Original Article

Identifying main interactions in marine predator–prey networks of the Bay of Biscay

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Identifying the role that environmental factors and biotic interactions play in species distribution can be essential to better understand and predict how ecosystems will respond to changing environmental conditions. This study aimed at disentangling the assemblage of the pelagic predator–prey community by identifying interspecific associations and their main drivers. For this purpose, we applied the joint species distribution modelling approach, JSDM, to the co-occurrence patterns of both prey and top predator communities obtained from JUVENA surveys during 2013–2016 in the Bay of Biscay. Results showed that the co-occurrence patterns of top predators and prey were driven by a combination of environmental and biotic factors, which highlighted the importance of considering both components to fully understand the community structure. In addition, results also revealed that many biotic interactions, such as schooling in prey (e.g. anchovy–sardine), local enhancement/facilitation in predators (e.g. Cory's shearwater–fin whale), and predation between predator–prey species (e.g. northern gannet–horse mackerel), were led by positive associations, although predator avoidance behaviour was also suggested between negatively associated species (e.g. striped dolphin–blue whiting). The identification of interspecific associations can therefore provide insights on the functioning of predators–prey network and help advance towards an ecosystem-based management.

Keywords: Bay of Biscay, co-occurrence patterns, environmental drivers, joint species distribution models, positive associations, predator–prey networks, species interactions

Introduction

Climate change has been identified as a major future threat for marine ecosystems (Collins *et al.*, 2013) and it has yet triggered shifts in the abundance, phenology, and distribution of organisms (Doney *et al.*, 2012; Poloczanska *et al.*, 2013). The assessment of these changes has been typically conducted considering only climatic factors, based on the assumption that biotic interactions might play a minor role in governing species distribution at regional to global scales (Pearson and Dawson, 2003). However, it is now generally accepted that interspecific interactions can strongly affect the biogeography of species beyond local extents (Araújo and Luoto, 2007; Wisz *et al.*, 2013). Therefore, it

is essential to understand the interplay between environmental factors and biotic interactions to better anticipate how ecosystems will respond (Gilman *et al.*, 2010; Blois *et al.*, 2013).

Biotic interactions are known to affect species spatial patterns via several mechanism such as predation, competition, parasitism, mutualism, and facilitation (Wisz *et al.*, 2013). Identifying such associations has long been a subject of ecological research that has been tackled by studying species co-occurrence patterns and specifically by comparing observed occurrences with null models to detect non-random patterns (for approaches based on randomized null models see Gotelli and Ulrich, 2010; for analytical null models see Veech, 2013). These conventional approaches,

however, do not allow to distinguish whether the resulting associations derive from the species having (dis-) similar habitat requirements or from a biotic relationship. In fact, a positive association may be caused by biotic interactions (e.g. facilitation) or by shared environmental requirements (e.g. similar habitat affinities) whereas negative associations may be driven by biotic interactions (e.g. competition) or reflect different habitat preferences (Ovaskainen *et al.*, 2010). Lately, new approaches including niche associations and network theory have been developed to infer species associations (Morueta-Holme *et al.*, 2016). In parallel, other methods consisting of incorporating species co-occurrence data into the classical species distribution model framework have emerged (Clark *et al.*, 2014; Pollock *et al.*, 2014; Warton *et al.*, 2015; Hui, 2016). By combining both components, joint species distribution models (JSDMs hereafter) allow the study of correlation patterns across taxa at the same time as studying environmental response (Warton *et al.*, 2015); as a result, species co-occurrence patterns can be decomposed into environmental responses and residual correlation not explained by the measured predictors (Hui, 2016). A key step consists then in attributing this residual correlation with biotic interactions, as there could also be non-biological explanations such as missing environmental variables or poor model fit (Zurell *et al.*, 2018). Some authors, however, have already succeed in identifying biotic interactions, including codominance in trees (Pollock *et al.*, 2014) and heterospecific attraction in river birds (Royan *et al.*, 2016). In contrast, the implementation of JSDMs on predator–prey co-occurrence patterns has been scarcely explored (Zurell *et al.*, 2018) and as a result, the potential to detect ecological processes such as predation or competition needs further investigation.

In the Bay of Biscay (BoB hereafter), the upwelling occurring mainly over the Iberian Shelf section and the river run-offs of the French shelf (Aquarone *et al.*, 2008) favours the occurrence of a rich community of small pelagic fishes, including European sardine *Sardina pilchardus*, European anchovy *Engraulis encrasicolus*, Atlantic mackerel *Scomber scombrus*, and Atlantic horse mackerel *Trachurus trachurus* (ICES, 2008). In addition, the BoB also holds a rich cetacean fauna (Kiszka *et al.*, 2007; Spitz *et al.*, 2011) and a highly diverse seabird population (Pettex *et al.*, 2017), including some endangered species such as fin whale *Balaenoptera physalus* (García-Barón *et al.*, 2019) and Balearic shearwater *Puffinus mauretanicus* (Pérez-Roda *et al.*, 2017) that make the identification of interspecific associations essential to advance towards an ecosystem-based management (Veit and Harrison, 2017). Acquiring simultaneous data for both predator and prey, however, is challenging and as a result, predator–prey interactions involving cetaceans and seabirds remains poorly understood in the area (but see Certain *et al.*, 2011; Lambert *et al.*, 2019).

Within this context, this work aims at better understanding the mechanisms underlying the assemblage of the pelagic predator–prey community of the BoB by identifying interspecific associations and their main drivers. For this purpose, we fitted JSDMs by combining the environmental conditions and the co-occurrence patterns of top predators and prey obtained from JUVENA surveys over the 2013–2016 period. In this way, we addressed the following specific questions: are species interactions, such as predator–prey, triggering the observed co-occurrence patterns? Or, in contrast, are environmental factors the main explanatory features of species co-occurrence? By answering to these questions, this study intends to provide relevant insights about the functioning of predators and prey

communities that may help the conservation of endangered species and the sustainable management of exploited species to advance ecosystem-based monitoring (Louzao *et al.*, 2019).

Material and methods
Multidisciplinary surveys
JUVENA (abbr. of Juvenile Anchovy) oceanographic survey takes place every September with the aim of evaluating the population of European anchovy and monitoring the abundance of other pelagic species in the BoB (Figure 1) (Boyra *et al.*, 2013). The sampling strategy is based on parallel transects arranged perpendicular to the coast, spaced at 15 nautical miles (nmi) and carried out by two oceanographic research vessels, *Ramon Margalef* and *Emma Bardan* (R/V RM and R/V EB, hereafter), surveying transects from the coast (20 m bottom depth) to beyond the shelf break (Figure 1). Data from plankton to predators, as well as environmental information are also collected to obtain an overall assessment of the marine ecosystem (Louzao *et al.*, 2019) (for a schematic flowchart of the entire Material and methods section see Figure 2).

