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1 **Marine megafauna niche coexistence and**  
2 **hotspot areas in a temperate ecosystem**

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30

## 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;

## 60 1. Introduction

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

75 Marine megafauna species have been proposed as indicators of the status of the  
76 marine environment (e.g. MAPAMA, 2012; Santos and Pierce, 2015). To aid in the  
77 management of megafauna, we need to identify those ecological descriptors that best  
78 explain species distribution. By obtaining spatial predictions for multiple species,  
79 ecologically meaningful areas could be defined to inform conservation efforts (Arcos et  
80 al., 2012). In the marine environment, niche models have been traditionally developed  
81 based on ecological descriptors such as chlorophyll *a* and sea surface temperature (e.g.  
82 Arrizabalaga et al., 2014; Louzao et al., 2013; McGowan et al., 2013; Pérez-Jorge et al.,  
83 2015; Redfern et al., 2006) since megafauna species may use oceanographic variables as  
84 cues for locating prey as well as responding directly to oceanographic conditions, for

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

90         Multidisciplinary oceanographic surveys provide a suitable monitoring platform  
91 to gather simultaneously oceanographic and biological information on the distribution  
92 and abundance of different trophic levels, from plankton to marine megafauna (Doray et  
93 al., 2017). The biological information recorded includes estimates of the biomass of  
94 species such as pelagic fishes, which are important prey for several marine megafauna  
95 species (e.g. Astarloa et al., 2019; Certain et al., 2011; Mèndez-Fernandez et al., 2012;  
96 Santos et al., 2014, 2013; Spitz et al., 2014). The PELACUS spring surveys of the  
97 Spanish Institute of Oceanography (IEO) have been conducted annually since the late  
98 1980s to inform the assessment of pelagic fish stocks in the northern and northwestern  
99 Atlantic continental shelf of the Iberian Peninsula using acoustic methods (Santos et al.,  
100 2013). Ancillary oceanographic and biological data (i.e. phytoplankton and zooplankton  
101 biomass) are collected to help characterise the structure, functioning and dynamics of  
102 the pelagic ecosystem. Since 2007, sightings of marine megafauna (e.g. marine  
103 mammals and seabirds) have been routinely collected by dedicated observers (Saavedra  
104 et al., 2018), in addition to the collection of information on the presence, type and  
105 abundance of different indicators of human pressures (e.g., fishing vessels, marine  
106 debris). Recently, marine litter sampling was also implemented within these surveys  
107 (Gago et al., 2015).

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

110 includes many megafauna species (Authier et al., 2018; García-Barón et al., 2019;  
111 Lambert et al., 2017; Pettex et al., 2017; Sims et al., 2009, 2003; Virgili et al., 2017). It  
112 represents an important migration flyway for European seabirds, thousands of which  
113 cross this biogeographic area (Arcos et al., 2009; Fort et al., 2012; Louzao et al., 2015).  
114 The study area also offers suitable habitats for a range of cetacean species, with a  
115 diverse physiographic environment that combines narrow and wide shelves indented  
116 with several canyon systems, seamounts and an extensive oceanic realm (Kiszka et al.,  
117 2007). In addition, there are multiple interacting oceanographic processes, such as slope  
118 currents, upwelling-downwelling processes, river plumes and various types of eddy-like  
119 structures (e.g. Charria et al., 2017; González-Pola et al., 2012; Kersalé et al., 2016;  
120 Koutsikopoulos and Le Cann, 1996).

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

## 134 **2. Methods**

135 2.1. *Data collection*

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

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

152 The Beaufort sea-state level ranged from 0 to 8 during the observation time of  
153 the seven surveys analysed (2007-2013, Fig. S1a). Mean overall conditions varied  
154 markedly among years (non-parametric Kruskal-Wallis test  $H_{6,65052} = 8340.56$ ,  $P <$   
155  $0.001$ ) (Fig. S1b, S1c). Sea state conditions were especially good in 2007 and 2011,  
156 whereas conditions were especially rough in 2008, 2010 and 2013. Beaufort state lower  
157 or equal to 3 is generally considered good sea state conditions to detect marine  
158 mammals (see Hammond et al., 2013). Based on this threshold, the mean percentage of



