Estuarine, Coastal and Shelf Science 273 (2022) 107912

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Mapping the habitats of a complex circalittoral rocky shelf in the Cantabrian Sea (south Bay of Biscay)

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ARTICLE INFO

Keywords:
Non-invasive methodologies
Benthos
Habitat models
Circalittoral communities
Bay of biscay

ABSTRACT

This work focuses on the study of habitats and communities of a high structural complexity area at different levels and scales. This gives us a better understanding of an area from an ecological point of view and at the same time provides us with tools that will facilitate management measures. It was developed in a complex circalittoral rocky platform of the central Cantabrian Sea (Bay of Biscay). The sampling was carried out using a towed photogrammetric vehicle and a rock dredge, which was used for the identification of the species. The first level of the study was the abiotic characterization of the area and the analysis of the communities. These analysis were developed using the unsupervised k-means classification method. For abiotic characterization we used the variables directly associated with the composition and morphology of the ground, such as backscatter, BPI (Bathymetric Position Index), roughness and slope. Depth was also included to discriminate between the circalittoral and bathyal zones. We obtained 5 different classes, which we related to the ground types observed by photogrammetry. In the analysis of the communities, the cluster was based on the sampling units extracted from the images (~10 m), from which 5 assemblages were obtained, providing information on the most abundant species of each class supplied by the abiotic study. The second level was carried out considering a management approach and was based on the modeling of the area at lower resolution, more suitable for the analysis of the habitat-fisheries interactions. Thus, the main habitat-forming species (HFS) of the entire circalittoral area were used to perform delta models based on GAMs (Generalize Additive Models). Obtaining the predictions of presence/absence and combining it with the predictions of densities, we got the zero inflated values density-based model. As all the identified habitats have vulnerable benthic species of a certain size settled on rocky bottoms, they can all be considered to belong to the designation 1170 reefs of the Habitats Directive.

1. Introduction

In recent years, the urgency of protecting threatened species and habitats of the marine space has grown while the knowledge of many of the most vulnerable habitats is still in a poor state of development or does not have the level of detail required for its assessment. This is especially important in the case of deep-sea, in which study it is required a greater amount of resources and effort. However, the use of techniques based on photogrammetry has allowed the identification of the detected gaps and the advancement in the knowledge of the most inaccessible areas (Danovaro et al., 2014).

This improvement of deep-sea knowledge is necessary for a better characterization of vulnerable habitats and species, which will help to determine the interactions of anthropic uses and activities with the environment, as well as to define and achieve the good environmental status of our seas, in accordance with the guidelines established by the Marine Strategy Framework Directive (MSFD, 2008/56/EC) through its quality descriptors. The International Guidelines for the Management of Deep-sea Fisheries in the High Seas (FAO, 2009), define in its paragraph 42 what a VME (Vulnerable Marine Ecosystem) must be considered, when says that "*A marine ecosystem should be classified as vulnerable based on the characteristics that it possesses. Functional significance of the habitat, fragility or structural complexity should be used as criteria in the identification of VMEs*" and details in the annex the habitats, communities or

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https://doi.org/10.1016/j.ecss.2022.107912
Received 30 December 2021; Received in revised form 8 May 2022; Accepted 18 May 2022
Available online 22 May 2022
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even groups that are likely to fall into this category, such as certain coldwater corals and hydroids or sponge dominated communities. According to this need, numerous studies have been developed based on the distribution and the knowledge of environmental characterization of different species of sponges (Gonzalez-Mirelis et al., 2021; Knudby et al., 2013; Ramiro-Sánchez et al., 2019; Ríos et al., 2020; Rodríguez-Basalo et al., 2021), and cold-water corals (Guinan et al., 2009; Lo Lo Iacono et al., 2019; Morato et al., 2020), mostly focusing on the requirement of studying the interactions of human uses and activities with the distribution of these species.

In addition, as the knowledge of benthic habitats advances, there is a need to unify the classification criteria so that the characterization of habitats starts from a supra-state point of view. Thus, with regard to the European zone, many efforts have being focused to adapt the reality of the habitats studied by the different states to a hierarchical classification (Galparsoro et al., 2012; Henriques et al., 2015), in accordance with that contemplated by EUNIS (European Union Nature Information System) (Moss, 2008). Further, at the national level, a major study has been carried out under the supervision of the Ministry of the Environment to classify the benthic habitats that surround the Iberian Peninsula, Balearic Islands and Canary Islands, publishing the Spanish Inventory of Marine Habitats (Templado et al., 2012).

The study of the megebenthic communities of the deep-sea habitats is essential as it is composed of species that play a decisive role in the exchange of energy between the pelagic and benthic ecosystems (Rossi et al., 2017). In the case of the Cantabrian circalittoral rocky shelf, previous studies have revealed that one of the communities of these three-dimensional habitats is formed by the yellow coral *Dendrophyllia cornigera* and the cup sponge *Phakellia ventilabrum* in areas of patchy rock and irregular distribution of sedimentary cover (Sánchez et al., 2008, 2009), which increases the complexity and makes the study of the communities and the distribution of the habitats more challenging (Prado et al., 2020). Furthermore, the presence of these two species assemblages has also been found in the waters of the Canary Islands (González-Porto et al., 2014).

The high-resolution studies of benthic habitats to characterize an area at different levels of resolution requires a wide knowledge of the area, especially in the deep-sea, which it is convenient to address with complementary samplings and different levels of analysis. In hard bottoms, a reliable approach for the quantification of species and communities is through photogrammetric analysis, although species identification problems are a known issue and it is required to be completed with rock dredge samplings (Buhl-Mortensen et al., 2012; Ríos et al., 2020).

In this study we analyze a way of selecting the different variables that can determine the structural complexity of a rocky circalittoral shelf to later study the communities related to each area. We develop this at two different levels according to the objectives pursued: i) on the one hand, we study the distribution of the different habitats at the biotope level at the highest resolution according to the data available. For this, we develop an abiotic characterization based on the variables most related to the ground types and analyze the sessile species that inhabit them and the factors that affect their distribution. ii) The second part of the study is developed taking into account the management aspects, that is, the main objective is to obtain the distribution of habitats according to the main habitat-forming species (HFS) to create a continuous map of vulnerable habitats and thus facilitate subsequent analyzes of interaction with the different human activities in the area to be developed in future studies.

2. Material and methods

2.1. Study area

The study area is a circalittoral rocky shelf located in the central Cantabrian Sea (south of the Bay of Biscay), north of the Peñas Cape (Fig. 1). The continental shelf in this sector is narrow and irregular, a characteristic feature of the Cantabrian continental margin (Ercilla et al., 2008), with very gentle slopes, less than 4°, and depths that reach 400 m, although the shelf brake is mainly located between 200 and 300 m, giving way to a short and abrupt continental slope, where the canyons of the Avilés canyon system have their origin. This area is characterized by rocky outcrops of different reliefs and morphologies, some of them intensely tectonized in an east-west direction that alternate with