Sightings of top predators
Since 2013 sightings of top predators have been recorded aboard R/V RM by a team of three experienced observers. By following the Distance sampling methodology (Buckland *et al.*, 2001), observers (2 at a time) searched for cetaceans and seabirds ahead of the bow within an angle of 180° and from a single observation platform located at 7.5 m above the sea level. For each observation, the radial distance to animal clusters (individual birds or groups of animals of the same species) and the angle of the cluster sighting with respect to the trackline were estimated based on a range finding stick (Heinemann, 1981) and an angle metre. Sightings were made with naked eye, except for the identification of species and counting of individuals, which was aided by 10 × 42 Swarovski binoculars. Time of observation, species composition, group size, movement direction, and behaviour (e.g. displacing, foraging, attracted) were also noted. In addition, environmental conditions affecting the detectability of species such as Beaufort sea-state, swell height, wind speed, visibility, or glare intensity were recorded at the beginning of each observation period (i.e. every hour) or whenever observation conditions changed. Sampling effort was performed only during daytime, at a constant speed and under sea-state conditions ≤6 and it was geographically located based on the vessel GPS which logs the coordinates of the vessel every 1 min.

Biomass estimates of pelagic prey species
Biomass of pelagic species (fish and crustaceans, prey hereafter) were estimated by means of acoustic methods and pelagic trawls for the 2013–2016 period to match in time with the available data of predators. The acoustic equipment used for that consisted on Simrad EK60 split-beam echosounders (Kongsberg Simrad AS, Kongsberg, Norway) located on both vessels that sampled the water column to depths of 200 m during daytime (Boyra *et al.*, 2013). Sampling started on the northern Spanish coast, from west to east, where each RV monitored the pelagic ecosystem simultaneously over different transects. Then, both RV moved to the north to sample French waters where the smaller R/V EB sampled the inner section of the transects, while the larger R/V RM
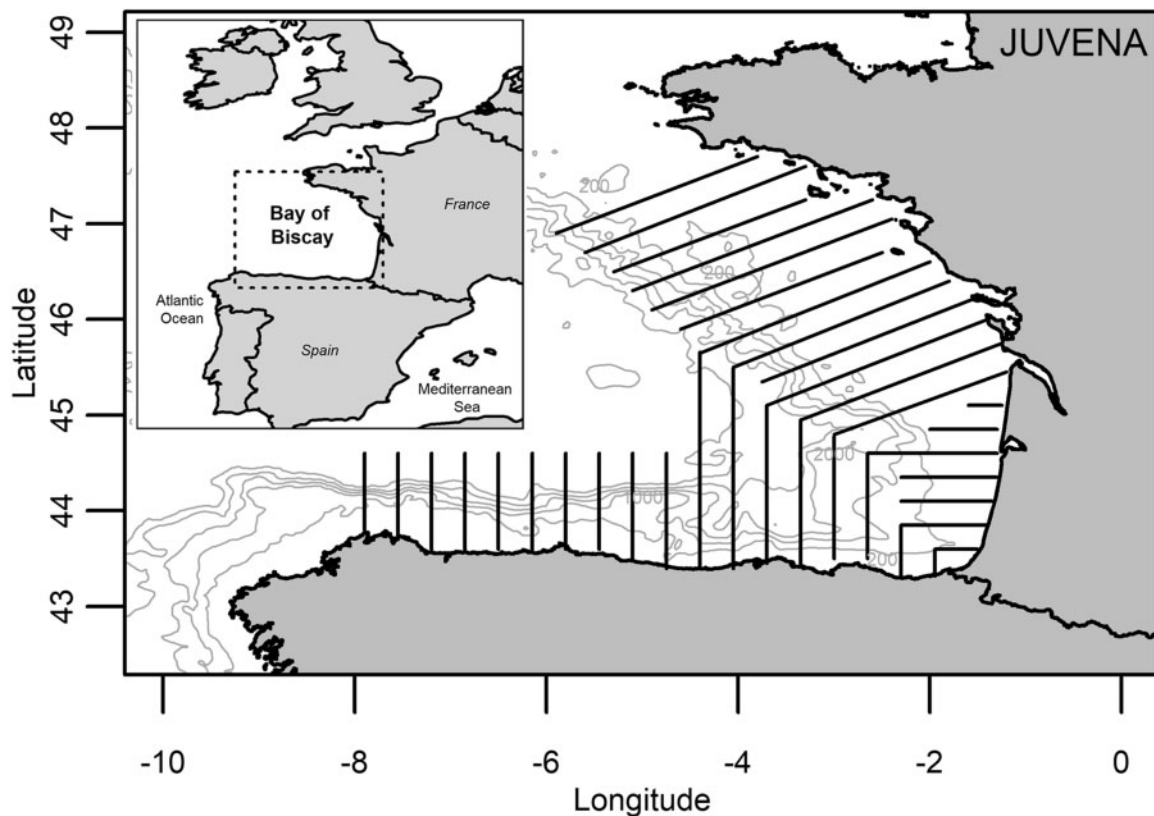
Figure 1. Overview of the study area and the sampling design of JUVENA survey. Isobaths of 200 m, 1000 m and 2000 m are indicated.

sampled the outer sector. The acoustic data collected by both vessels were then processed together: abundance estimates were obtained processing the collected acoustic data in the positive strata by layer echo integration and using an ESDU (Echo integration Sampling Distance Unit) of 0.1 nmi, whereas identification of organisms and population size structure was determined using net sampling and echo trace characteristics. Finally, abundance in number of individuals was multiplied by the mean weight, obtaining biomass estimates per age, and length class for each ESDU [more details can be found in Boyra *et al.* (2013)].

Oceanographic characterization of the pelagic realm

During the survey, oceanographic data were also collected using a CTD profiler. For each transect, a minimum of three profiles were performed (coastal, continental shelf, and oceanic waters) measuring the water column from the surface to 200 m depth. Temperature, salinity, and water density were directly inferred from CTD casts. The depth of the maximum temperature gradient (as a proxy of the mixing layer depth) and geostrophic velocities were derived from temperature and density data following Rubio *et al.* (2009) and Caballero *et al.* (2016), respectively. Horizontal fields of these variables were obtained using Optimal Statistical Interpolation scheme described in Gomis *et al.* (2001) over a spatial grid with regular node distances of $0.15 \times 0.15°$ latitude–longitude. To obtain 3D matrix fields, horizontal analysis were performed independently at 5 dbar intervals from 10 to 200 m. In this way, we obtained temperature, salinity, and geostrophic velocities values for the surface (T_s, SAL_s, and GV_s) and for the water column up to 200 m by estimating the median value

(T_{200}, SAL_{200}, GV_{200}), making them suitable for the study of seabirds and cetaceans. For the depth of maximum temperature gradient (DTG), no additional estimates were made, since it is a two-dimensional field. Finally, distance to the coast (DIS) and depth values (DEP) were extracted from NOAA database using the *marmap* R package V.: 1.0.2 (Pante and Simon-Bouhet, 2013) and added to the analysis.

