pelagic ecosystem components (i.e. phytoplankton, zooplankton, pelagic fishes and marine megafauna) is collected throughout the survey (Saavedra et al., 2018; Santos et al., 2013).

For marine megafauna, sightings are recorded during navigation at constant heading and speed (around 10 knots) during the daytime acoustic transects. Two experienced observers from a team of three continuously scan the water to the front of the vessel, each one covering an area of 90° from the track-line to port or starboard (Table 1). Observers record environmental conditions, as well as information on the sightings such as distance to the vessel, angle, species, group size, heading direction and behaviour (Saavedra et al., 2018).

The Beaufort sea-state level ranged from 0 to 8 during the observation time of the seven surveys analysed (2007-2013, Fig. S1a). Mean overall conditions varied markedly among years (non-parametric Kruskal-Wallis test $H_{6,65052} = 8340.56$, $P < 0.001$) (Fig. S1b, S1c). Sea state conditions were especially good in 2007 and 2011, whereas conditions were especially rough in 2008, 2010 and 2013. Beaufort state lower or equal to 3 is generally considered good sea state conditions to detect marine mammals (see Hammond et al., 2013). Based on this threshold, the mean percentage of

good sea state conditions during an annual PELACUS survey was 38.0 %, ranging between 18.0% (in 2013) and 65.3% (in 2011). To increase sample size, we analysed those observations recorded with a Beaufort sea-state from 0 to 4, corresponding to an average sampling effort of 62% (ranging between 42% and 84%).

2.2. Ecological descriptors

2.2.1. Multi-trophic survey information

The multi-level trophic information collected during the PELACUS surveys comprised estimates of phytoplankton, zooplankton and pelagic fish biomass. Both types of plankton data were collected during the night at coastal, mid-shelf and outer-shelf sampling stations located along the acoustic transects using vertical hauls from the surface down to 100 m depth (or down to 5m above the bottom in shallower stations) (Bode et al., 2003). An index of phytoplankton abundance was obtained based on chlorophyll *a* values measured from acetonic extracts of samples collected with a bongo-type conical net (mouth diameter 30 cm, 40 μ m mesh-size) following Neveux and Panouse (1987). Zooplankton (meso: 200-2000 μ m) was collected with a triple-WP2 net (mouth diameter 60 cm, 200 μ m mesh-size). In every haul, one of the samples was selected to obtain the zooplankton biomass and frozen for later laboratory processing (Rodriguez et al., 2009). Dry weight of zooplankton biomass was obtained after drying the samples in an oven (50°C, 24 h), and standardised to mg m^{-2} .

During the surveys, the acoustic energy reflected by marine organisms was recorded continuously at a constant vessel speed of 10 knots, using a scientific split beam echosounder EK60 (SIMRAD), working at 38 kHz (Santos et al., 2013). Acoustic sampling was performed from sunrise to sunset over the entire continental shelf.

Pelagic trawls provided information on the relative abundances of different fish species present in the area and their length-frequency distributions (LFD). Acoustic data were integrated for each elementary distance sampling unit (EDSU, set to one nautical mile), using the Echoview (MyriaxLtd.) software. The result of the echo integration was estimated as the nautical-area scattering coefficient (s_A in $m^2 \text{ mile}^{-2}$) (Simmonds and MacLennan, 2005). Then, s_A was then divided between the various fish species present based on their abundance and LFDs in the trawl catches, applying the Nakken and Dommasnes (1975) method for multiple species. Total s_A was translated into abundance (numbers of fish) by applying the target strength relationship for each pelagic species. Abundance was transformed into biomass using weight–length relationships.

In total, the six families of pelagic fishes most commonly detected in the survey were included in the analysis: Clupeidae (sardine *Sardina pilchardus* and European anchovy *Engraulis encrasicolus*, representing on average 13% and 0.5% of the total estimated biomass, respectively), Scombridae (Atlantic mackerel *Scomber scombrus* and Atlantic chub mackerel *S. colias*; 68% and 1.3%, respectively), Carangidae (Atlantic horse mackerel *Trachurus trachurus*, Mediterranean horse mackerel *T. mediterraneus*, and blue jack mackerel *T. picturatus*; 5.2%, 0.8% and 1.3%, respectively), Sparidae (bogue *Boops boops*; 3%), Gadidae (blue whiting *Micromesistius poutassou*; 1.5%) and Caproidae (boarfish *Capros aper*; 4%).