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

163

## 164 2.2. *Ecological descriptors*

### 165 2.2.1. *Multi-trophic survey information*

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

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

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

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

202

### 203 2.2.2. Independent oceanographic variables

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

207 used for the development of marine species distribution models. This dataset is a  
208 comprehensive assemblage (e.g., satellite-based and *in situ* measured data of high-  
209 resolution, approximately 9.2 km) and readily usable package of 23 global  
210 climatological environmental rasters (Tyberghein et al., 2012). We selected those  
211 environmental variables expected to be related to marine megafauna distribution in the  
212 study area, namely sea surface temperature (SST, °C) and chlorophyll *a* (CHL, mg m<sup>-3</sup>),  
213 to describe, respectively, overall water mass distribution and productivity domains. In  
214 addition, we used the annual ranges (difference between maximum and minimum) of  
215 both oceanographic variables within the climatological time series (Tyberghein et al.,  
216 2012). Finally, spatial gradients of averaged SST and CHL (SSTG and CHLG) were  
217 estimated as the proportional changes (SG) in these variables within a surrounding 3x3  
218 cell grid using a moving window as follows:  $SG = [(maximum\ value - minimum\ value)$   
219  $\times 100] / (maximum\ value)$  (Louzao et al., 2006).

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

232 2.3. *Data processing*

233 We created a standard grid over the study area (latitudinal range: 42°-44°N;  
234 longitudinal range: 10°-1°W) to map biological observations with a spatial cell size of  
235 0.0833° (approximately 9 km covering ca. 81km<sup>2</sup>) to match the spatial resolution of  
236 environmental variables. For each megafauna species, we overlaid all sightings for the  
237 2007-2013 period over the standard grid and grid cells with at least one observation  
238 were coded as “presence”, while the remaining cells were coded as “absence”. For each  
239 species, we counted the number of cells with presence across the 7-year period. Due to  
240 the high number of species with low numbers of presence records (even when data were  
241 pooled across years), we established a cut-off of 20 presence records (NCPs) when  
242 selecting the megafauna species for further niche modelling. This number was  
243 considered as a good compromise to increase the number of species characterising the  
244 megafauna community. We mapped the observed species richness by counting the  
245 number of species present in each grid cell.

246 Biomasses of phytoplankton, zooplankton and pelagic fish (after log-  
247 transforming) were overlaid over the standard grid and interpolated based on the inverse  
248 distance weighted interpolation using the *gstat* package (Pebesma, 2004; Gräler et al.,  
249 2016). Synthetic ecological descriptors were obtained by estimating the mean and the  
250 standard deviation (i.e. variability) per grid cell across all available years for each  
251 descriptor. Therefore, three trophic layers were obtained describing overall (i.e. mean)  
252 spatial patterns of phytoplankton, zooplankton and pelagic fish biomass (PHY, ZOO  
253 and FISH), as well as their variability (i.e. standard deviation, PHYSD, ZOOSD and  
254 FISHSD) (see Table 2 and Fig. 2).

255 2.4. *Marine megafauna distribution models*

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

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

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

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

287

288

### 289 2.5. Marine megafauna assemblages and community hotspots

290 Marine megafauna niche preference was described at the community and  
291 assemblage level. These analyses are based on the relative predictor importance for  
292 each megafauna species obtained from niche modelling. At the community level, we  
293 identified the relative importance of ecological descriptors by the mean and standard  
294 deviation (i.e. SD) across all species. Overall niche preference was characterised by the  
295 mean  $\pm$  SD of the main ecological descriptors contributing more than 0.10%. At the  
296 assemblage level, we firstly performed a hierarchical clustering analysis based on the  
297 averaged predicted presence of each megafauna species to identify megafauna  
298 assemblages sharing similar niche preferences. For this, we used the *Pvclust* package,  
299 specifying the Euclidean distance and Ward agglomeration method (Suzuki and  
300 Shimodaira, 2006). *Pvclust* calculates *P-values* for hierarchical clustering via multi-  
301 scale bootstrap resampling and significant clusters with probability  $P \geq 0.95$  were  
302 extracted. Secondly, niche preferences of each assemblage (i.e. cluster) were described  
303 by the mean  $\pm$  SD of the main non-correlated ecological descriptors (Louzao et al.,  
304 2014).

305 In order to identify megafauna hotspots, we estimated the threshold probability  
306 at which both predicted presence (sensitivity) and absence (specificity) were maximized  
307 for each species. For each megafauna species, the predicted presence probability ranging  
308 from 0 to 1 was transformed into suitable and non-suitable areas corresponding to grid  
309 cell values higher and lower than the threshold probability, respectively (Louzao et al.,  
310 2006). Then, we estimated the predicted megafauna species richness index for each cell  
311 by summing all suitable areas across species and within grid cells. Megafauna hotspots  
312 were identified as the marine areas where a higher number of megafauna species was  
313 predicted to be present.