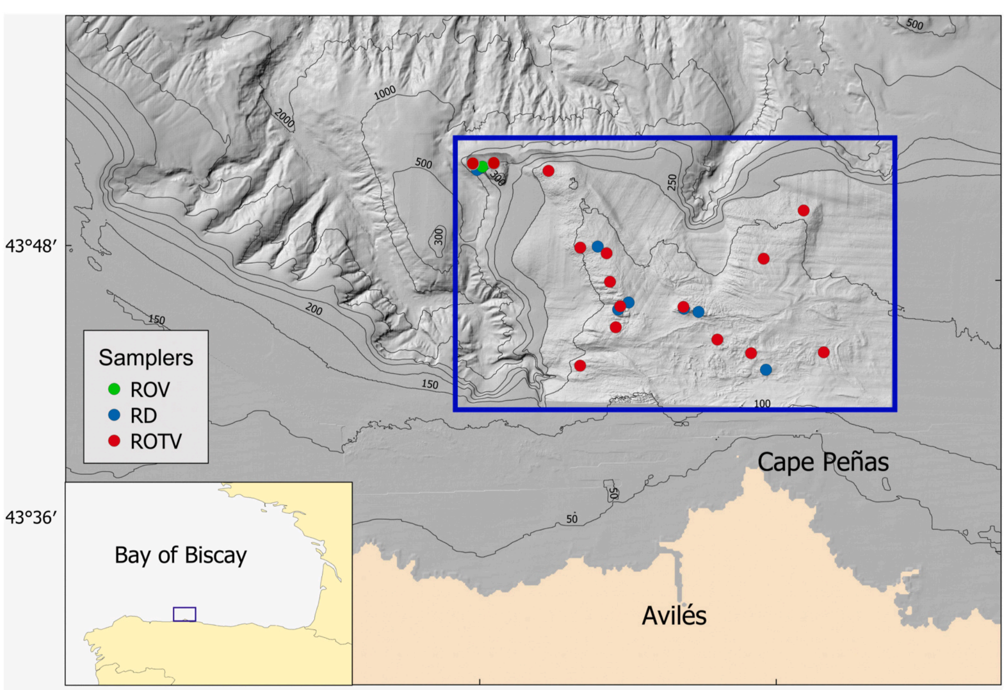

Fig. 1. Study area and sampling effort. Samplers were made by the ROV Liropus 2000 (green mark), a rock dredge (blue marks), and the ROTV Politolana (red marks). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

depressed areas with high sedimentary coverage (Gómez-Ballesteros et al., 2014). In its northwesternmost part, this rocky shelf extends beyond 600 m depth, a slight slope of rocky substrate, boulders and sediments.

2.2. Sampling methods

The area was sampled between 2010 and 2022 in 8 different surveys (Fig. 1) and was developed combining two different methodologies, one non-invasive through images captured by a ROTV (Remote Operated Towed Vehicle) and a ROV (Remote Operated Vehicle), and a direct sampling, the rock dredge, which allowed us to complement the information obtained by the underwater images, since it facilitated the identification of some of the species observed in addition to allowing access to species whose size makes them hardly detectable by non-invasive methods.

The analysis of the circalittoral shelf was developed by photographic images taken by the ROTV Politolana (Sanchez and Rodriguez, 2009), an underwater photogrammetry vehicle equipped with a transponder that allows the georeferencing of images, as well as a photographic camera with four lasers that enable the scaling of the images to calculate the area. For each picture, the number of specimens and their density were obtained according to the area covered. All those species both mobile and sessile, with a size greater than 5 cm were selected. If the classification of species or genus could not be reached, they were classified according to the most specific taxonomic group. Additionally, the bathyal zone was sampled by video recording and analyzed using OFOP software (Huetten and Greinert, 2008). Transects were divided into 10 m sections and the swept area was calculated as described in Prado et al. (2020) for the estimation of species and groups and thus integrate the studies with the sampling carried out in the circalittoral area.

A total of 16 visual transects were carried out, covering all the areas with different environmental characteristics in order to collect all the heterogeneity of habitats in the area. The average route of transects was approximately 500 m, and the total area covered by the sampling was just over 6000 m^2.

2.3. Preparation of environmental variables and abiotic characterization

Previous studies on the area carried out with a multibeam echosounder resulted in a 10 m resolution DEM (Digital Elevation Model). From this layer, the bathymetric derivatives considered relevant for the settlement of HFS according to previous studies (Brown et al., 2011; Prado et al., 2020) were extracted. These layers were depth, Bathymetric Position Index (BPI), slope and roughness. In addition, we included the backscatter at the same resolution as DEM.

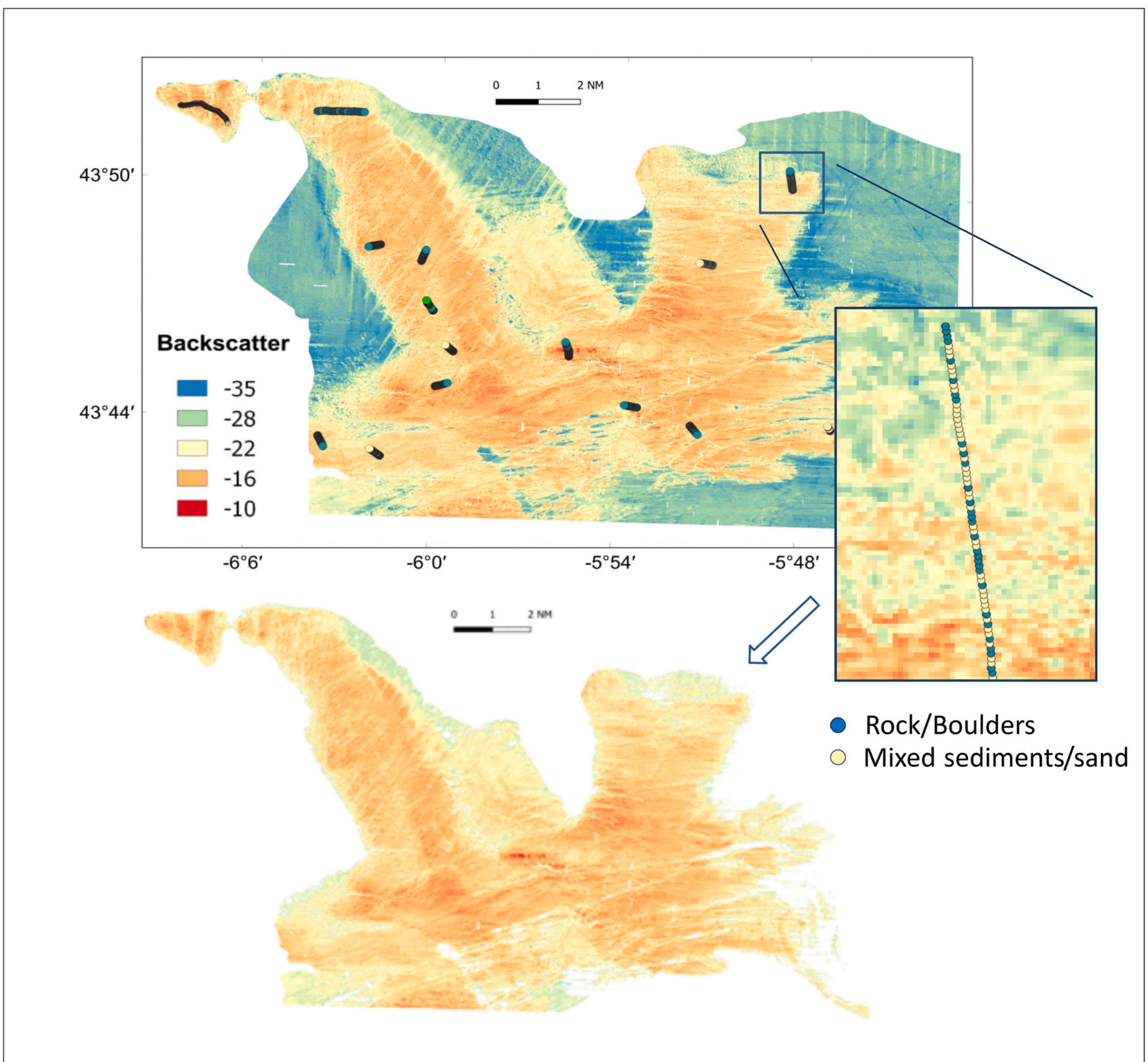

Fig. 2. Selection of hard substrata by backscatter and visual transects ground-truthing.

As our study only concerns to the habitats and communities living in hard substrata, by ground-truthing we searched the limit value for the settlement of hard substrata HFS. Thus, to obtain the area occupied by rock, rock with sediments and rock with boulders, and exclude the one where the rock does not appear, the lowest backscatter value in which hard substrata and boulders appear was selected to mask the rocky bottom (Fig. 2). This mask was shaped with the help of ground-truthing derived from the image analysis (Fig. 3).