2.2.2. Independent oceanographic variables

Additional environmental variables were obtained from different sources (Table 2). Dynamic oceanographic variables were obtained from the Bio-ORACLE environmental data set (Tyberghein et al., 2012)(Fig. S2), which has been previously

used for the development of marine species distribution models. This dataset is a comprehensive assemblage (e.g., satellite-based and *in situ* measured data of high-resolution, approximately 9.2 km) and readily usable package of 23 global climatological environmental rasters (Tyberghein et al., 2012). We selected those environmental variables expected to be related to marine megafauna distribution in the study area, namely sea surface temperature (SST, °C) and chlorophyll *a* (CHL, mg m⁻³), to describe, respectively, overall water mass distribution and productivity domains. In addition, we used the annual ranges (difference between maximum and minimum) of both oceanographic variables within the climatological time series (Tyberghein et al., 2012). Finally, spatial gradients of averaged SST and CHL (SSTG and CHLG) were estimated as the proportional changes (SG) in these variables within a surrounding 3x3 cell grid using a moving window as follows: $SG = [(maximum\ value - minimum\ value) \times 100] / (maximum\ value)$ (Louzao et al., 2006).

Regarding static environmental variables, bathymetric data (BAT) obtained from ETOPO (<http://coastwatch.pfeg.noaa.gov/erddap/griddap/etopo180.html>) was resampled to match the spatial resolution of dynamic environmental variables (Fig. S3). Then bathymetric spatial gradients were computed as previously described (BATG). We also included distances to the coast and shelf-break (COAST and BREAK, respectively) in order to account for ecological processes associated to these topographic features. The shelf-break was defined by the 200 m isobath and the distance between the centroid of each cell and this reference line was estimated. The coastline was obtained from the NOAA/National Geophysical Data Center (<http://www.ngdc.noaa.gov/mgg/shorelines/gshhs.html>) and the distance between the centroid of each cell and the coastline was estimated. See Table 2 for a comprehensive list of environmental variables and their biological interpretation.

2.3. Data processing

We created a standard grid over the study area (latitudinal range: 42°-44°N; longitudinal range: 10°-1°W) to map biological observations with a spatial cell size of 0.0833° (approximately 9 km covering ca. 81km²) to match the spatial resolution of environmental variables. For each megafauna species, we overlaid all sightings for the 2007-2013 period over the standard grid and grid cells with at least one observation were coded as “presence”, while the remaining cells were coded as “absence”. For each species, we counted the number of cells with presence across the 7-year period. Due to the high number of species with low numbers of presence records (even when data were pooled across years), we established a cut-off of 20 presence records (NCPs) when selecting the megafauna species for further niche modelling. This number was considered as a good compromise to increase the number of species characterising the megafauna community. We mapped the observed species richness by counting the number of species present in each grid cell.

Biomasses of phytoplankton, zooplankton and pelagic fish (after log-transforming) were overlaid over the standard grid and interpolated based on the inverse distance weighted interpolation using the *gstat* package (Pebesma, 2004; Gräler et al., 2016). Synthetic ecological descriptors were obtained by estimating the mean and the standard deviation (i.e. variability) per grid cell across all available years for each descriptor. Therefore, three trophic layers were obtained describing overall (i.e. mean) spatial patterns of phytoplankton, zooplankton and pelagic fish biomass (PHY, ZOO and FISH), as well as their variability (i.e. standard deviation, PHYSD, ZOOSD and FISHSD) (see Table 2 and Fig. 2).

2.4. Marine megafauna distribution models

We developed species distribution models (SDMs) for marine megafauna to identify suitable marine areas at the species level in the study area. SDMs were developed based on Generalized Additive Models (GAMs) developed within the information theoretic approach using the *mgcv* package (Wood 2011). Prior to modelling, ecological descriptors were standardized (subtracting the mean and dividing by the standard deviation) and the Variance Inflation Factor (VIF) estimated to detect highly collinear predictors (VIF value > 5; Zuur et al., 2007). This approach led to the removal of average CHL, COAST, PHY and SSTR.

For each species, the presence/absence response variable was fitted following a binomial distribution, limiting the smoothing splines of predictors to a maximum of 3 degrees of freedom to capture non-linear associations, but avoiding complex functional relationship between the probability of presence and environmental descriptors. Afterwards, models were developed for all possible combinations of predictors based on *MuMin* package (Barton 2016), and were ranked based on the second-order Akaike Information Criterion (AICc) (Guisan & Zimmermann 2000). We obtained averaged coefficients and variance estimators from those models included in the 95% confidence set (i.e. the models for which the cumulative sum of AICc weights was ≥ 0.95) (Burnham & Anderson 2002).

For each species, we present the GAM output as follows: (1) the relative importance of ecological descriptors measured by summing the AICs weights for all models within the confidence set containing a specific ecological descriptor (Burnham & Anderson 2002), (2) functional relationships between the presence probability of megafauna species and non-correlated ecological descriptors constructed based on averaged coefficients, (3) average spatial predictions and their uncertainty and (4) an assessment of the model evaluation. Spatial predictions were obtained over the standard

grid for the sampled geographical extension restricted to depths lower than 500 m. The predictive performance of SDMs was assessed by evaluating GAM predictions using the Area Under the receiver operating characteristic Curve (AUC) [AUC of 0.9 excellent, 0.9–0.8 good, 0.8–0.7 reasonable, 0.7–0.6 poor and 0.6–0.5 unsuccessful; (Swets, 1988)]. We also estimated the adjusted R-squared of the model with the lowest AICc value.