314

### 315 **3. Results**

#### 316 *3.1. Megafauna community*

317 Sightings of the megafauna community in the northwestern and northern Iberian  
318 shelf during spring included at least 10 species of cetaceans, 28 species of seabirds and  
319 2 genus of pelagic fish (see Table 1). The fish seen by the observers were sunfish *Mola*  
320 spp., which was recorded as present in 37 grid cells and triggerfish *Balistes* spp. (present  
321 in only 1 cell). The cetacean species with the highest occupancy were common dolphin  
322 *Delphinus delphis*, bottlenose dolphin *Tursiops truncatus* and long-finned pilot whale  
323 *Globicephala melas*. The seabird species with the highest occupancy (with more than  
324 100 cells with presence records) were northern gannet *Morus bassanus*, yellow-legged  
325 gull *Larus michahellis*, lesser black-backed gull *L. fuscus*, great skua *Stercorarius skua*,  
326 followed by (with less than 100 cells with presence records) sandwich tern *Thalasseus*  
327 *sandvicensis*, razorbill *Alca torda*, Balearic shearwater *Puffinus mauretanicus*,  
328 Mediterranean gull *Ichthyophaga melanocephalus*, European shag *Phalacrocorax*  
329 *aristotelis* and common guillemot *Uria aalge*.

330 Following the criterion of a minimum number of cells with presence records  
331 (<20), 14 taxa were considered for further analysis (see Table 1). The highest observed  
332 species richness (i.e. highest number of megafauna species/taxa) was located in the  
333 western sector of the study area, in Galicia, followed by a smaller local concentration in  
334 the eastern Cantabrian Sea (Fig. 1).

### 335 3.2. *Megafauna assemblages*

336 The megafauna distribution models yielded a reasonable predictive performance  
337 since models for most species showed an AUC value higher than 0.7 (Table 3), with an  
338 overall community average of 0.751 (SD = 0.070) . The adjusted R-squared varied from  
339 0.121 (long-finned pilot whale) to 0.674 (European shag). The mean sensitivity and  
340 specificity values were 0.749 (0.641 – 0.895) and 0.754 (0.623 – 0.900), respectively,  
341 indicating high proportions of both true predicted presences and true predicted  
342 absences.

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



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

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

378 .

379

### 380 3.3. *Marine megafauna hotspots*

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

388

## 389 4. Discussion

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

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

408

#### 409 4.1. *Marine megafauna community*

410 In the southern sector of the Bay of Biscay (N and NW Iberian Peninsula), the  
411 marine megafauna community investigated in this study was characterised by the  
412 presence of at least 10 species of cetaceans and 28 species of seabirds, as well as two  
413 genus of pelagic fishes. . Most of these species have also been detected in the French  
414 sector of the Bay of Biscay during the spring PELGAS surveys (Authier et al., 2018),  
415 with a similar survey design and characteristics as PELACUS. In both Spanish and  
416 French sectors, the cetacean species with the highest number of records were common  
417 dolphins, bottlenose dolphins, and long-finned pilot whales (this study; Authier et al.,  
418 2017). Among the seabirds, northern gannets, lesser black-backed gulls and great skuas  
419 were the species with the highest number of records in both sectors of the Bay of Biscay  
420 (this study; Authier et al., 2017). Due to differences in survey timing with respect to the  
421 annual phenology of seabirds (which is broadly similar in all species sighted in the  
422 present study), the PELACUS surveys (i.e. March-April) generally coincide with the  
423 pre-breeding migration while the PELGAS surveys (i.e. May) coincide with the start of  
424 the breeding season (this study; Authier et al., 2017). In addition, the most abundant  
425 species detected in each sector differed, reflecting biogeographical limits. Thus, yellow-  
426 legged gulls were highly abundant in northern Iberian waters while northern fulmars  
427 were mostly present in the French sector (this study; Authier et al., 2018; Lambert et al.,  
428 2018).

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

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

443

#### 444 *4.2. Niche segregation*

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

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

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

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

466 Cluster 2 included a taxonomically diverse group of species, with the common  
467 dolphin, great skua and sunfish occurring in the Atlantic sector of the study area.  
468 Common dolphins have been previously linked to the presence of three species of  
469 pelagic fishes (i.e. anchovy, sprat *Sprattus sprattus*, and small sardine) (Certain et al.,  
470 2011). The association of great skuas with pelagic fishes was also been suggested by  
471 Certain et al. (2011), who proposed an association with fishing discards, which are  
472 likely to be highly available in the western sector of the study area due to a hotspot of  
473 trawling activity (Pennino et al., 2019). Cluster 3 was formed by species of shallow  
474 waters associated with frontal systems, in agreement to previous studies modelling auk  
475 (and razorbill) (Lambert et al., 2017) and shag (Virgili et al., 2017) abundance. In  
476 addition, the Balearic shearwater is a typical shelf seabird species, highly associated  
477 with cool marine waters in its non-breeding distribution range in the NE Atlantic  
478 (Araújo et al., 2017; Pérez-Roda et al., 2017). The relationship between SST conditions