BPI has turned out to be one of the most important layers in recent studies involving spatial distribution models in the central Cantabrian Sea (Sánchez et al., 2017). It is defined as the relative position of an area with respect to the surrounding area, so valley zones and elevations are represented. In some local studies it has been used in two different resolutions to highlight, on the one hand, the large geomorphological structures of canyons and seamounts with a wide BPI, and by other, smaller-scale structural accidents with a fine BPI, which will be determined by the maximum radius in which the layer is obtained (García-Alegre et al., 2014; Sánchez et al., 2014). However, our study area is very uniform and the outcrops have similar characteristics all over the area, so we maintained the structural integrity without neglecting their internal complexity. Thus, we selected BPIs at different resolutions, 30 m, 200 m, and 500 m radius, and obtained different profiles that we compared with the observations of the samplings to verify which of them best fit the ground types and sediments distribution of the terrain (Fig. 4).

For the abiotic characterization of the study area, a clustering technique based on the selected variables, depth, backscatter, BPI, roughness and slope was developed. To study the relationship among the different predictors, the correlation between each pair of variables was calculated. Finally, roughness was discarded as it correlated with slope by more than 90%. The correlation between the rest of the variables was below 50%. A VIF (Variance inflation Factor) was also performed to rule out multicollinearity between the set of variables (Zuur et al., 2009), but all values were below 3, which implies that there is no multicollinearity. Values were standardized using Min-max technique as recommended for groups overlapping (Nogueira, 2021; Visalakshi and Suguna, 2009) to apply the unsupervised classification algorithm k-means. The number of groups was determined using the WCSS (Within Cluster Sum of Squares) method (Pollard, 2007) (Figure A1), showing 5 different cluster groups as the best fit (Table 1).

2.4. Analysis of the communities

The study of the benthic communities was developed by integrating the densities of the species by video sections and groups of photographs taken every 10 m obtaining a total of 370 samples. We selected sessile species and those species with low mobility that characterize specific habitats, such as the brittle stars *Ophiotrix fragilis* and *Ophiocomina nigra* (Connor et al., 1997). The list of species analyzed in the study is shown in Table A1, and the species marked with an asterisk are those selected for the communities study. Species occurring in less than three stations were disregarded, as well as those stations with less than three species. A hierarchical clustering was then performed using the Bray-Curtis similarity index and UPGMA algorithm to calculate the distance matrix. The optimal cut-off was at 20% Bray-Curtis similarity, resulting in a division of 5 separate groups following the same methodology that was used for the abiotic cluster. To select the species or taxa that contributes most to the difference between groups, we performed a Similarity Percentage Analysis (SIMPER).

Finally, to check the variables responsible for the aggregations of the different samples, an ordination method was performed. For its selection, we checked the length of the DCA (Detrended Correspondence Analysis) axes. Axis 1 presented a value of 4, which advised the use of a unimodal method, so a CCA (Canonical Correspondence Analysis) was

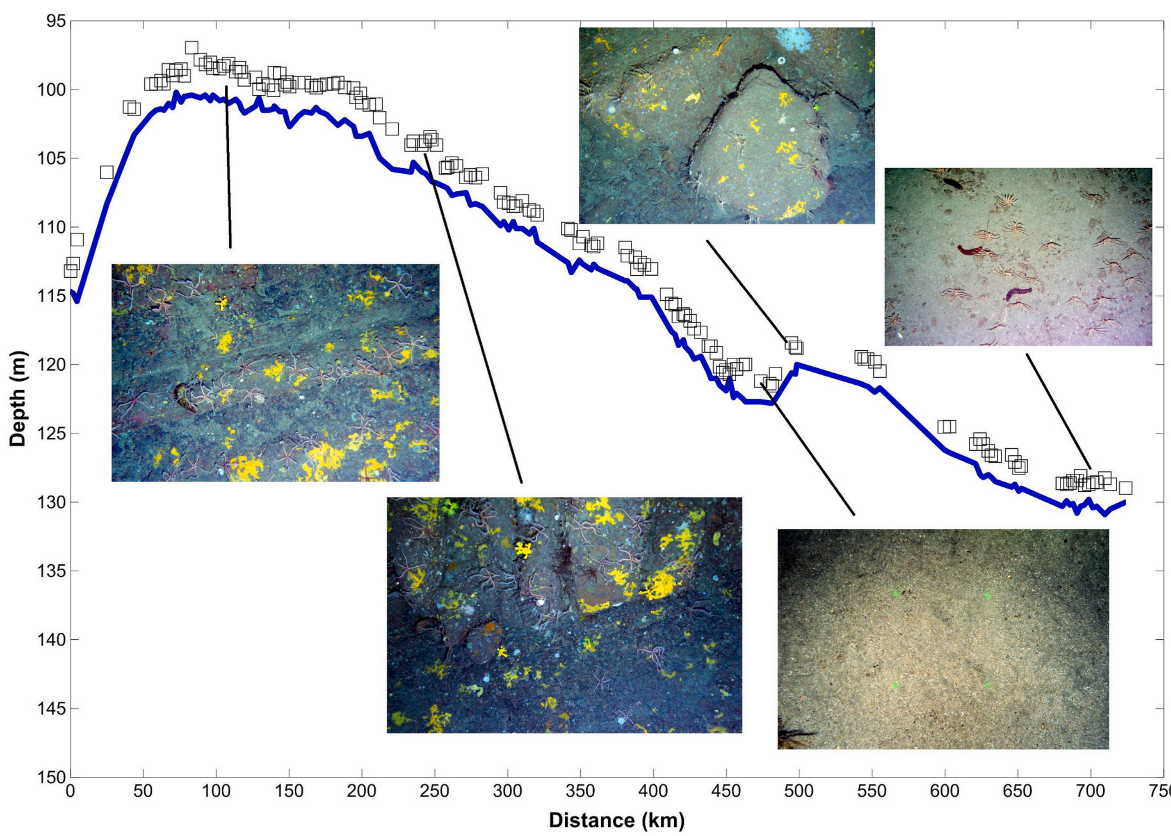

Fig. 3. Ground type selection by ground-truthing. It can be seen in the images that the upper part of the outcrop is formed by living bedrock, as well as the accumulation of sediments in the valleys.

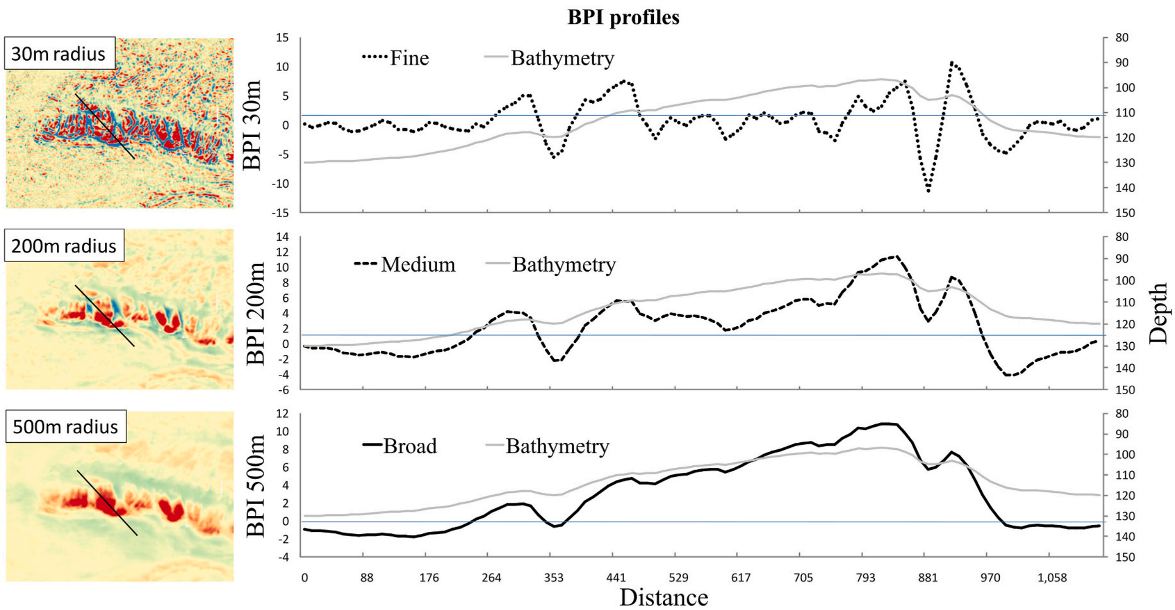

Fig. 4. Profiles drawn in one of the outcrops for three different BPI resolution according to the external radius: 30 m, 200 m and 500 m. The bathymetric profile is also displayed in each of the figures.