Data selection and assemblage

Initially, top predator's data were filtered by including only those sightings where the identification was made at species level and by removing sightings considered to be attracted by the vessel (i.e. those individuals coming directly to the boat). In the case of prey, all species for which a biomass estimate was available were selected. Predator and prey data (i.e. number of sightings and biomasses) were then transformed to presence–absence and overlaid per year over a standard grid covering the study area (latitudinal range: 43.2–48°N; longitudinal range: 1–9°W) with a cell size of 0.1° spatial resolution. At this point, a second filter was applied, selecting only those prey and predator data with common sampling effort within the same year. In addition, species with <25 presences over the total survey period were removed with the aim of avoiding problems related to small sample size (Wisz *et al.*, 2008; Authier *et al.*, 2018). As a whole, 28 species were chosen, 17 top predators and 11 prey (Table 1) that were arranged as a community matrix where columns were species and rows were each 0.1° cell of the standard grid by year (sites hereafter). Some species within the prey group could be also acting as predators over other prey species, e.g.
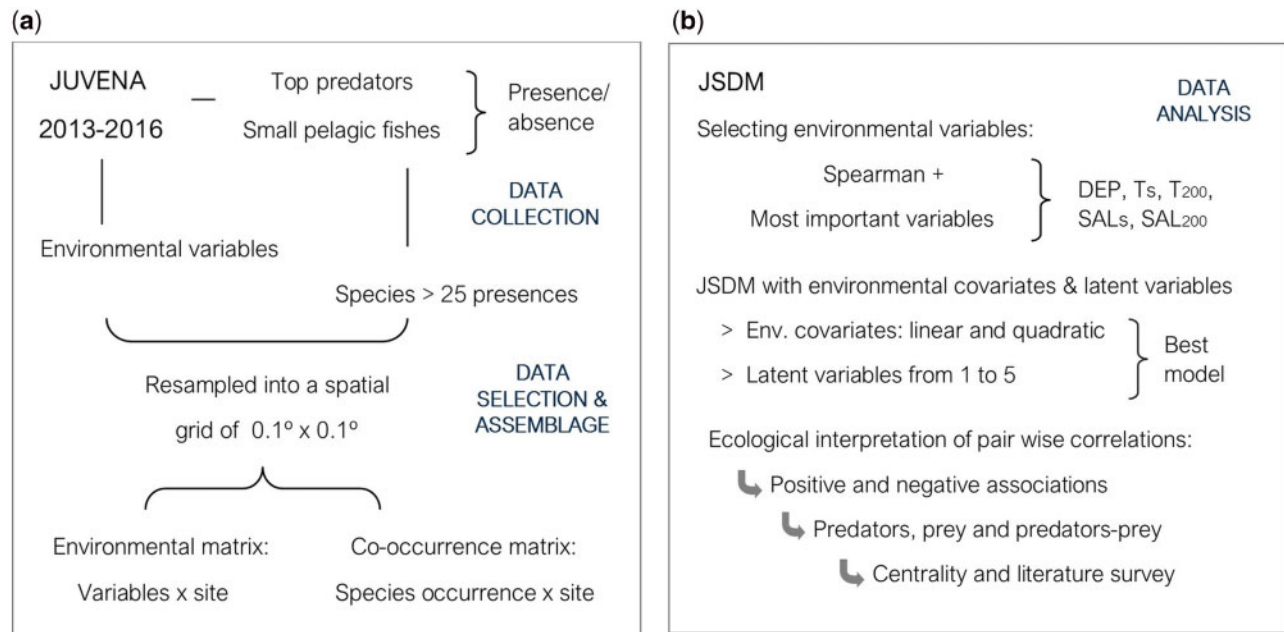
Figure 2. Workflow showing the steps taken through the study including data collection, data selection and assemblage, and data analysis.

mackerel–blue whiting (Olaso *et al.*, 2005). However, to avoid misunderstandings, predators and prey in this study will only refer to those species defined as such in Table 1. Finally, environmental variables were resampled with the *raster* package V.: 2.9.5 (Hijmans *et al.*, 2017) to match the standard grid of predators and prey and arranged in a matrix of environmental variables (columns) vs. sites (rows).

Predator–prey networks

To uncover the community structure behind predator–prey networks and identify interspecific associations, we fitted a series of JSDMs using the *boral* package V.: 1.7 (Hui, 2018). JSDMs are extensions of the generalized linear modelling (GLMs, McCullagh and Nelder, 1989) framework, which is widely used for modelling species distribution data (Guisan *et al.*, 2002). A key feature of JSDMs is that they comprise both environmental variables and latent variables, where the latter can be understood as a set of unobserved predictors that induce correlation between species. Latent variables, similarly to ordination axes, aim at representing the main axes of covariation across taxa and that is why they are used as a tool for estimating the underlying causes of covariation as well as for studying the factors driving co-occurrence (Warton *et al.*, 2015). We refer the reader to Warton *et al.* (2015, 2016) or to Ovaskainen *et al.* (2017), among others, for more comprehensive overviews of latent variables aimed at ecologists.

Latent variables

A critical issue when fitting JSDMs is the choice of the number of latent variables: a small number of latent variables means a simpler model, but risks a potentially too poor approximation of the true correlation structure, while more latent variables means an inherently more complex model (Wilkinson *et al.*, 2018). Previous literature suggests that a small number (<5) of latent variables is often enough for a good approximation to the species

correlation structure (Warton *et al.*, 2015). Therefore, to obtain the best model, we fitted a series of JSDMs using from 1 to 5 latent variables.

Environmental covariates

Species distribution modelling is fundamental to understand the realized niche of species, which theoretically assumes a symmetric Gaussian-shaped response (Austin, 2007). When fitting GLMs for each species via the *boral* package, fitting a quadratic polynomial function can be a possible solution in the absence of more sophisticated nonlinear methods (Jamil and Ter Braak, 2013). However, adding quadratic terms to the already available covariates could potentially lead to model overfitting (Harris, 2015). To overcome this problem, we identified the most important variables by using two complementary approaches (based on the Multi-Model Inference Approach and the JSDM approach) and limited the selection to five variables at most to avoid excessive complexity (D'Amen *et al.*, 2018) (for detailed variable selection approach see Supplementary File SA).