2.5. Marine megafauna assemblages and community hotspots

Marine megafauna niche preference was described at the community and assemblage level. These analyses are based on the relative predictor importance for each megafauna species obtained from niche modelling. At the community level, we identified the relative importance of ecological descriptors by the mean and standard deviation (i.e. SD) across all species. Overall niche preference was characterised by the mean $\pm$ SD of the main ecological descriptors contributing more than 0.10%. At the assemblage level, we firstly performed a hierarchical clustering analysis based on the averaged predicted presence of each megafauna species to identify megafauna assemblages sharing similar niche preferences. For this, we used the *Pvclust* package, specifying the Euclidean distance and Ward agglomeration method (Suzuki and Shimodaira, 2006). *Pvclust* calculates *P-values* for hierarchical clustering via multi-scale bootstrap resampling and significant clusters with probability $P \geq 0.95$ were extracted. Secondly, niche preferences of each assemblage (i.e. cluster) were described by the mean $\pm$ SD of the main non-correlated ecological descriptors (Louzao et al., 2014).

In order to identify megafauna hotspots, we estimated the threshold probability at which both predicted presence (sensitivity) and absence (specificity) were maximized for each species. For each megafauna species, the predicted presence probability ranging from 0 to 1 was transformed into suitable and non-suitable areas corresponding to grid cell values higher and lower than the threshold probability, respectively (Louzao et al., 2006). Then, we estimated the predicted megafauna species richness index for each cell by summing all suitable areas across species and within grid cells. Megafauna hotspots were identified as the marine areas where a higher number of megafauna species was predicted to be present.

3. Results

3.1. Megafauna community

Sightings of the megafauna community in the northwestern and northern Iberian shelf during spring included at least 10 species of cetaceans, 28 species of seabirds and 2 genus of pelagic fish (see Table 1). The fish seen by the observers were sunfish *Mola* spp., which was recorded as present in 37 grid cells and triggerfish *Balistes* spp. (present in only 1 cell). The cetacean species with the highest occupancy were common dolphin *Delphinus delphis*, bottlenose dolphin *Tursiops truncatus* and long-finned pilot whale *Globicephala melas*. The seabird species with the highest occupancy (with more than 100 cells with presence records) were northern gannet *Morus bassanus*, yellow-legged gull *Larus michahellis*, lesser black-backed gull *L. fuscus*, great skua *Stercorarius skua*, followed by (with less than 100 cells with presence records) sandwich tern *Thalasseus sandvicensis*, razorbill *Alca torda*, Balearic shearwater *Puffinus mauretanicus*, Mediterranean gull *Ichthyophaga melanocephalus*, European shag *Phalacrocorax aristotelis* and common guillemot *Uria aalge*.

Following the criterion of a minimum number of cells with presence records (<20), 14 taxa were considered for further analysis (see Table 1). The highest observed species richness (i.e. highest number of megafauna species/taxa) was located in the western sector of the study area, in Galicia, followed by a smaller local concentration in the eastern Cantabrian Sea (Fig. 1).

3.2. *Megafauna assemblages*

The megafauna distribution models yielded a reasonable predictive performance since models for most species showed an AUC value higher than 0.7 (Table 3), with an overall community average of 0.751 (SD = 0.070). The adjusted R-squared varied from 0.121 (long-finned pilot whale) to 0.674 (European shag). The mean sensitivity and specificity values were 0.749 (0.641 – 0.895) and 0.754 (0.623 – 0.900), respectively, indicating high proportions of both true predicted presences and true predicted absences.

Regarding overall niche preferences, community structure was mainly described (mean $\pm$ SD) by three dynamic variables that contributed on average more than 0.10 % (Table 4). The main ecological descriptors were preyscape-related variables such as FISH and FISHSD, which highlights the importance of pelagic fish in explaining megafauna distribution (Table 2). The spatial distribution of fish biomass showed higher values in the central sector of the study area, mainly in twestern Asturias and the eastern coast of Cantabria (Fig. 2e), whereas fish biomass variability showed the highest values in Galicia (Fig. 2f). In addition, SST, which plays a major role in describing the characteristics of water masses, showed a longitudinal gradient across the study area, from lower values in the west to higher values in the east (Fig. S2). The other ecological descriptors with relatively high importance were BAT, BATG, BREAK, SSTG, CHLG, ZOO and ZOOSD. However, the relative importance of

individual ecological descriptors varied widely within the megafauna community, suggesting clear species-specific niche preferences (as seen in a plot of the normalised values of the relative importance, Fig.3).