Table 1
Average values and standard deviations of cluster groups for every environmental variable of the k-means classification technique according to abiotic factors.

Clusters	Depth		Slope		Backscatter		BPI	
	Center	sd	Center	sd	Center	sd	Center	sd
A	129.41	13.45	0.96	0.82	−17.17	1.22	−0.19	0.54
B	303.91	60.41	6.45	2.80	−18.00	0.06	−0.07	1.07
C	147.28	22.43	1.02	0.73	−25.50	1.43	−0.16	0.60
D	138.13	17.26	1.04	0.78	−20.89	1.17	−0.11	0.59
E	131.79	19.77	1.44	1.32	−17.48	1.66	1.11	0.71

selected.

2.5. Bathial and circalittoral habitat modeling for management studies

To address future strategies in the study of the interaction of habitats with anthropic uses and activities, we developed the modeling of the main HFS (habitat-forming species) of both the circalittoral zone and the bathyal zone, at a scale suitable for the development of the monitoring plan. Thus, the circalittoral area have as dominant species the sponge *Phakellia ventilabrum* and the yellow coral *Dendrophyllia cornigera,* an assemblage that has already been analyzed in previous studies (González-Porto et al., 2014; Sánchez et al., 2009). Therefore, these are the species that have been taken into account for the development of the habitat distribution models at EUNIS level 4 (Moss, 2008) by adding their presences and abundance. For the bathyal domain, we can highlight two main HFS, the antipatharian *Antipathes dichotoma* and the sponge *Asconema setubalense,* for their density and for being the species that have defined habitats in previous studies (Lo Iacono et al., 2019). Their occurrences and abundances have also been combined to obtain the spatial distribution at EUNIS level 4.

For the proposed models, in addition to the variables used in the cluster for the abiotic characterization of the bottoms, we added the layers most associated with the exposure and intensity of the dominant currents of the area, such as the aspect or orientation of the terrain, the kinetic energy of the deep layer and the profile curvature. The orientation of the terrain has been disaggregated into its north and east components calculated as the sine and cosine of the aspect respectively. Furthermore, bottom currents play an important role in habitat selection for sessile benthic species as they largely condition the food supply and larval dispersion (Davies et al., 2008; Juva et al., 2020), and kinetic energy was used as a proxy for seabed hydrodynamics. This predictor variable was derived from water velocity data from the COPERNICUS operational model IBI (Iberian Biscay Irish) Ocean Analysis and Forecasting system (Sotillo et al., 2015), and has a spatial resolution of $0.028^{\circ} \times 0.028^{\circ}$. Nearest bottom velocity data layers (u and v components) were generated based on the DEM, and mean kinetic energy for 2014 was calculated from monthly means. The profile curvature is the concavity/convexity of the terrain parallel to the aspect, and was an important variable in the studies of microhabitats in the area (Prado et al., 2020). Finally, new correlation and VIF analysis were carried out between variables, showing that there is a very high negative correlation (more than 80%) between depth and kinetic energy, so the latter was not included in the models for being at a lower resolution. The VIF values were below 3, indicating that there was no multicolinearity.

The species selected were modeled together for each area in two steps, modeling the presence/absence on the one hand, and densities on the other. This allows us, through the union of the two layers, to model the distribution of densities in zero inflated data (Zuur et al., 2009) through the use of GAMs (Generalized Additive Models). This SDM (Spatial Distribution Model) uses partial smooth functions that are not necessarily linear to relate the dependent variable with the different predictors (Hastie and Tibshirani, 1987), and lets us to work with both presence/absence values and densities. Models have been run with the R package “mgcv” (Wood and Wood, 2015). The selection of variables was carried out by the forward-backward stepwise selection method, adding and eliminating variables in such a way as to minimize the value of AIC (Akaike Information Criterion). The maximum number of smooth functions for each predictor (knots) was set to 5 to avoid overfitting. The distribution used for presence/absence data was binomial, and negative binomial for density. Finally, we changed the resolution of the predictors to 30 m to mitigate the spatial autocorrelation derived from the sampling method and a Moran's I test was performed, which values were lower than 0.022 besides being not significant, so we assumed the absence of spatial autocorrelation.

For the evaluation of the presence/absence models, 70% of the data was randomly selected for the training data and the other 30% was reserved for the test data. 10 repetitions were carried out, calculating the AUC (Area Under the Curve) for each one, which represents the sensitivity *versus* specificity, and the average was calculated for both circalittoral and bathyal models.

3. Results

3.1. Characterizing habitat/biotopes level

The map in Fig. 5 shows the distribution of the different groups that have been obtained from the abiotic cluster: group A represents low BPI areas of boulders and sediments and high backscatter, group B is the bathyal one representing deep areas of boulders and sediments and steep slopes, group C are low BPI areas of high sedimentary coverage and low backscatter, group D are flat areas of hard substrate with high sedimentary coverage, and finally the group E shows the top of the outcrops, high BPI areas of living rock with scarce boulders and sediments. The average values of the different variables for each group and the standard deviations are in Table 1.

The clustering of the samples carried out for the study of the communities also resulted in 5 groups (Fig. 6), showing a disaggregated distribution of the stations according to the different abiotic predictors. For a clear representation in the CCA, GR1 was removed, as it is characterized by the species of the bathyal zone and strongly influenced by depth (Table 2). Thus, Fig. 7 shows that GR2 is clearly influenced by depth and low backscatter, and GR4 by slope and BPI. GR3 and GR5 do not show a clear influence of any variable, except that it represents an area with low variability of slope and BPI. As for the communities of groups GR3 and GR5, both belong to the majority group of Fig. 5, group A, the one corresponding to the circalittoral with boulders and sediment.

The representative species of each of the groups selected by the SIMPER method are shown in Table 2. The mean density of *P. ventilabrum* is similar throughout the circalittoral area, while *D. cornigera* is more characteristic of groups GR4 and GR5. The most strongly differentiated groups are GR1 and GR4, the first characterized mainly by depth, since it represents the bathyal zone of the study area, with the presence of species absent in the circalittoral at these latitudes, such as the hexactinellid sponge *Asconema setubalense* and the antipatharian *Antipathes dichotoma*. GR4, in which a high density of different species of ophiuroids was observed, is characteristic of the upper part of the outcrops, highlighting its high backscatter and BPI. GR3 and GR5 are more overlapping, although the latter has a lower BPI and slope, as well as a greater presence of boulders, contributing to high concentrations of brachiopods. In GR2, the most characteristic sedimentary bottom community, the mollusk *Neopycnodonte cochlear* is very abundant as it finds in the exposed rocks an extensive surface to adhere to.