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

482

483 Finally, cluster 4 was composed by species that appeared to preferentially  
484 inhabit the Cantabrian Sea, especially the eastern sector, such as bottlenose dolphins  
485 and common guillemots, mainly driven by higher SST values within the study area.  
486 While offshore bottlenose dolphin population preferred the slope areas of the Bay of  
487 Biscay (Lambert et al., 2017), the southern population off Galicia (differentiated from  
488 the northern population off Galicia in a stable isotope study by Fernández et al. (2011))  
489 is known to inhabit the coastal inlets (i.e. rías) in southern Galicia. However, PELACUS  
490 surveys did not well cover the inshore waters of these coastal inlets. The common  
491 guillemot was also present in coastal areas of the eastern Cantabrian Sea (Le Rest et al.,  
492 2016), associated with frontal systems (Lambert et al., 2017).

493

#### 494 4.3. *Megafauna diversity hotspots*

495 The frequent co-occurrence of different marine megafauna species allows the  
496 identification of hotspots of biodiversity in the NW and N Iberian waters. While cluster  
497 1 grouped wide-ranging species, the remaining assemblages were geographically more  
498 restricted, with cluster 2 and 3 species occurring mainly in shelf/slope and coastal/shelf  
499 waters, respectively of Galicia and Cluster 4 containing species with higher niche  
500 preferences in the Cantabrian Sea. Even though different species differed in their  
501 predicted habitats, we were able to provide a consistent description of megafauna  
502 hotspot areas. The highest predicted megafauna diversity was found in the western  
503 sector, covering both the continental shelf and shelf-break. In the Cantabrian Sea,

504 megafauna hotspots were predicted in scattered small areas over the narrow continental  
505 shelf. Even with the methodological limitations of our study (e.g., aggregation of  
506 several years to increase the number of species that could be considered, and the use of  
507 general ecological descriptors), our results complement those of previous studies of  
508 megafauna hotspots. The eight marine Important Bird Areas (IBAs) identified over the  
509 northwestern and northern Iberian continental shelf during early autumn (Arcos et al.,  
510 2009) roughly corresponded to the high biodiversity areas we have identified in spring.  
511 These results seem to indicate temporal persistency, at least during two seasonal  
512 periods, of megafauna biodiversity hotspots.

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

528

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543

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545

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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	<b>Common dolphin</b>	<b>DELDEL</b>	<b><i>Delphinus delphis</i></b>	<b>58</b>	<b>11.18</b>
	<b>Long-finned pilot whale</b>	<b>GLOMEL</b>	<b><i>Globicephala melas</i></b>	<b>34</b>	<b>6.55</b>
	<b>Bottlenose dolphin</b>	<b>TURTRU</b>	<b><i>Tursiops truncatus</i></b>	<b>34</b>	<b>6.55</b>
	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	<b>Northern gannet</b>	<b>MORBAS</b>	<b><i>Morus bassanus</i></b>	<b>383</b>
<b>Yellow-legged gull</b>		<b>LARMIC</b>	<b><i>Larus michahellis</i></b>	<b>309</b>	<b>59.54</b>
<b>Lesser black-backed gull</b>		<b>LARFUS</b>	<b><i>Larus fuscus</i></b>	<b>288</b>	<b>55.49</b>
<b>Great skua</b>		<b>STESKU</b>	<b><i>Stercorarius skua</i></b>	<b>133</b>	<b>25.63</b>
<b>Sandwich tern</b>		<b>THASAN</b>	<b><i>Thalasseus sandvicensis</i></b>	<b>80</b>	<b>15.41</b>
<b>Razorbill</b>		<b>ALCTOR</b>	<b><i>Alca torda</i></b>	<b>33</b>	<b>6.36</b>
<b>Balearic shearwater</b>		<b>PUFMAU</b>	<b><i>Puffinus mauretanicus</i></b>	<b>32</b>	<b>6.17</b>
<b>Mediterranean gull</b>		<b>ICTMEL</b>	<b><i>Ichthyaetus melanocephalus</i></b>	<b>29</b>	<b>5.59</b>
<b>European shag</b>		<b>PHAARI</b>	<b><i>Phalacrocorax aristotelis</i></b>	<b>28</b>	<b>5.39</b>
<b>Common guillemot</b>		<b>URIAAL</b>	<b><i>Uria aalge</i></b>	<b>21</b>	<b>4.05</b>
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	<b>Sunfish</b>	<b>MOLSPP</b>	<b><i>Mola</i> spp.</b>	<b>37</b>	<b>7.13</b>
	Baliste	-----	<i>Balistes</i> spp.	1	0.19

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783 **Table 2.** List of the ecological descriptors used to characterise the niches of marine  
 784 megafauna species in the northern and northwestern Iberian Peninsula. Descriptors  
 785 indicated by an asterisk were removed due to collinearity with other descriptors (VIF >  
 786 5).