Hierarchical clustering analysis identified one significant assemblage (indicated by the red rectangle, Fig. 4), but we applied the 35% similarity level to obtain community level megafauna assemblages (clusters 1 to 4). Cluster 1 was formed by one cetacean species (the long-finned pilot whale) and 3 species of birds (i.e. yellow-legged and lesser black-backed gulls and northern gannets). The main contributing descriptors (contribution higher than 0.10%) were SSTG and FISHSD (Table 4). A higher presence of these megafauna species was predicted in areas of increasing variability of both SST (SSTG) and FISH (FISHSD), i.e. along the slope-shelf band of the entire study area (Fig. S4). Cluster 2 was taxonomically diverse with one seabird species (great skuas), one cetacean (common dolphins) and the sunfish. . The main contributing variables were FISH and BREAK . The presence probability was higher in the slope-shelf area of Galicia, especially in the southernmost sector (Table 4, Fig. S4). Cluster 3 contained five species of birds (razorbill, Balearic shearwater, European shag, sandwich tern and Mediterranean gull) for which the most relative important variables were SST and FISHSD (Table 4). The probability of presence of these megafauna species was higher in highly localized coastal areas, especially in Galicia (Fig. S4). Cluster 4 was formed by one species of bird (common guillemots) and one cetacean (bottlenose dolphins) for which SST, BAT, CHLG and FISHSD have a higher relative importance (Table 4). The probability of presence of this assemblage presence was higher in the Cantabrian Sea, especially in the eastern sector of the study area (Fig. S4).

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3.3. *Marine megafauna hotspots*

The threshold probability for predicted presences and absences for individual species ranged between 0.040 and 0.740 (Table 3). The predicted areas of the highest megafauna diversity (i.e. the highest number of species) were found in Galicia, covering the whole continental shelf and shelf-break (Fig. 5), largely corresponding to the areas of the highest observed megafauna diversity (Fig. 1) and areas of highest FISH values (Fig. 2). In the Cantabrian Sea, where the continental shelf is narrow, megafauna hotspots consisted of small areas close to the coast (Fig. 5).

4. Discussion

We have integrated distributional information on multiple megafauna species to describe community niche coexistence based on multi-trophic ecological information. We have thus provided the first integrated picture of marine megafauna distribution during early spring across the northwestern and northern Iberian shelf ecosystem. Previous studies in the area focused on specific taxa, such as seabirds (Valeiras, 2003), cetaceans (López et al., 2004; Spyrakos et al., 2011), demersal fishes (García-Alegre et al., 2014; Sánchez et al., 2008) and pelagic fishes (Santos et al., 2013). Our approach is possible based on the availability of data gathered through synoptic integrated surveys (Certain et al., 2011; Doray et al., 2017; Louzao et al., 2019) and allows us to show that prey abundance data collected concurrently using acoustic methods can improve distribution models for megafauna. In our analyses, both static and dynamic ecological descriptors, including preyscapes, affected megafauna distribution patterns. Prey distribution was described based on acoustic data, which likely gives more suitable information, for the purpose of modelling predator distribution relative to that of their prey, than can be obtained from trawl hauls (results from which have been shown to be

a poor predictor of cetacean distribution, Torres et al., 2008). Acoustic data can be collected simultaneously with megafauna observations, data collection is continuous and the sampling methodology does not affect fish distribution.

4.1. Marine megafauna community

In the southern sector of the Bay of Biscay (N and NW Iberian Peninsula), the marine megafauna community investigated in this study was characterised by the presence of at least 10 species of cetaceans and 28 species of seabirds, as well as two genus of pelagic fishes. . Most of these species have also been detected in the French sector of the Bay of Biscay during the spring PELGAS surveys (Authier et al., 2018), with a similar survey design and characteristics as PELACUS. In both Spanish and French sectors, the cetacean species with the highest number of records were common dolphins, bottlenose dolphins, and long-finned pilot whales (this study; Authier et al., 2017). Among the seabirds, northern gannets, lesser black-backed gulls and great skuas were the species with the highest number of records in both sectors of the Bay of Biscay (this study; Authier et al., 2017). Due to differences in survey timing with respect to the annual phenology of seabirds (which is broadly similar in all species sighted in the present study), the PELACUS surveys (i.e. March-April) generally coincide with the pre-breeding migration while the PELGAS surveys (i.e. May) coincide with the start of the breeding season (this study; Authier et al., 2017). In addition, the most abundant species detected in each sector differed, reflecting biogeographical limits. Thus, yellow-legged gulls were highly abundant in northern Iberian waters while northern fulmars were mostly present in the French sector (this study; Authier et al., 2018; Lambert et al., 2018).