Model fit

Five JSDMs ranging from 1 to 5 latent variables were fitted to the species co-occurrence matrix, assuming the binomial error distribution with a probit-link function and the aforementioned five environmental covariates as explanatory predictors. All environmental covariates were standardized to have a mean of zero and a standard deviation of one (Zuur *et al.*, 2007) before entering them as both linear and quadratic terms in the model. In addition, a random row effect for both site and year was also included to address the variability between sites and years. To address the issue of non-convergence due to complete separation in binary variables, we used an informative prior on the regression coefficients (Ghosh *et al.*, 2018), specifically $\beta \sim N(0, 1)$, as recommended by Wilkinson *et al.* (2018). We adopted the default MCMC configuration in *boral*, that is, running Bayesian MCMC

Table 1. List containing the family, scientific name, common name, and acronym of the selected species of pelagic prey and top predators.

Family	Scientific name	Common name	Acronym
Prey			
Caproidae	*Capros aper*	Boarfish	BOC
Carangidae	*T. mediterraneus*	Mediterranean horse mackerel	HMM
	T. trachurus	Atlantic horse mackerel	HOM
Clupeidae	*S. pilchardus*	European pilchard	PIL
	S. sprattus	European sprat	SPR
Engraulidae	*E. encrasicolus*	European anchovy	ANE
Euphausiidae	*Euphasia* spp.	Krill	KRX
Gadidae	*M. poutassou*	Blue whiting	WHB
Scombridae	*S. scombrus*	Atlantic mackerel	MAC
	Scomber japonicus	Pacific chub mackerel	MAS
Sternoptychidae	*M. muelleri*	Mueller's pearlside	MAV
Predators			
Balaenopteridae	*B. physalus*	Fin whale	BALPHY
Delphinidae	*Delphinus delphis*	Common dolphin	DELDEL
	S. coeruleoalba	Striped dolphin	STECOE
Hydrobatidae	*Hydrobates pelagicus*	European storm-petrel	HYDPEL
Laridae	*L. michahellis*	Yellow-legged gull	LARMIC
	L. fuscus	Lesser black-backed gull	LARFUS
	Xema sabini	Sabine's gull	XEMSAB
Procellariidae	*Ardenna gravis*	Great shearwater	ARDGRA
	A. grisea	Sooty shearwater	ARDGRI
	C. borealis	Cory's shearwater	CALBOR
	P. mauretanicus	Balearic shearwater	PUFMAU
	Puffinus puffinus	Manx shearwater	PUFPUF
Stercorariidae	*Stercorarius parasiticus*	Arctic jaeger	STEPAR
	S. skua	Great skua	STESKU
Sternidae	*Sterna hirundo*	Common tern	STEHIR
	T. sandvicensis	Sandwich tern	THASAN
Sulidae	*M. bassanus*	Northern gannet	MORBAS

Acronym for prey refers to FAO code, whereas acronym for predators holds the abbreviation, widely used by observers, of the scientific name.

Table 2. The ecological interpretation given to pairwise associations based on their environmental and residual response (inspired by D'Amen *et al.*, 2018).

Environmental correlation of species pair	Residual correlation of species pair	Ecological interpretation of pairwise associations
0	+	Positive interactions causing aggregation
−	+	Positive interactions despite habitat differentiation
+	+	Positive interactions and similar environmental preferences causing aggregation
+	0	Similar habitat preferences
0	−	Negative interactions causing segregation
−	−	Negative interactions and habitat filtering causing segregation
+	−	Negative interactions despite shared environmental preferences
−	0	Habitat differentiation
0	0	Random pair

sampler with 40 000 iteration, with the first 10 000 discarded as burn in and the remaining thinned by a factor of 30 (Hui, 2018). For checking MCMC convergence, a combination of trace plots and the Geweke diagnostic (Geweke, 1992) was used. Finally, estimated residual correlations, their uncertainty (defined as the width of their corresponding 95% credible interval) and a variation partitioning was obtained for each JSDM to assess the best model in terms of the number of latent variables required.

Ecological interpretation
Significant environmental and residual correlations resulting from the best model (those whose 95% credible interval does not contain zero) were first analysed at the community level and then separately in predator, prey and predator–prey assemblies. To uncover the community structure behind each assembly, pairwise correlations were ecologically interpreted following D'Amen *et al.* (2018) approach (Table 2). To identify species with a high number of associations, degree centrality—defined as the number of species a given species interacts with—was assessed for each trophic guild using both positive and negative associations. For this purpose, the *igraph* package V.: 1.2.4.1 (Csardi and Nepusz, 2006) was used, which enabled the visualization of all associations and in addition, assigned a larger weight to those species with higher number of positive or negative associations.

In addition, a literature survey was conducted with the aim of contrasting results and to identify biotic interactions from those associations driven by missing predictors. Specifically, scientific papers focusing primarily in the North Atlantic and describing species diet and feeding behaviour were searched to evidence predator–prey interactions, mutualistic relationships or interspecific competition. Nevertheless, the difficulty to assign mutualistic or competition evidences to pairwise species lead us to only quantify trophic evidences.

Results
Predator–prey network structure
The comparison among the five candidate JSDMs (where the number of latent variables varied from 1 to 5) showed that the models tended to stabilize in terms of their residual correlations from three latent variables onwards. We decided in the end to select the JSDM with four latent variables, given that the model with three latent variables showed small evidence (based on the Geweke diagnostic) that the MCMC sampling algorithm had failed to converge within the current sampling configuration (to compare the different JSDMs see Supplementary File SB).

At the community level, the significant environmental correlations (58%) resulting from the selected model showed a homogeneous distribution of positive and negative correlations (Figure 3a), followed by a homogenous distribution of their uncertainty (Figure 3b) and a percentage of accounted variance ranging from 8% (lesser black-backed gull) to 70% (blue whiting) (Supplementary File SC). In contrast, the significant residual correlations (45%) showed that positive correlations occurred mainly between pairwise species of prey or predators and negative correlations especially among predator–prey species (Figure 3c). Similarly, estimates of residual uncertainty also showed more contrasting results, pointing out some species with a higher uncertainty, e.g. northern gannet *Morus bassanus*, striped dolphin *Stenella coeruleoalba* or Cory's shearwater *Calonectris borealis* (Figure 3d). This was consistent with the relatively lower percentage of variance accounted for the latent variables in these species (Supplementary File SC). A similar pattern was found when environmental and residual correlations between species pairs were compared: both prey and predators showed a general positive response to environmental and residual correlations, while predator–prey group responded negatively in most of the cases (Figure 4a–c). This last group, however, showed a more diverse response that contrasted with the twofold pattern shown by the prey guild and that corresponded to neritic–oceanic species pairs (Figure 4a and c). More detailed information was obtained when attributing an ecological meaning to every pairwise correlation (Figure 5). The twofold pattern seen in prey (Figure 4a), for instance, was found to be mainly driven by the combined effect of positive interactions and similar environmental preferences (49%) and by the combination of negative interactions and habitat differentiation (22%). Predator guild, although in a minor extent, also showed a high number of positive correlations (54%), attributed mainly to similar habitat preferences and positive interactions separately. Negative correlations, in contrast, were very low (14%) and in most of the cases were caused by different environmental preferences. In the predator–prey group, positive correlations were less abundant (30%) and mainly driven by similar habitat preferences, whereas the proportion of negative correlations was higher (42%) and more diverse. Although no specific

driver was detected in this group, for first time all possible negative associations were described here, including those classified as negative interactions despite shared environmental preferences.