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Ecological descriptor	Source	Methodology	Time window	Ecological process
<b>Dynamic</b>				
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
<b>Static</b>				
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
<b>Distance to shelf</b>	ETOPO		----	Influence of the shelf-break

break (BREAK, km)

788

ACCEPTED MANUSCRIPT

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

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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

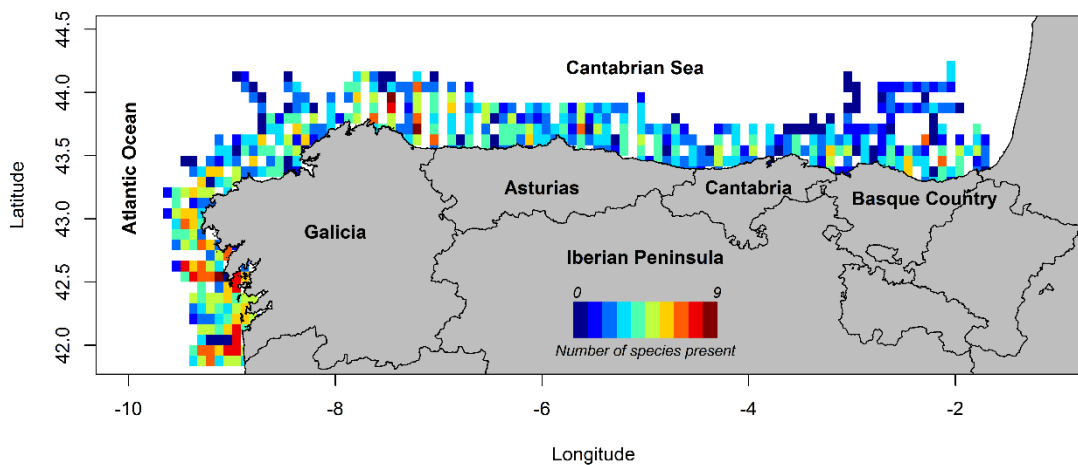
795 **Table 4.** Mean  $\pm$  SD of relative importance of ecological descriptors for the overall  
 796 community and each megafauna cluster. Contributions higher than 0.10% are highlighted  
 797 in bold. See table 2 for acronyms.

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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	<b>0.110 <math>\pm</math> 0.028</b>
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	<b>0.116 <math>\pm</math> 0.045</b>
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	<b>0.110 <math>\pm</math> 0.007</b>	0.076 $\pm$ 0.038	0.057 $\pm$ 0.007
FISH	<b>0.103 <math>\pm</math> 0.033</b>	0.095 $\pm$ 0.036	<b>0.131 <math>\pm</math> 0.009</b>	0.099 $\pm$ 0.041	0.090 $\pm$ 0.005
FISHSD	<b>0.104 <math>\pm</math> 0.045</b>	<b>0.115 <math>\pm</math> 0.042</b>	0.096 $\pm$ 0.056	<b>0.103 <math>\pm</math> 0.048</b>	<b>0.100 <math>\pm</math> 0.071</b>
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	<b>0.124 <math>\pm</math> 0.030</b>	0.055 $\pm$ 0.031	0.096 $\pm$ 0.051	0.051 $\pm$ 0.007
SST	<b>0.100 <math>\pm</math> 0.046</b>	0.066 $\pm$ 0.037	0.089 $\pm$ 0.040	<b>0.105 <math>\pm</math> 0.058</b>	<b>0.132 <math>\pm</math> 0.022</b>
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