As hypothesised, both dynamic and static ecological descriptors influenced the megafauna community distribution patterns. Few attempts have been made to include prey abundance in megafauna distribution models (see Benoit-Bird et al., 2013; Louzao et al., 2019) due to the difficulty of obtaining simultaneous information on both trophic levels. The results of the present study demonstrate the added value of simultaneously collected biological information, which is only possible by using monitoring systems such as integrated oceanographic surveys (Doray et al., 2017).

Our main objective was to characterise the spatial overlap in species niches but it is important to recognise that species coexistence also has temporal dimensions, and pooling data from several years will have prevented us from capturing the inter-annual variability shown by certain species in the BoB (Lambert et al., 2018). Species with narrower and wider habitat preferences have previously been shown to display lower (bottlenose dolphins and auks) and higher (gannets) variability among years, respectively (Lambert et al., 2018).

4.2. Niche segregation

Habitat models for species in the megafauna community were characterised by a high variability in the relative importance of different environmental descriptors, suggesting species-specific niche preferences. In fact, the community was segregated in four different ecological groups in terms of niche preference, shaped by the main overall niche descriptors in addition to other prey fields (zooplankton and phytoplankton biomass).

All clusters of megafauna were influenced primarily by preyscape (FISH and FISHSD) biomass and additional dynamic descriptors (SST and SSTG). Even with the present results on niche segregation were based on presence/absence data, our results

were in agreement with results on preferred oceanographic habitats of certain species based on abundance data collected in the study area and French Atlantic waters (see below). Summarising pelagic fish biomass in a synthetic descriptor helped us understand the role of preyscapes in driving overall community distribution patterns, and paves the way for future analyses of specific megafauna-prey relationships.

Species of cluster 1 such as the northern gannet, yellow-legged and lesser black-backed gulls, and long-finned pilot whales, were widely distributed over the entire shelf and slope areas. All three bird species are widely distributed over the study area, as also observed in the Bay of Biscay (Certain et al., 2011; Lambert et al., 2018). Northern gannets and yellow-legged gulls have been identified as central species within the autumn marine megafauna and pelagic prey community of the Bay of Biscay (Astarloa et al., 2019).

Cluster 2 included a taxonomically diverse group of species, with the common dolphin, great skua and sunfish occurring in the Atlantic sector of the study area. Common dolphins have been previously linked to the presence of three species of pelagic fishes (i.e. anchovy, sprat *Sprattus sprattus*, and small sardine) (Certain et al., 2011). The association of great skuas with pelagic fishes was also been suggested by Certain et al. (2011), who proposed an association with fishing discards, which are likely to be highly available in the western sector of the study area due to a hotspot of trawling activity (Pennino et al., 2019). Cluster 3 was formed by species of shallow waters associated with frontal systems, in agreement to previous studies modelling auk (and razorbill) (Lambert et al., 2017) and shag (Virgili et al., 2017) abundance. In addition, the Balearic shearwater is a typical shelf seabird species, highly associated with cool marine waters in its non-breeding distribution range in the NE Atlantic (Araújo et al., 2017; Pérez-Roda et al., 2017). The relationship between SST conditions

and Balearic shearwater Atlantic distribution might be a result of food web links at intermediate trophic levels (e.g. involving plankton and forage fish species such (Luczak et al., 2011; Wynn et al., 2007).

Finally, cluster 4 was composed by species that appeared to preferentially inhabit the Cantabrian Sea, especially the eastern sector, such as bottlenose dolphins and common guillemots, mainly driven by higher SST values within the study area. While offshore bottlenose dolphin population preferred the slope areas of the Bay of Biscay (Lambert et al., 2017), the southern population off Galicia (differentiated from the northern population off Galicia in a stable isotope study by Fernández et al. (2011)) is known to inhabit the coastal inlets (i.e. rías) in southern Galicia. However, PELACUS surveys did not well cover the inshore waters of these coastal inlets. The common guillemot was also present in coastal areas of the eastern Cantabrian Sea (Le Rest et al., 2016), associated with frontal systems (Lambert et al., 2017).

4.3. *Megafauna diversity hotspots*

The frequent co-occurrence of different marine megafauna species allows the identification of hotspots of biodiversity in the NW and N Iberian waters. While cluster 1 grouped wide-ranging species, the remaining assemblages were geographically more restricted, with cluster 2 and 3 species occurring mainly in shelf/slope and coastal/shelf waters, respectively of Galicia and Cluster 4 containing species with higher niche preferences in the Cantabrian Sea. Even though different species differed in their predicted habitats, we were able to provide a consistent description of megafauna hotspot areas. The highest predicted megafauna diversity was found in the western sector, covering both the continental shelf and shelf-break. In the Cantabrian Sea,

megafauna hotspots were predicted in scattered small areas over the narrow continental shelf. Even with the methodological limitations of our study (e.g., aggregation of several years to increase the number of species that could be considered, and the use of general ecological descriptors), our results complement those of previous studies of megafauna hotspots. The eight marine Important Bird Areas (IBAs) identified over the northwestern and northern Iberian continental shelf during early autumn (Arcos et al., 2009) roughly corresponded to the high biodiversity areas we have identified in spring. These results seem to indicate temporal persistency, at least during two seasonal periods, of megafauna biodiversity hotspots.