Predator–prey network associations
The attribution of ecological associations to pairwise species enabled us to identify species individual role and assess species degree centrality. This led to the identification of many central species within the prey guild that interacted similarly in terms of positive associations (Figure 6a). Krill and Mueller's pearlside *Maurolicus muelleri*, were the exception and accounted for the highest number of negative associations (Figure 6d). Among predators, many interacting species were found too, with sandwich tern *Thalasseus sandvicensis*, great skua *Stercorarius skua*, and sooty shearwater *Ardenna grisea* as main central species. Among species with the lowest number of positive associations, fin whale and Cory's shearwater were identified, followed by the endangered Balearic shearwater (Figure 6b). These species were also found to have negative associations, although the species with the highest proportion of negative associations were fin whale and striped dolphin (Figure 6e). In both cases (Figure 6b and e), two new associations not present in the prey guild showed up, i.e. similar habitat preferences and segregation by the environment, that accounted for the highest proportion of associations in this guild (Figure 5). Among predators–prey group, northern gannet, Balearic shearwater, and yellow-legged gull *Larus michahellis* seabirds together with Mediterranean horse mackerel *Trachurus mediterraneus* were identified as central species, followed in a minor extent by krill *Euphasia* spp. (Figure 6c). In the opposite side, species previously found to have negative associations such as Cory's shearwater, fin whale, striped dolphin, or lesser black-backed gull *L. fuscus* were identified, accompanied by blue whiting *Micromesistius poutassou*, horse mackerel *T. trachurus* and sprat *Sprattus sprattus* (Figure 6f). In this case (Figure 6f), a new association not previously described in the other guilds came out, i.e. negative interactions despite shared environmental preferences.

In addition, the literature survey based on 36 scientific papers focusing on all the predator–prey associations (those represented in Figure 6c and f) revealed that evidences of predation (mainly based on regurgitates, pellets, and stomach content) tended to be found more often between positively associated predator–prey species (59%) than between negatively associated pairs (27%) (Figure 7 and Supplementary File SD).

Discussion
Environmental factors vs. biotic interactions
The reported significant associations resulting from the JSDM at the community level showed a slightly larger proportion of correlations due to (dis)similarity in environmental preferences (58% of environmental correlations vs. 45% of residual correlations), which may indicate a higher weight of the environmental conditions in driving the co-occurrence patterns of the overall predator–prey network. Similar results were also found by Royan *et al.* (2016) in river bird communities, who concluded that species interactions were of secondary importance in comparison to habitat structure. In this work, however, the proportion of residual correlations did not greatly differ from the former, meaning that biotic interactions might also be an important driver. It is important to keep in mind that in the JSDM, like with all statistical
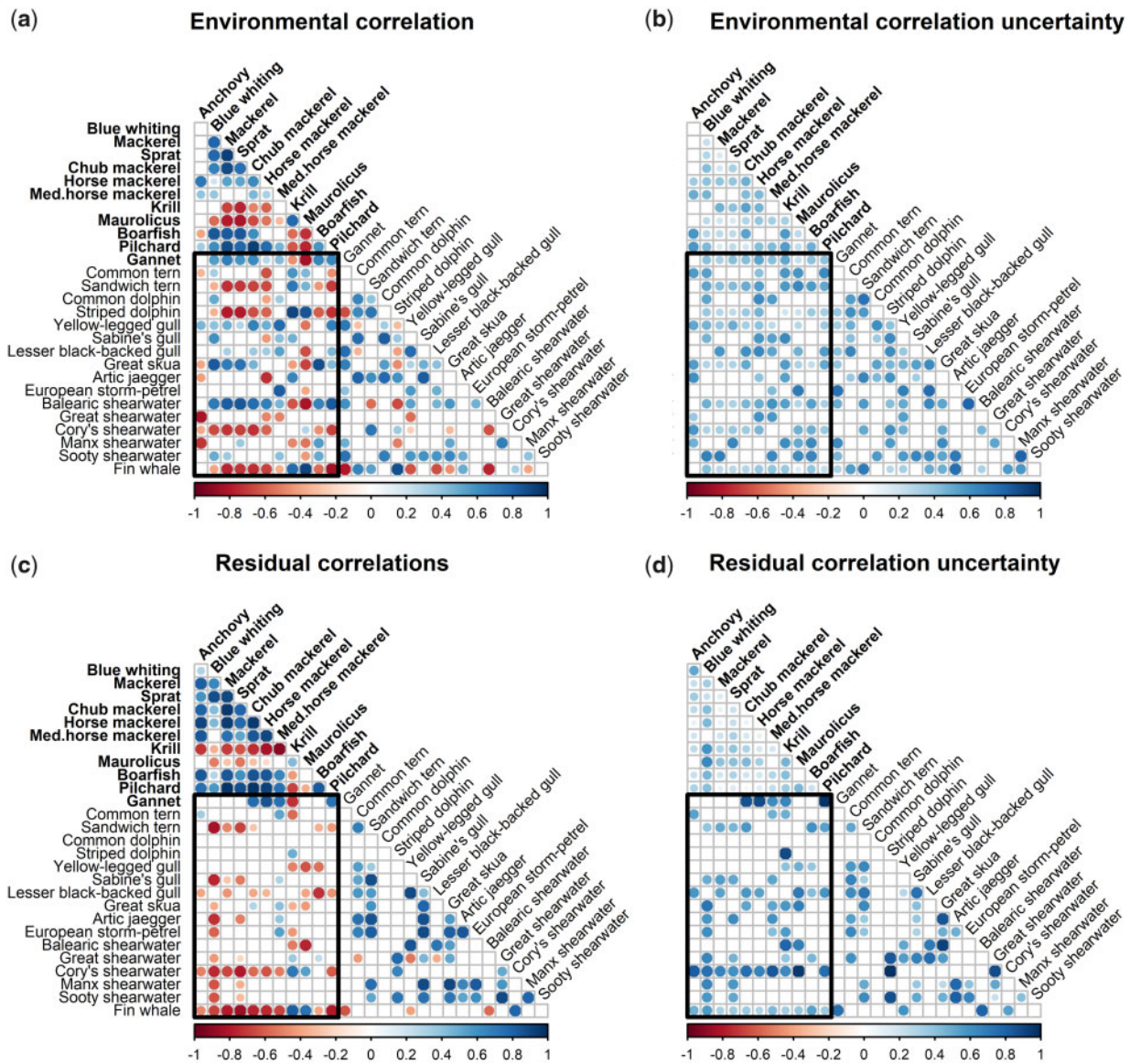
Figure 3. Environmental and residual correlations (a-c) and their corresponding uncertainty (b-d) for each species pair. The rectangle defined under the black lines corresponds to correlations among predator–prey species (for interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