3.2. Modeling densities on EUNIS level 4

The contribution of the variables and the deviations explained are detailed in Table 3. Presence/absence and density of circalittoral full models explain 72% and 37.3% deviation respectively, and bathyal full models, 41.6% and 55.3%. Depth is the main variable for three of the four models, especially for predicting the presence of the species in the circalittoral, where it explains 20% of the variance. The trend is negative in the circalittoral and positive in the bathyal (Fig. 8). The northern component is the next most important in the circalittoral, and eastern for the bathyal domain density model. The trend curves are negative for the northern component and positive for the eastern component, except in the model of densities in the bathyal zone, which is favored by west-

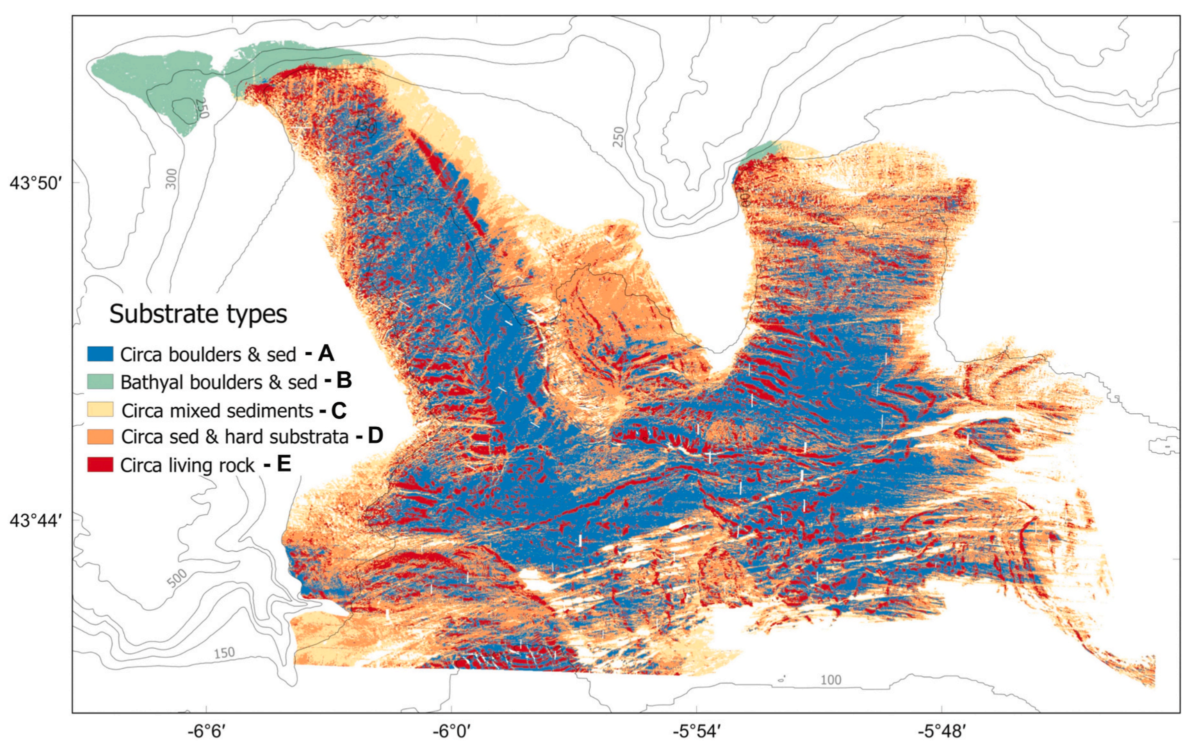

Fig. 5. Distribution of the different groups according to the k-means unsupervised classification technique. Group A (blue): circalittoral with boulders and mixed sediment; group B (green): Bathyal with boulders and mixed sediment; group C (light orange): Circalittoral with mixed sediments; group D (orange): circalittoral rock with mixed sediments; and group E (red): Circalittoral living rock. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

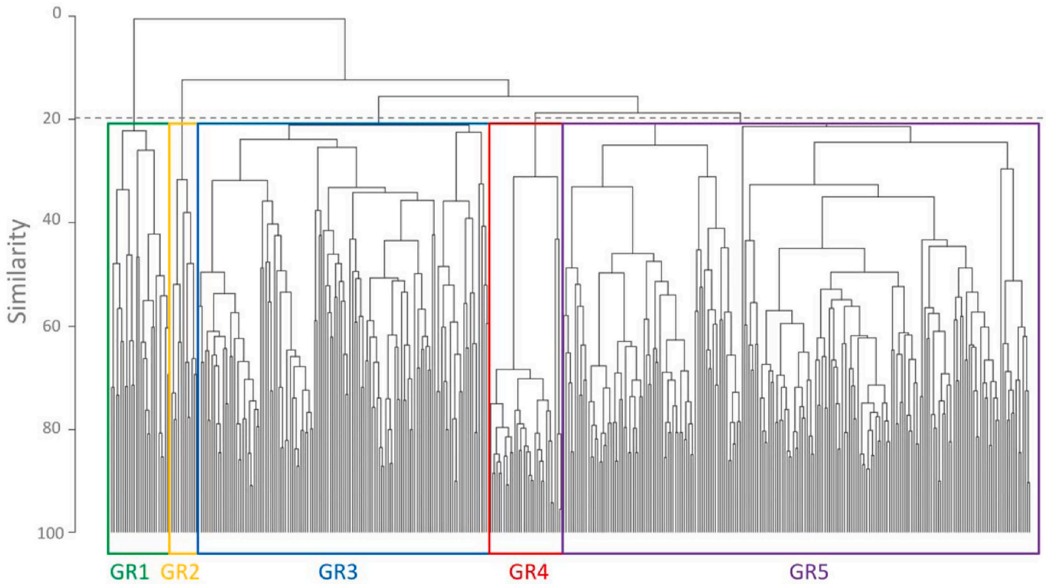

Fig. 6. Hierarchical clustering dendrogram of the stations according to HFS species densities. Each group of stations corresponds to a specific assemblage of species.

Table 2
Species and average density values (N/100 m) of the main species representative of the dissimilarity between groups of the SIMPER analysis.

Species	AV	Species	AV
GR1		GR3	
Antipathes dichotoma	69.5	*Artemisina transiens*	72.7
Stylocordyla pellita	62.1	*Halicnemia* spp.	49.0
Asconema setubalense	29.8	*Phakellia ventilabrum*	45.3
Ophiotrix spp.	15.2	*Dendrophyllia cornigera*	7.5
Cerianthus spp.	14.5	Yellow Demospongiae sp1.	7.4
Geodia spp.	12.0	**GR4**	
Hymedesmia paupertas	4.6	*Ophiotrix* spp.	1103.0
GR2		*Halicnemia* spp.	246.0
Neopycnodonte cochlear	712.6	*Phakellia ventilabrum*	173.0
Undetermined brachiopods	193.1	Undetermined brachiopods	154.7
Halicnemia spp.	95.0	*Ophiocomina nigra*	130.1
Phakellia ventilabrum	78.1	*Artemisina transiens*	74.5
Guitarra solorzanoi	43.7	*Dendrophyllia cornigera*	59.0
Geodia spp.	19.1	**GR5**	
Axinella infundibuliformis	16.7	Undetermined brachiopods	313.4
Ophiotrix spp.	11.1	*Halicnemia* spp.	161.5
White Demospongiae sp1.	6.4	*Dendrophyllia cornigera*	149.3
Phakellia hirondellei	5.6	*Phakellia ventilabrum*	90.5
Hymedesmia paupertas	5.6	*Artemisina transiens*	68.6
		Hymedesmia sp1.	38.2
		Haliclona spp.	15.8

facing slopes. Backscatter explains 4.1% of the variance of the circalittoral model with a positive trend stabilizing from a value of −21, which indicates that the habitat is favored by hard bottoms. Regarding BPI, its contribution is important specially for the bathyal zone, showing clearly positive trends.

To convert the probability values into presence/absence, we used the value that maximizes the Kappa (de la Torriente et al., 2019), which is 0.51 and 0.34 in the circalittoral and bathyal respectively. The mean AUC obtained in the repetitions carried out for the validation of the circalittoral model is 0.97 and for the bathyal it is 0.9. Fig. 9 shows the maps resulted in the predictions of densities and presence/absence full models, and the result of their union to obtain the zero inflated values delta model.

4. Discussion

The methodology combining the study of the seabed with visual transects and the collection of specimens with rock dredge and/or ROVs is essential in the configuration of habitats and rocky bottom communities in morphostructurally complex areas of the deep-sea. In this study it has been developed in a circalittoral shelf for its abiotic characterization and the analysis of its associated communities at the habitat/biotope level, equivalent to EUNIS level 5, as well as to represent the spatial distribution of the predicted densities of habitat level 4 main species in circalitoral and bathyal domain for the development of management studies. In addition, this study has enabled the disaggregation of the main HFS of the circalittoral, in order to determine the biotic and abiotic affinities of the main species, *P. ventilabrum* and *D. cornigera*.