Similar spatial assessments have been performed in the study area (McClellan et al., 2014) and these authors acknowledged the limitation of not including preyscapes. Our study suggests a way forward whereby prey abundance data based on acoustic estimates is used to obtain prey fields simultaneously to the sightings of megafauna, an approach which is not possible with other sampling techniques (i.e. trawling, Torres et al., 2008), and provides a more suitable data set for modelling predator distribution in relation to their prey. Our approach highlights the advantage of using multidisciplinary oceanographic surveys to collect information on ecological descriptors for spatial ecological assessments. Further development could also integrate the in-situ collected oceanographic descriptors from integrated ecosystem surveys, which might be more suited to match the timescales of annual monitoring schemes (Louzao et al., 2019). The integration of information on ecosystem structure and dynamics would allow the future development of spatial abundance models that can contribute to ecosystem-based management (McClellan et al., 2014), that could inform management measures such as those related to the EU's Marine Strategy Framework Directive (MSFD).

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775 **Table 1.** List of the marine megafauna taxa observed during the IEO PELACUS surveys (2007-
 776 2013), ordered by the Number of Cells with Presence (NCP). The percentage occupancy (Occ) was
 777 estimated as the number of cells occupied divided by the number of cells in the standard grid
 778 (composed by 461 cells). The species that meet the criterion of presence in at least 20 grid cells (out
 779 of 461) are indicated in bold and their acronyms are provided.

Group	Common name	Acronym	Scientific name	NCP	Occ (%)
Cetaceans	Common dolphin	DELDEL	<i>Delphinus delphis</i>	58	11.18
	Long-finned pilot whale	GLOMEL	<i>Globicephala melas</i>	34	6.55
	Bottlenose dolphin	TURTRU	<i>Tursiops truncatus</i>	34	6.55
	Small dolphins	-----	Delphinidae	23	4.43
	Risso's dolphin	-----	<i>Grampus griseus</i>	5	0.96
	Mesoplodon whales	-----	<i>Mesoplodon</i> spp.	2	0.39
	Common porpoise	-----	<i>Phocoena phocoena</i>	2	0.39
	Striped dolphin	-----	<i>Stenella coeruleoalba</i>	2	0.39
	Minke whale	-----	<i>Balaenoptera acutorostrata</i>	1	0.19
	Fin whale	-----	<i>Balaenoptera physalus</i>	1	0.19
	Baleen whales	-----	<i>Balaenoptera</i> spp.	1	0.19
	Sperm whale	-----	<i>Physeter macrocephalus</i>	1	0.19
	False killer whale	-----	<i>Pseudorca crassidens</i>	1	0.19
	Beaked whale	-----	Ziphiidae	1	0.19
Seabirds	Northern gannet	MORBAS	<i>Morus bassanus</i>	383	73.80
	Yellow-legged gull	LARMIC	<i>Larus michahellis</i>	309	59.54
	Lesser black-backed gull	LARFUS	<i>Larus fuscus</i>	288	55.49
	Great skua	STESKU	<i>Stercorarius skua</i>	133	25.63
	Sandwich tern	THASAN	<i>Thalasseus sandvicensis</i>	80	15.41
	Razorbill	ALCTOR	<i>Alca torda</i>	33	6.36
	Balearic shearwater	PUFMAU	<i>Puffinus mauretanicus</i>	32	6.17
	Mediterranean gull	ICTMEL	<i>Ichthyaeus melanocephalus</i>	29	5.59
	European shag	PHAARI	<i>Phalacrocorax aristotelis</i>	28	5.39
	Common guillemot	URIAAL	<i>Uria aalge</i>	21	4.05
	Terns	-----	<i>Sterna</i> spp.	17	3.28
	Cory's/Scopoli's shearwater	-----	<i>Calonectris borealis/C. diomedea</i>	14	2.70
	Manx shearwater	-----	<i>Puffinus puffinus</i>	13	2.50
	Black-headed gull	-----	<i>Chroicocephalus ridibundus</i>	11	2.12
	Cormorants	-----	<i>Phalacrocorax</i> spp.	10	1.93
	Common tern	-----	<i>Sterna hirundo</i>	9	1.73