approaches aimed at attributing sources of species covariation, the identification of biotic interactions is sensitive to the choice of environmental covariates (D'Amen *et al.*, 2018). Unexplained deviance due to missing predictors could result in the effect of biotic interactions (Hui, 2016), and hence, contrasting the results with an additional source of information, such as literature, is recommended. In our case, the literature survey conducted, despite referring only to predator–prey guild, could indicate that some of the residual correlations do not correspond to a truly biotic interaction. If so, a higher percentage of predation would be expected. Nevertheless, it must be considered that obtaining information on predators' diet may have some limitations too. Indeed, most of the top predators of this study are protected species under different Conservation Agreements, and most of the seabird species observed do not breed in the BoB, which does not make possible colony-based field studies that would contribute to the collection

of trophic evidences. Diet studies, therefore, are limited to the analysis of stomach contents of opportunistically stranded or bycaught animals (Spitz *et al.*, 2006; Pusineri *et al.*, 2007) or to the application of indirect methods such as stable isotope analysis, genetics, or fatty acids (Navarro *et al.*, 2009; Käkelä *et al.*, 2010). Consequently, the information used to contrast the results can be incomplete, leading to an underestimation.

Ecological interpretation of associations

While acknowledging its limitations, the JSDM approach has been seen to provide general patterns of species co-occurrence such as environmental filtering (D'Amen *et al.*, 2018), competition (Zurell *et al.*, 2018), or mutualism (Royan *et al.*, 2016). In our case, the mutualistic associations derived from the aggregation behaviour of both prey and predators could also explain a large proportion of positive interactions. Among pelagic fishes,
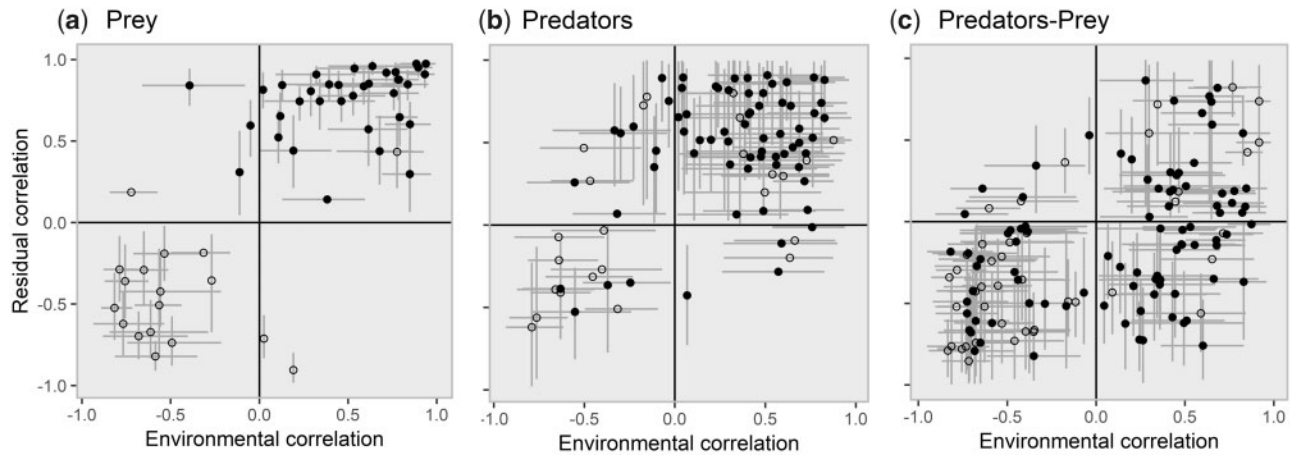
Figure 4. Significant environmental and residual correlations (those whose 95% credible interval does not contain zero) between pairs of prey (a), predators (b), and predator-prey (c) species. The error bars represent 95% credible intervals. White circles indicate neritic–oceanic species pairs, while black points represent either neritic–neritic or oceanic–oceanic species pairs.
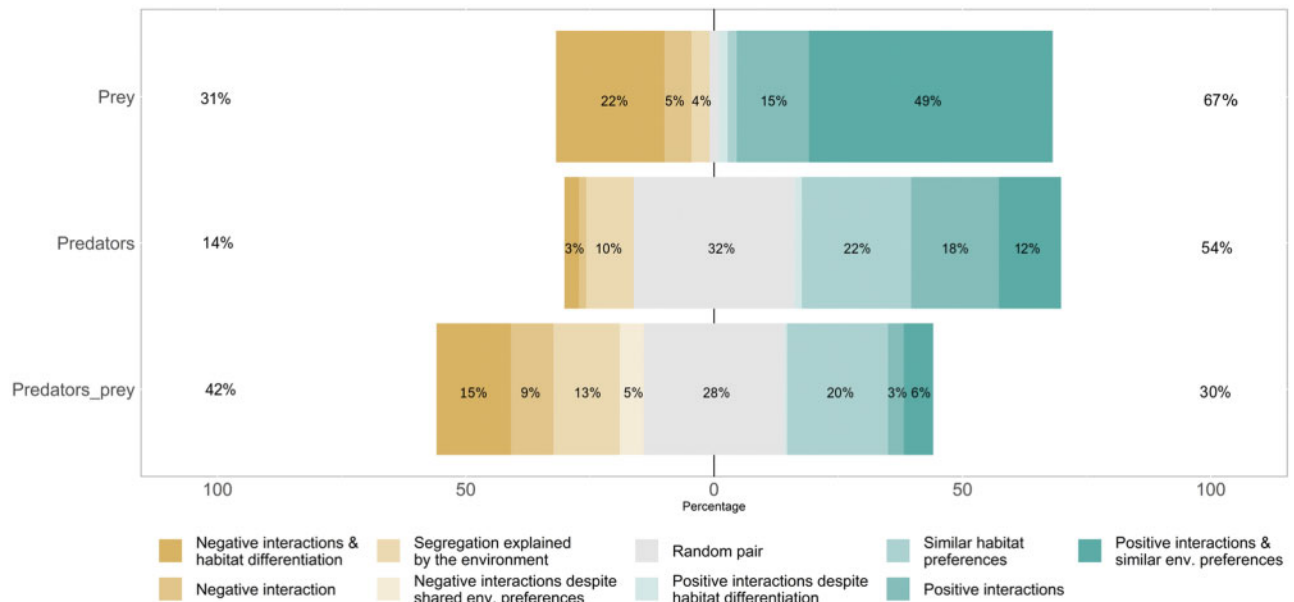

Figure 5. Ecologically interpreted associations (explained in Table 2) displayed by trophic guild with their corresponding proportion (percentages smaller than 3% are not shown). Random associations are displayed in the centre of the figure, whereas associations to the right refer to positive associations and associations to the left refer to negatives (for interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

for instance, schooling behaviour has been long described, including mixed schools among engraulids, clupeids, carangids, and scombroids (Pitcher, 1986). In the BoB, Boyra *et al.* (2013) reported that European anchovy could be found mixed with European sardine, Atlantic horse mackerel, Atlantic mackerel, and European sprat, explaining up to some extent the positive interactions detected in this study.