An essential work for the success of the characterization of benthic habitats is the taxonomic analysis of the specimens obtained with direct samplings such as the rock dredge, in order to optimize the identification of the species that appear in the analysis of the images captured by the photogrammetric vehicle. However, despite the efforts made in sampling, a large number of species are not collected by rock dredge due to its lower catchability, what makes it inefficient for species quantification. This can be complemented with the use of ROVs, which allows the selective collection of species. These sampling strategies are necessary for getting the bottom fauna and its functionality, and for providing a complete picture of the GES (Good Environmental Status) of seafloor integrity (Buhl-Mortensen et al., 2015).

For the biotope level analysis, we have excluded the sedimentary zone by applying a cut-off point as detailed in Brown et al. (2011). This allowed us to make a first approach by selecting the variables that give more information on the ground composition of the terrain at this scale. For this first analysis, the energy derived from the tides was not included due to its low resolution and its high correlation with depth. This lack of adequate resolution results in a limitation for the study of the deep circalittoral (Henriques et al., 2015) despite being an important feature in defining representative circalittoral habitats. In addition, according to EUNIS, the absence of foliose red algae corresponds to the lower circalittoral zone (Ellwood et al., 2011), in which we are located, and has a very low range of kinetic energy values. However, this range of values may not be entirely faithful to reality, since the proximity of the submarine canyons is affecting in a very localized way, which would not be

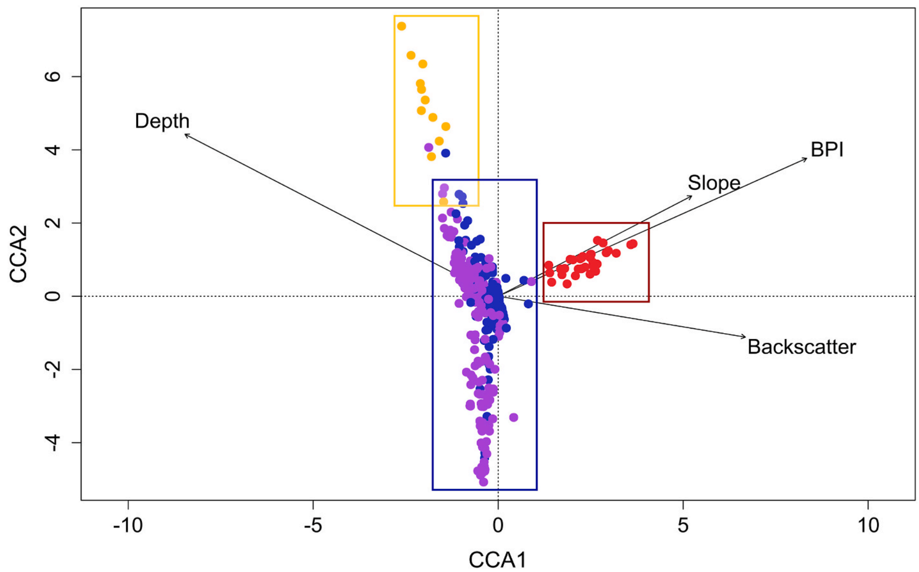

Fig. 7. Distribution of the samples according to the environmental variables of the Canonical Correspondence Analysis (CCA). The different colors correspond to those of the dendrogram clusters. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 3
Deviance contribution of the predictors to the presence/absence and density models of both areas and total deviance explained by the full models. The absence of data means that the variable has not been selected for the full model.

	Circalittoral				Bathial			
	Pres/Abs		Densities (N/m^2)		Pres/Abs		Densities (N/m^2)	
	Dev (%)	p-value	Dev (%)	p-value	Dev (%)	p-value	Dev (%)	p-value
Depth	20	**	14.5	***	11.8	.	4.1	**
Slope	3.3	*						
BPI			0.2	>0.1	4.6	***	3.1	***
North	4.4	***	7.4	***	1	*		
East	0.6	>0.1	5.4	**	0.3	>0.1	11.2	***
Curv					2	*	0.9	*
Backscatter	4.1	**						
Full Model	72		37.3		41.6		55.3	

reflected at the real scale of the currents. Therefore, depth can provide with more information as a proxy of the kinetic energy.

For this study we also developed an analysis of the BPI resolution by selecting the most suitable radius through the transects and the ground-truthing to get the ground composition of the characteristic outcrops of the study area. Depth itself does not affect the distribution of species, but it does influence other variables, such as temperature or bottom dynamic, which do affect habitats, and slope is essential in the sediments transport process. These four layers helped us to predict the distribution of the seafloor characteristics following strategy 1 abiotic surrogates only (Brown et al., 2011; Buhl-Mortensen et al., 2015; Ferrier and Guisan, 2006). This is a requirement to be considered because the different habitat classification systems used have as reference the environmental variables in the first hierarchical levels.

Table 4 shows the relationship of habitats according to the results obtained. In habitats in which no equivalences have been found in EUNIS, the code has been created with the previous level and the EU country code was completed with correlative numbers to create a new habitat that can be inventoried as was done in Sánchez et al. (2017). The companion species have been obtained from the SIMPER and from the total inventory of analyzed species (Table A1). Abiotic group A comprises two different communities, GR3 and GR5. The former has as main species the sponges *P. ventilabrum* and *A. transiens,* and according to visual transects and previous studies of microhabitats (Prado et al., 2020), they have preference for more open areas with greater sedimentary cover; however, in GR5, where the predominant species are *D. cornigera* and some brachiopod species, the bottoms are more irregular with high presence of stone blocks. The main companion species of this area are *Marthasterias glacialis, Parazoanthus* spp. and *Poecillastra compressa*. Brachiopods are specially abundant as this and previous studies of the images collected by the photogrammetric vehicle in the area have highlighted (Sánchez et al., 2008, 2009). According to the rock dredge samples, *Megerlia truncata* and *Novocrania anomala* are the most abundant among all the species of brachiopods observed, although the species *Macandrevia cranium* and *Terebratulina retusa* can also be found in the western zone of the study area.

A. setubalense and *A. dichotoma* are the main species of the bathyal zone assemblage (GR1) due to their abundance, size and representativeness. Thus, Lo Iacono et al. (2019), define a volcanic ridge habitat as dominated by the glass sponge *Asconema setubalense* and antipatharians. The main accompanying species of the bathyal habitat are the lollipop sponge *Stylocordyla pellita* and several species of genus *Geodia*.

The difference between groups C and D of the cluster according to Table 1 are not very significant. It is likely that cluster C is a transition zone towards the sedimentary shelf, since there is no correspondence with any assamblage. Thus, we can find species typical of sedimentary substrates such as *Anseropoda placenta* or *Funiculina quadrangularis*. In group D we find the GR2 assemblage, where along with *P. ventilabrum* and *N. cochlear* there are large diversity of sponges, such as *Guitarra solorzanoii*, species of genus *Geodia*, and *Axinella infudibuliformis*. In addition, *Acanthogorgia armata*, *M. glacialis* or species of the genus *Epizoanthus* can also be found.