	Sooty shearwater	-----	<i>Ardenna grisea</i>	8	1.54
	Shearwaters	-----	<i>Puffinus</i> spp.	7	1.35
	Guillemot / Razorbill	-----		6	1.16
	Northern fulmar	-----	<i>Fulmarus glacialis</i>	6	1.16
	Great cormorant	-----	<i>Phalacrocorax carbo</i>	6	1.16
	Arctic skua	-----	<i>Stercorarius parasiticus</i>	6	1.16
	Atlantic Puffin	-----	<i>Fratercula arctica</i>	4	0.77
	Skuas	-----	<i>Stercorarius</i> spp.	4	0.77
	Pomarine skua	-----	<i>Stercorarius pomarinus</i>	4	0.77
	Black-legged kittiwake	-----	<i>Rissa tridactyla</i>	3	0.58
	Black tern	-----	<i>Chlidonias niger</i>	2	0.39
	Arctic tern	-----	<i>Sterna paradisaea</i>	2	0.39
	European storm petrel	-----	<i>Hydrobates pelagicus</i>	1	0.19
	European Herring Gull	-----	<i>Larus argentatus</i>	1	0.19
	Common gull	-----	<i>Larus canus</i>	1	0.19
	Great black-backed gull	-----	<i>Larus marinus</i>	1	0.19
	Little gull	-----	<i>Hydrocoloeus minutus</i>	1	0.19
	Litter tern	-----	<i>Sterna albifrons</i>	1	0.19
Fish es	Sunfish	MOLSPP	<i>Mola</i> spp.	37	7.13
	Baliste	-----	<i>Balistes</i> spp.	1	0.19

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Table 2. List of the ecological descriptors used to characterise the niches of marine megafauna species in the northern and northwestern Iberian Peninsula. Descriptors indicated by an asterisk were removed due to collinearity with other descriptors (VIF > 5).

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Ecological descriptor	Source	Methodology	Time window	Ecological process
Dynamic				
Phytoplankton (PHY)*	PELACUS surveys	Net sampling	2005-2011	Mean chlorophyll concentration of microplankton (40-200µm size-fraction)
PHY standard deviation (PHYSD)	PELACUS surveys	Net sampling	2005-2011	Inter-annual variability of PHY
Zooplankton (ZOO)	PELACUS surveys	Net sampling	2007-2013	Mean biomass of zooplankton (dry weight for the 200-2000µm size-fraction)
ZOO standard deviation (ZOOSD)	PELACUS surveys	Net sampling	2007-2013	Inter-annual variability of ZOO
Pelagic fish (FISH)	PELACUS surveys	Acoustic surveys	2007-2011	Mean biomass of pelagic fish
FISH standard deviation (FISHSD)	PELACUS surveys	Acoustic surveys	2007-2011	Inter-annual variability of FISH
Chlorophyll a (CHL)*	Bio-ORACLE	Satellite imagery & interpolation	2003-2011	Ocean productivity domains (satellite-derived surface chlorophyll a as proxy)
CHL's spatial gradient (CHLG)	Bio-ORACLE	Satellite imagery & interpolation		Frontal systems
CHL range (CHLR)	Bio-ORACLE	Satellite imagery & interpolation		Inter-annual variability of CHL
Sea surface temperature (SST)	Bio-ORACLE	Satellite imagery & interpolation		Water bodies
SST gradient (SSTG)	Bio-ORACLE	Satellite imagery & interpolation		Frontal systems
SST range (SSTR)*	Bio-ORACLE	Satellite imagery & interpolation		Inter-annual variability of SST
Static				
Bathymetry (BAT, m)	ETOPO		----	Coastal versus pelagic domains
BAT gradient (BATG)	ETOPO		----	Presence of physiographic features (e.g., shelf-break, seamounts)
Distance to coast (COAST, km)*			----	Onshore–offshore distribution patterns
Distance to shelf	ETOPO		----	Influence of the shelf-break

break (BREAK, km)

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Table 3. Generalized Additive Modelling output, highlighting the predictive performance of megafauna distribution models based on the adjusted R-squared (AdjR), sensitivity, specificity, threshold probability and the Area Under the Curve (AUC). See Table 1 for acronyms.

Species	AdjR	Sensitivity	Specificity	Threshold	AUC
PHAARI	0.674	0.895	0.900	0.040	0.898
ALCTOR	0.466	0.844	0.855	0.110	0.850
LARMIC	0.420	0.726	0.727	0.640	0.727
DELDEL	0.381	0.810	0.782	0.160	0.796
MOLSPP	0.293	0.784	0.807	0.090	0.795
MORBAS	0.277	0.705	0.705	0.740	0.705
ICTMEL	0.275	0.815	0.827	0.090	0.821
PUFMAU	0.259	0.700	0.752	0.090	0.726
URIAAL	0.215	0.800	0.796	0.060	0.798
STESKU	0.191	0.682	0.681	0.280	0.681
LARFUS	0.165	0.641	0.665	0.590	0.653
TALSAN	0.163	0.689	0.623	0.160	0.656
TURTRU	0.162	0.727	0.731	0.090	0.729
GLOMEL	0.121	0.667	0.699	0.080	0.683

Table 4. Mean $\pm$ SD of relative importance of ecological descriptors for the overall community and each megafauna cluster. Contributions higher than 0.10% are highlighted in bold. See table 2 for acronyms.