Similarly, the positive interactions found in seabirds, which are known to heavily rely on other seabirds and cetaceans to locate prey and increase fishing success (Fauchald, 2009), would also indicate mutualistic associations such as local enhancement or facilitative mechanisms. Among predator–prey group, positive interactions could indicate predation, based on the trophic evidences found in

the literature. In contrast, negative interactions could be related to the aggregation behaviour of prey and predators described above, which may induce local peaks in predators' densities, leaving other zones free of predators and leading to spatial mismatches between predators and prey (Ballance *et al.*, 2001; Fauchald, 2009). Alternatively, a second reason could be a predator avoidance behaviour, described by Lambert *et al.* (2019) for the cetaceans–prey of the BoB and suggested by Logerwell and Hargreaves (1996) for seabirds–prey species. In our case, the smaller percentage of trophic evidences found among negative interactions might indicate that predation leads positive spatio-temporal associations, but also might support the avoidance behaviour hypothesis, since several predator–prey pairs have been identified.
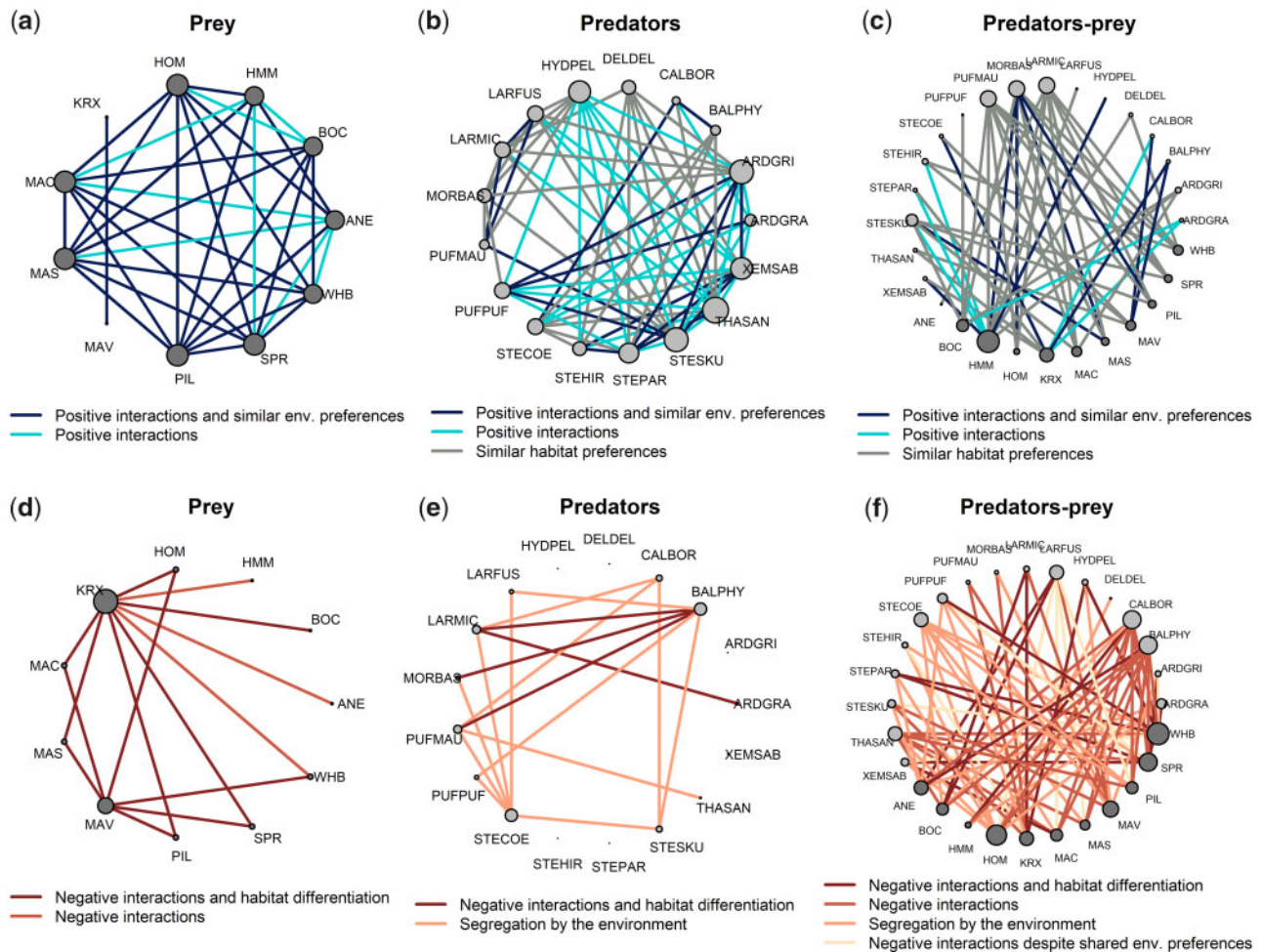
Figure 6. Networks graphs showing the ecologically interpreted associations in prey (a-d), predators (b-e), and predators-prey (c-f) trophic guilds (associations occurring two times or less have not been shown to simplify the visualization). First row refers to positive associations, second row refers to negatives, and the size of the circles represents species degree centrality (for interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article). Acronyms can be found in Table 1.

Among prey, the negative interactions in krill could also indicate some kind of avoidance, since most of the neritic species targeted in this study could feed on euphausiids (Bachiller and Irigoien, 2015). However, the effect of habitat segregation cannot be omitted, since the highest number of negative interactions was found in oceanic species (krill and Mueller's pearlside). Habitat differentiation was also found to be the main driver among predators, where the fin whale and striped dolphin (oceanic species) accounted for the highest proportion of negative associations. Competition, in contrast, might not be occurring (e.g. due to a non-limiting resource) or might be hidden by indirect effects; if two competing species share a positive relationship to the same resource, their occurrence could be positively correlated, when the true effect should be negative (Morueta-Holme et al., 2016). In predator species that typically feed on flock, the relative effects of competition have been suggested to be negligible (Tremblay et al., 2014); the prey species of the study, in contrast, were found to have a high diet overlap which would allow the possibility of indirect effects (Bachiller and Irigoien, 2015).