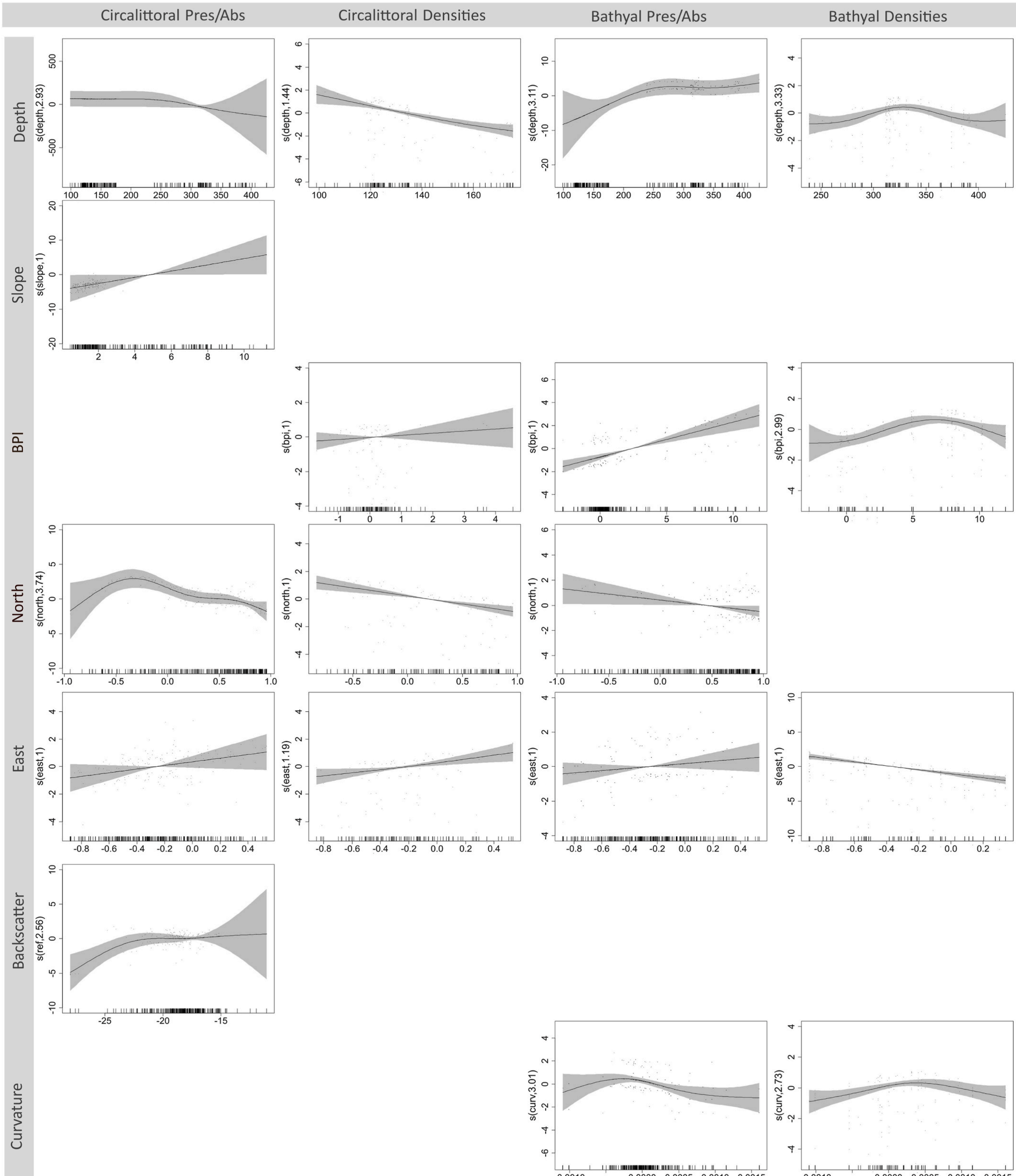

Fig. 8. Response curves of circalittoral and bathyal GAM models in their two steps, presence/absence and densities, showing the smoothed functions and confidence intervals. The absence of figures means the exclusion of the variable for the full model.

Finally, the rocky outcrops with little sedimentary cover is represented by group E, in which we find the GR4 assemblage. It is characterized by the presence of living rock and positive BPIs and has a great abundance of brittle stars, being *Ophiotrix fragilis* one of the most abundant. The species of the genus *Ophiotrix* and *Ophiocomina nigra* are the only mobile species included in the studies of communities since they are dominant species that have defined biotope in the Marine Biotope Classification for Britain and Ireland in the moderately or low exposed circalittoral (Connor et al., 1997). Studies in the phylogeographic patterns of mitochondrial DNA have demonstrated the existence

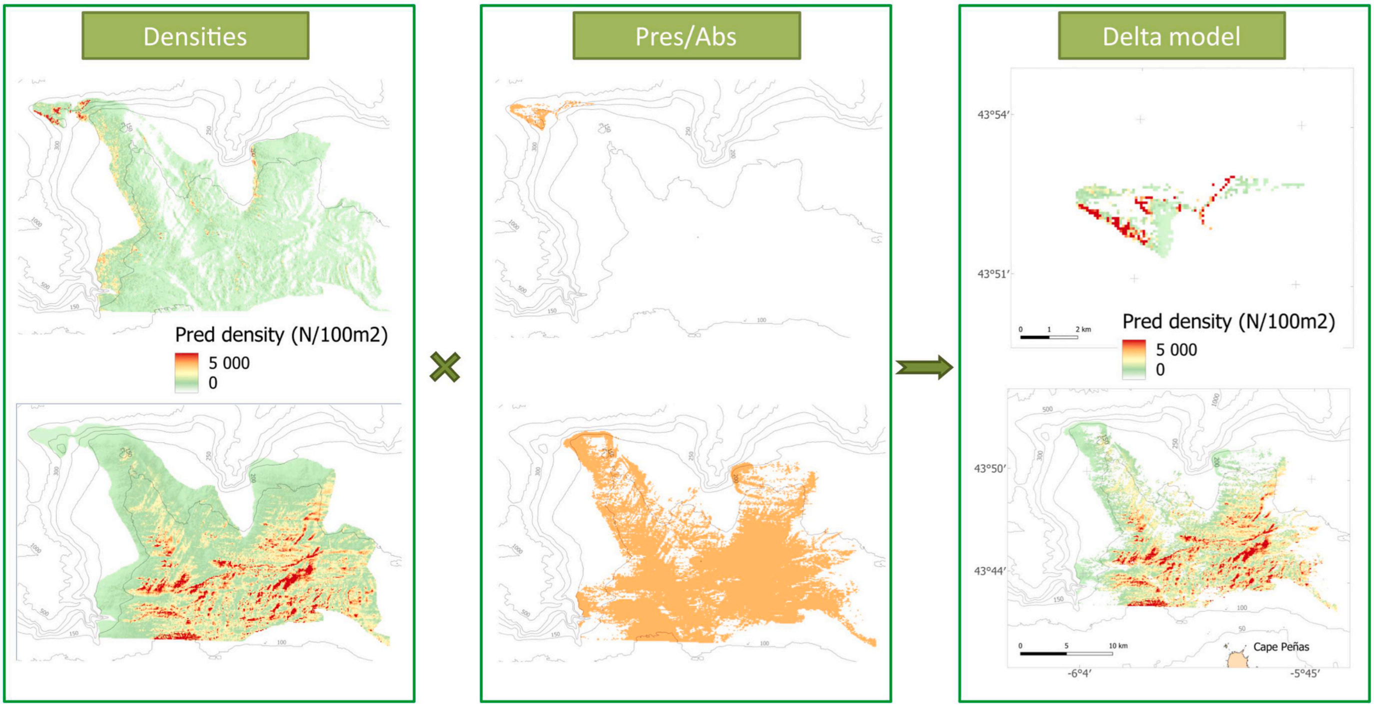

Fig. 9. Maps of the elaboration process of delta models for the bathyal and circalittoral zones. First maps on the left are the predicted densities for both areas, the maps in the middle are the presence/absence ones, and on the right, the zero inflated factor model maps.

Table 4
Designation of the studied habitats and equivalences according to the Spanish inventory and EUNIS classification.

Unit designation	Community group	Abiotic cluster	EUNIS level	EUNIS code	Spanish inventory
Atlantic upper bathyal rock dominated by invertebrates	GR1	B	4	A6.11	4010208
Asconema setubalense and *Antipathes dichotoma* on bathyal rock with boulders and sediments	GR1	B	5	A6.11_SP1	4010106
Phakellia ventilabrum and *Dendrophyllia cornigera* on Atlantic offshore circalittoral rock	GR2, GR3, GR4, GR5	A, C, D, E	4	A4.121	3020213
Phakellia ventilabrum and the mollusc *Neopycnodonte cochlear* on offshore circalittoral mixed sediments	GR2	D	5	A4.121_SP1	
Sponges *Phakellia ventilabrum* and *Artemisina transiens* on offshore circalittoral rock and mixed sediments	GR3	A	5	A4.121_SP2	3020214
Phakellia ventilabrum and *Dendrophyllia cornigera* with brittle stars *Ophiothrix* spp. And *Ophiocomina nigra* on offshore circalittoral living rock	GR4	E	5	A4.121_SP4	
Dendrophyllia cornigera and brachiopods *Megerlia truncata* and *Novodina pandina* on offshore circalittoral rock and boulders	GR5	A	5	A4.121_SP3	3020218

of three species of *Ophiothrix* in what had originally been classified as *O. fragilis* (Taboada and Pérez-Portela, 2016). The samples collected by the rock dredge in this area are still being analyzed, so the main species of this habitat are yet to be determined.