Variable	Overall	Cluster 1	Cluster 2	Cluster 3	Cluster 4
BAT	0.090 $\pm$ 0.039	0.089 $\pm$ 0.047	0.096 $\pm$ 0.047	0.079 $\pm$ 0.040	0.110 $\pm$ 0.028
BATG	0.071 $\pm$ 0.035	0.087 $\pm$ 0.033	0.053 $\pm$ 0.050	0.073 $\pm$ 0.035	0.060 $\pm$ 0.018
CHLG	0.083 $\pm$ 0.036	0.073 $\pm$ 0.038	0.088 $\pm$ 0.042	0.075 $\pm$ 0.033	0.116 $\pm$ 0.045
CHLR	0.065 $\pm$ 0.024	0.062 $\pm$ 0.026	0.055 $\pm$ 0.018	0.069 $\pm$ 0.032	0.074 $\pm$ 0.005
BREAK	0.086 $\pm$ 0.034	0.097 $\pm$ 0.038	0.110 $\pm$ 0.007	0.076 $\pm$ 0.038	0.057 $\pm$ 0.007
FISH	0.103 $\pm$ 0.033	0.095 $\pm$ 0.036	0.131 $\pm$ 0.009	0.099 $\pm$ 0.041	0.090 $\pm$ 0.005
FISHSD	0.104 $\pm$ 0.045	0.115 $\pm$ 0.042	0.096 $\pm$ 0.056	0.103 $\pm$ 0.048	0.100 $\pm$ 0.071
PHYSD	0.067 $\pm$ 0.028	0.070 $\pm$ 0.032	0.076 $\pm$ 0.032	0.059 $\pm$ 0.028	0.067 $\pm$ 0.031
SSTG	0.089 $\pm$ 0.045	0.124 $\pm$ 0.030	0.055 $\pm$ 0.031	0.096 $\pm$ 0.051	0.051 $\pm$ 0.007
SST	0.100 $\pm$ 0.046	0.066 $\pm$ 0.037	0.089 $\pm$ 0.040	0.105 $\pm$ 0.058	0.132 $\pm$ 0.022
ZOO	0.074 $\pm$ 0.029	0.061 $\pm$ 0.014	0.083 $\pm$ 0.036	0.083 $\pm$ 0.039	0.061 $\pm$ 0.022
ZOOSD	0.074 $\pm$ 0.035	0.062 $\pm$ 0.035	0.068 $\pm$ 0.032	0.083 $\pm$ 0.037	0.085 $\pm$ 0.057

Fig. 1. Map of the study area showing observed megafauna richness obtained by summing presences across all taxa considered for each spatial cell within the standard grid.

806 **Fig. 2.** Average values of ecological descriptors obtained during the IEO PELACUS surveys: (a) 40-200 μm phytoplankton chlorophyll
807 concentration (2005-2011), (c) zooplankton biomass (mg m^{-2}) (2005-2013) and (e) pelagic fish (t m^{-2}) (2007-2011). (b), (d) and (f) represent the
808 corresponding temporal variability represented by the coefficient of variation during the study period for microplankton, zooplankton and pelagic
809 fish, respectively. See Fig. 1 for geographical references.

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813 **Fig. 3. Relative importance of ecological descriptors for each megafauna taxa. See**
814 **Table 1 and 2 for species and descriptor acronyms.**

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Fig.4. Identification of megafauna clusters depending on the predicted presence probability based on hierarchical clustering. Significant clusters with probability $P \geq 0.95$ are indicated by red rectangles, and the 35% similarity level by a black dotted line.

Fig. 5. Identification of biodiversity hotspots for the megafauna community using predicted megafauna species richness index by summing all species predicted presence and absence values based on the threshold probabilities at which predicted presence (sensitivity) and absence (specificity) were maximized. Isobaths of 100 m, 200 m, 500 m and 1000 m are shown. See Fig. 1 for geographical references.

Highlights:

- Synoptically collected acoustic-based preyscapes were the most important variables explaining megafauna niche preference
- Four distinct megafauna assemblages constituted by wide-ranging species and more restricted species present in specific areas
- Megafauna richness higher in the western shelf and shelf-break sectors.
- Advantage of using integrated monitoring schemes to collect simultaneous information on ecosystem components for spatial assessments.