It must be taken into account that overall biotic interactions are scale dependent. Positive interactions (e.g. mutualism), for instance, can be manifested across scales, whereas negative

interactions (e.g. competition) are unlikely to be discernible beyond local and regional scales (Araújo and Rozenfeld, 2013). Many studies focusing on predator–prey relationships have found that spatial correlations increase with increasing scales. At large scales, prey may be aggregated on predictable areas linked to mesoscale oceanographic features, leading to positive correlations, whilst at smaller scales, prey may be further congregated in dense and unpredictable schools to avoid predation, inducing negative correlations (Rose and Leggett, 1990; Fauchald et al., 2000). In this work, we have characterized mesoscale processes (phenomenon of spatial scales between ~10 and 100 km and timescales from several days up to 1 month) as a result of analysing synoptically the data of this regional survey (Louzao et al., 2019). However, the analysis of spatial associations at finer scales is still possible using the same dataset but different approaches (see Lambert et al., 2019).

Main association components

In graph theory, indicators of centrality are used to identify the most important vertices within a graph. During the last decades, a growing number of studies has applied these measures in species co-occurrence networks to assess the species contribution to
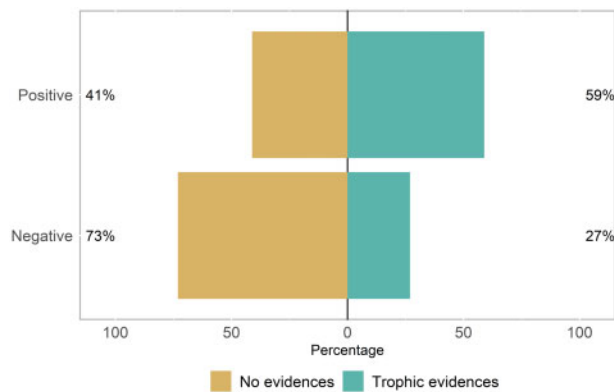
Figure 7. Proportion of trophic evidences (and no evidences) found in the literature for all the positive and negative associations occurring within predators–prey trophic guild.

network robustness (Araújo *et al.,* 2011) or to identify keystone species (Martín González *et al.,* 2010; Berry and Widder, 2014). The analyses conducted in this study did not enable the identification of keystone species (sensu Paine, 1969), but pointed out those species with an important role within their own community (Morueta-Holme *et al.,* 2016). In the predator's guild, for instance, the high centrality shown by the sandwich tern, sooty shearwater, and great skua may be related to their role within the flock as catalysts (species that initiate the flock and attract other seabirds with their presence; Camphuysen *et al.,* 2007), facilitators (species that drive prey to surface and make available to others; Veit and Harrison, 2017), and kleptoparasites (species that steal prey from other seabirds; Camphuysen *et al.,* 2007), respectively. However, these roles are not limited to the three central species; instead, they can be found widespread along the top predator community. Fin whale and striped dolphins for instance, can act as facilitators too, leading to some positive interactions previously described by other authors, e.g. fin whale–Cory's shearwater (Veit and Harrison, 2017) or striped dolphin–great shearwater–Cory's shearwater (Clua, 2001) and also found in this study. Due to their limited ability to dive, species such as terns and storm-petrels also tend to interact with cetaceans or shearwaters; it is the case, for instance, of the interaction between the storm petrel and the Manx shearwater detected in this study and also described by Skov *et al.* (1995). Similarly, the lower centrality showed by other species such as the northern gannet, could be also a consequence of their role as suppressors (species whose presence decreases the availability of prey to other predators), since they take over the surface-feeding opportunities from smaller species (Camphuysen *et al.,* 2007).

In the prey guild, the degree centrality measure did not show any outstanding species but reflected species spatial distribution, making difference between neritic and oceanic species. In predator–prey guild, the analysis detected highly interacting species but did not identify most predatory species or most consumed prey, since predation evidences were spread into both positive and negative interactions. Based on the literature, we could also identify some predator–prey associations potentially occurring in the BoB such as the northern gannet predating upon the Atlantic mackerel (Lewis *et al.,* 2003). This association had been previously detected in the BoB during spring by Certain *et al.* (2011), who also found the northern gannet associated with the horse mackerel. In

addition, we also found trophic evidences for striped dolphin feeding on krill and Mueller's pearlside and for two endangered predator species occurring in the BoB only during late summer–autumn; i.e. the fin whale feeding upon krill and Mueller's pearlside (Bravo Rebolledo *et al.,* 2016) and the Balearic shearwater potentially feeding on sardine (Yésou, 2003; Navarro *et al.,* 2009; Käkelä *et al.,* 2010), Atlantic mackerel, horse mackerel, and on blue whiting according to stable isotopes (Meier *et al.,* 2017). These results, together with other additional associations where krill and Mueller's pearlside were reported as prey, could indicate that these species are more important for seabirds than initially thought; indeed, recent studies suggest that mesopelagic fishes constitute a considerable amount of the food of shearwaters and storm petrels, especially for those exploiting oceanic habitats (Watanuki and Thiebot, 2018).

The JSDMs are therefore able to detect consistent predator–prey associations that can be complemented by including ancillary information such as traits or phylogeny when available (Ovaskainen *et al.,* 2017; Hui, 2018). In addition, some of the detected interactions can be used for the conservation of top predators, as suggested by Veit and Harrison (2017) or for a sustainable management of exploited and potentially exploited species (St John *et al.,* 2016) based on their predators and competitors.

Conclusions

According to our results, the co-occurrence patterns of top predators and prey in the BoB would be driven by a combination of environmental factors and biotic interactions. These biotic interactions tended to be positive in predators and prey and negatives in predators–prey group, suggesting: (i) mutualism and facilitation are very important processes in species with aggregation behaviours, (ii) this aggregation behaviour potentially leads to spatial mismatch in predator–prey species. Furthermore, the literature survey revealed that predation is likely driven by positive associations, although trophic evidences suggesting a possible predator avoidance behaviour have also been found. The use of JSDM in predator–prey networks can therefore provide valuable information on ecosystem functioning, community structure, and help advance towards an ecosystem-based management. In addition, the combination of biotic and environmental drivers found in this study highlights the species vulnerability to climate change variability and hence, to the potential modification of the network's links. As a result, further research is needed to project how species will respond under changing conditions.

Supplementary data

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

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