Fig. 10 shows the most representative images of the assemblages. In all of them, the bottom is characterized by presenting rock with boulders and sediments in different percentages, including the bathyal community (assemblage GR4). In previous studies of this habitat, many sponges of the species *A. setubalense* appeared with obvious damage caused by longline fishing (Rodríguez-Basalo et al., 2021). The fact that it is an habitat degraded by human activities makes the distribution mapping process more delicate, since it depends largely on the pressure of the fisheries with which it interacts, so in future studies it would be advisable to incorporate the monitoring of part of this habitat as no-take area.

All the identified habitats have vulnerable benthic species of a certain size settled on rocky bottoms. Combining the results of the four assemblages of the circalittoral rocky shelf, yellow coral *D. cornigera* and the sponge *P. ventilabrum* are the most abundant, being accompanied by other benthic species, especially by sponges. On the bathyal rocky habitat, in addition to *A. dichotoma*, two of the structuring species are the large sponges *Asconema setubalense* and *Geodia barreti*. Due to these dominant species, all habitats mentioned in this work are considered as belonging to the management unit of the Habitats Directive (Annex I) called 1170 Reefs. LIFE + INTEMARES project (https://intemares.es/) is one of the drivers who are trying to contribute to the development of a methodology that allows advances in the knowledge of the current state of Natura (2000) network habitats and their conservation needs throughout the Spanish territory, as well as the governance and the involvement of the different actors and stakeholders in the processes of creation and monitoring of protected areas. This is the framework within which, an effort to unify criteria for the study, characterization and designation of the habitats studied is being developed (de la Torriente et al., 2019; Sánchez et al., 2014, 2017). Thus, the administrations responsible for the protection of vulnerable habitats will be provided with studies of these vulnerable benthic habitats and their distribution to be able to develop each Special Area of Conservation (SAC) Management Plan for the adequate protection of these areas.

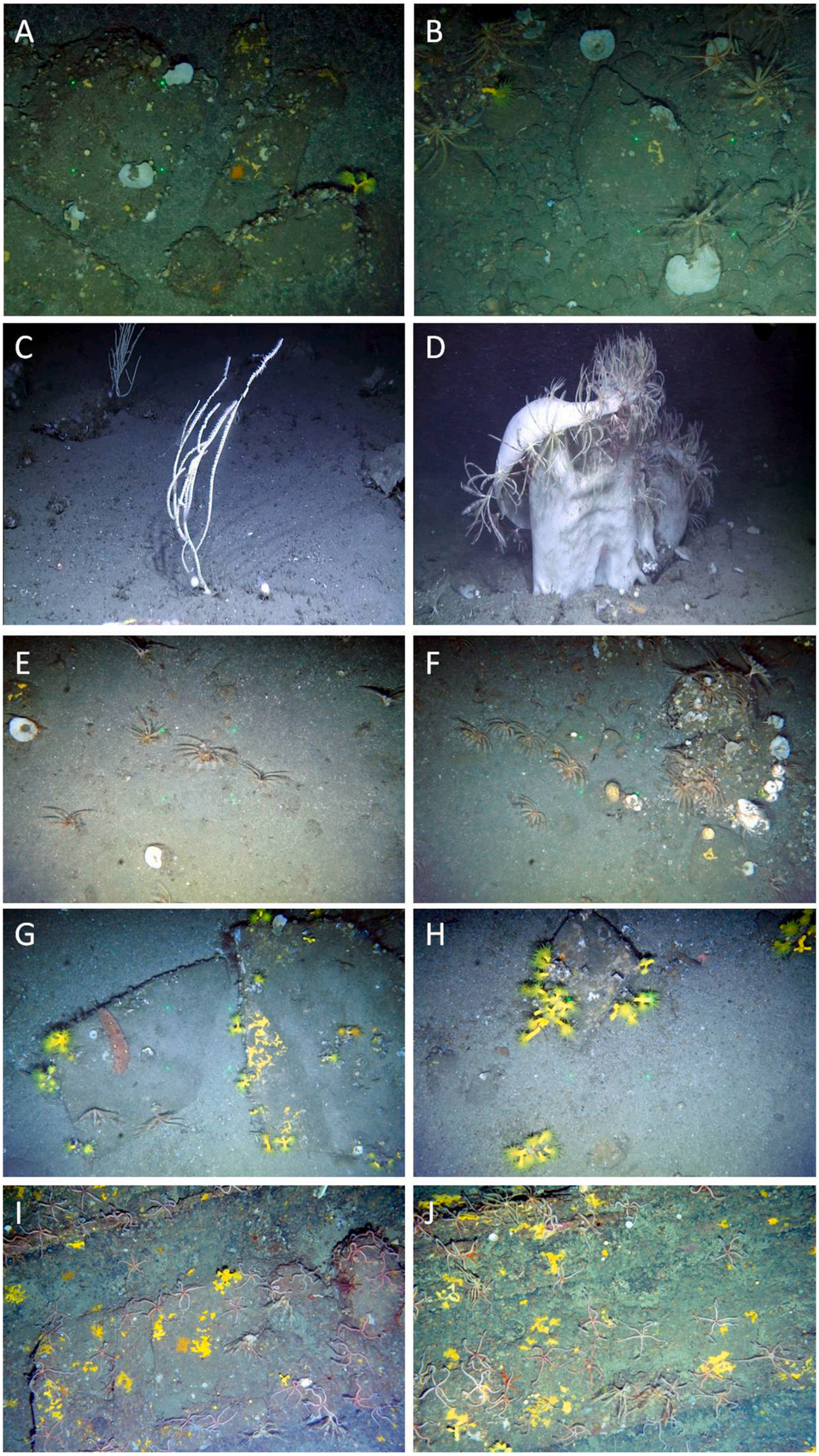

Fig. 10. Images selection of the assemblages. Images A and B: sponges *Phakellia ventilabrum* and *Artemisina transiens* on offshore circalittoral rock and mixed sediments; images C and D: *Asconema setubalense* and *Antipathes dichotoma* on bathyal rock with boulders and sediments; images E and F: *Phakellia ventilabrum* and the mollusc *Neopycnodonte cochlear* on offshore circalittoral mixed sediments; images G and H: *Dendrophyllia cornigera* and brachiopods *Megerlia truncata* and *Novodina pandina* on offshore circalittoral rock and boulders; images I and J: *Phakellia ventilabrum* and *Dendrophyllia cornigera* with brittle stars *Ophiothrix* spp. And *Ophiocomina nigra* on offshore circalittoral living rock.

CRediT authorship contribution statement

A. Rodríguez-Basalo: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **P. Ríos:** Writing – review & editing, Formal analysis, Data curation, Conceptualization. **B. Arrese:** Writing – review & editing, Formal analysis, Data curation. **A. Abad-Uribarren:** Writing – review & editing, Methodology, Formal analysis. **J. Cristobo:** Writing – review & editing, Funding acquisition, Data curation. **T.P. Ibarrola:** Writing – review & editing, Data curation. **M. Gómez-Ballesteros:** Writing – review & editing, Formal analysis, Data curation. **E. Prado:** Methodology, Formal analysis, Data curation. **F. Sánchez:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This study was made possible thanks to the invaluable work of all the participants in the five surveys involved and the crews of the R/Vs Ramón Margalef and Angeles Alvariño. The authors also appreciate the helpful assistance of the technicians of the ROTV Politolana and ROV Liropus 2000 for their skill in executing the dangerous visual transects very close to the rough bottoms of the study area.

This research has been performed in the scope of the INTEMARES project. INTEMARES was partially funded by the European Commission LIFE C “Nature and Biodiversity” call (LIFE15 IPE ES 012). The Biodiversity Foundation, of the Ministry of Environment, was the institution responsible for coordination this project.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2022.107912.

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