800

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



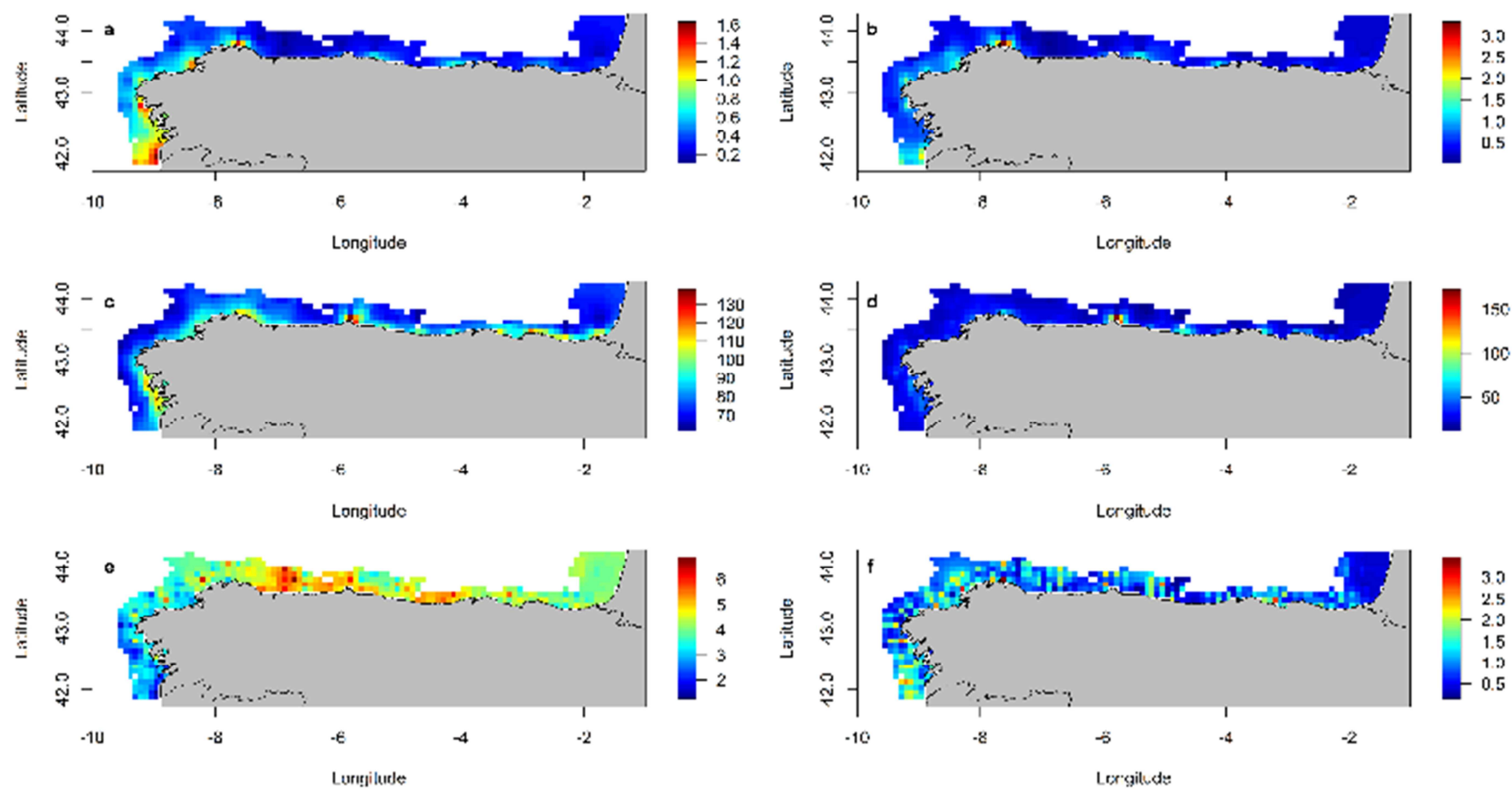
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806 **Fig. 2.** Average values of ecological descriptors obtained during the IEO PELACUS surveys: (a) 40-200  $\mu\text{m}$  phytoplankton chlorophyll  
807 concentration (2005-2011), (c) zooplankton biomass ( $\text{mg m}^{-2}$ ) (2005-2013) and (e) pelagic fish ( $\text{t m}^{-2}$ ) (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.

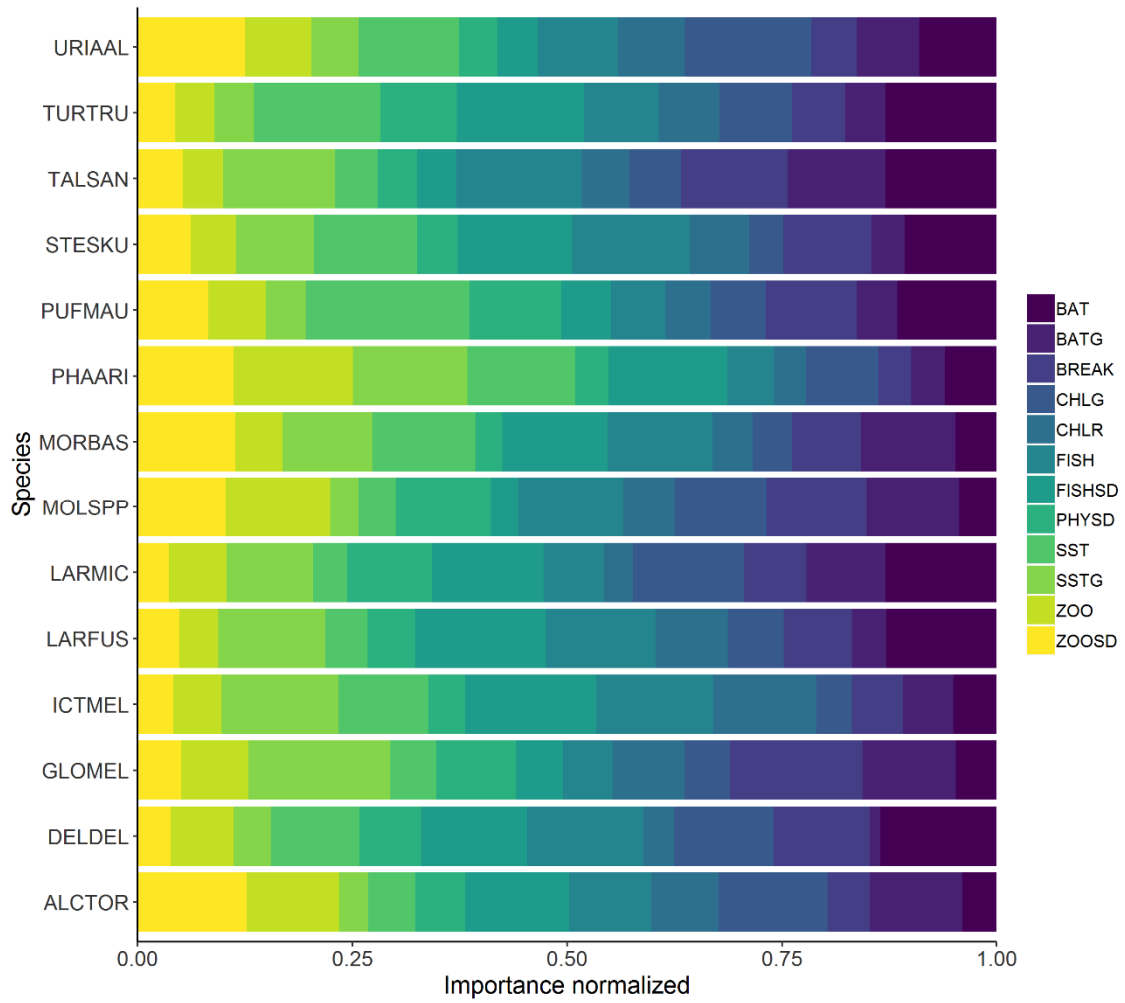
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813 **Fig. 3. Relative importance of ecological descriptors for each megafauna taxa. See**

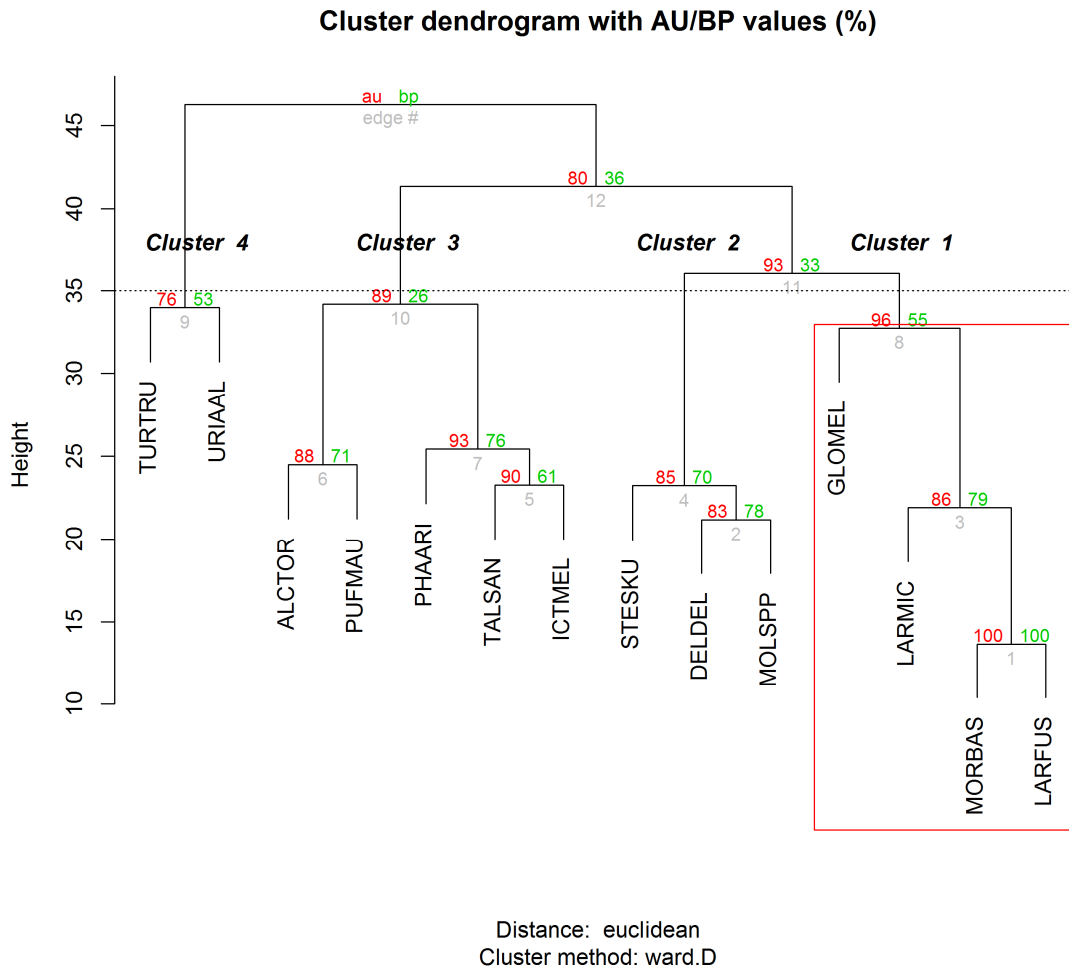
814 Table 1 and 2 for species and descriptor acronyms.



815

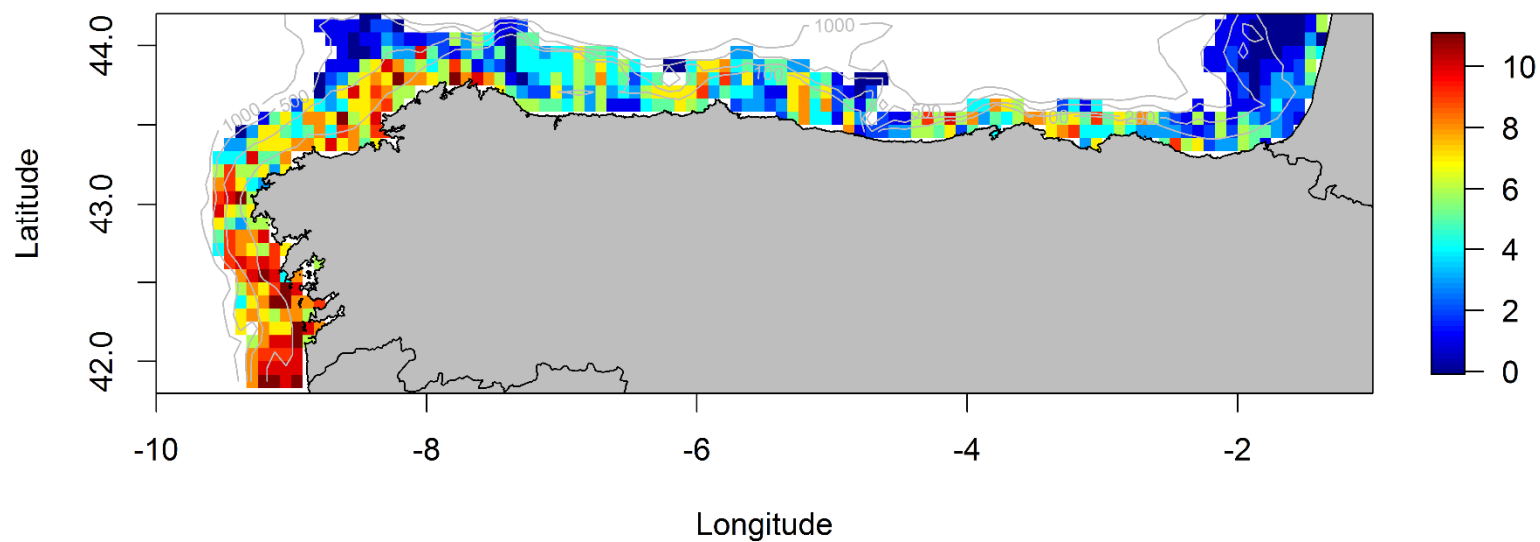


816 **Fig.4.** Identification of megafauna clusters depending on the predicted presence  
 817 probability based on hierarchical clustering. Significant clusters with probability  $P \geq$   
 818 0.95 are indicated by red rectangles, and the 35% similarity level by a black dotted line.  
 819



820

**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.