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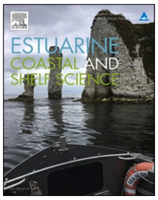

Mapping the macrofauna communities of Portugal's continental shelf north of Nazaré Canyon using Community Distribution Modelling (CDM)

Renato Mamede [a], Leandro Sampaio [b,c], Fernando Ricardo [a], Luísa Magalhães [d], Marta Lopes [a], Roberto Martins [d], Ana Maria Rodrigues [d], Rosa Freitas [d], Victor Quintino [d,*]

[a] *ECOMARE, CESAM - Centre for Environmental and Marine Studies and Department of Biology, University of Aveiro, 3810-193, Aveiro, Portugal*

[b] *CIIMAR Interdisciplinary Centre of Marine and Environmental Research of the University of Porto, Novo Edifício do Terminal de Cruzeiros do Porto de Leixões, Avenida General Norton de Matos, Matosinhos, Portugal*

[c] *Department of Biology, Faculty of Sciences, University of Porto, Porto, Portugal*

[d] *CESAM - Centre for Environmental and Marine Studies and Department of Biology, University of Aveiro, 3810-193, Aveiro, Portugal*

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ABSTRACT

The conservation and sustainable use of marine ecosystems is a worldwide concern, and to achieve it, managers and decision-makers require detailed environmental and biological information, namely supplied as maps of the seafloor. This work was conducted on Portugal's continental shelf located north of Nazaré Canyon. Sediment data was obtained in 226 grab samples, of which 169 were used to study the macroinvertebrate benthic communities. Acoustic transects were run for more than 2500 Km to obtain depth and maps of environmental variables were produced through spatial interpolation of the point data. A multivariate analysis of the biological data identified seven benthic communities, characterized by different species and environmental conditions (i.e., sediment type and depth). The spatial distribution of each biological community was modelled as the response to environmental variables using generalized linear models with a binomial distribution. Depth was the variable more often significantly related to the distribution of the benthic communities, selected in 5 of the 7 Community Distribution Models (CDM). Using the CDM expressions and maps of the environmental variables, probability maps were produced for the distribution of each community. Their combination allowed to obtain a final map of the most probable benthic communities throughout the study area, showing a high agreement (81%) between the observed and the predicted distributions. The maps produced in this study are valuable tools for the decision-making process involved in the management of the marine environment and their resources, for instance to classify these habitats according to the European nature information system (EUNIS) and in the scope of the Marine Strategy Framework Directive.

1. Introduction

The conservation and sustainability of the oceans, seas and marine resources comprise one of the main goals of the 2030 Agenda for Sustainable Development of the United Nations (United Nations, 2016). The need to protect marine ecosystems was also emphasized by European authorities through several pieces of legislation (European Commission, 2007, 2008a; 2008b). Detailed environmental and biological information are essential to assist their implementation and the decision-making management (Galparsoro et al., 2015; Reiss et al., 2015), such as to identify and classify marine habitats according to the European nature information system (EUNIS) and in the scope of the Marine Strategy Framework Directive (MSFD).

Due to the difficulty of collecting data in the marine environment, it is common that managers are confronted with sparse data on species and habitats. The development of new statistical methods and geographic information system tools coupled to the need for more detailed and spatially continuous data for environmental managing, led to the increasing use of spatial interpolation methods (e.g. kriging) and Species Distribution Models (SDM) (Li and Heap, 2011; Reiss et al., 2015; Melo-Merino et al., 2020).

Spatial interpolation methods, such as kriging, permit to produce continuous surfaces (i.e. maps) from point sampling data (Li and Heap, 2011), issued from the traditional seafloor sampling approaches.

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* Corresponding author.
E-mail address: victor.quintino@ua.pt (V. Quintino).

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Environmental maps can be combined with species distribution models (SDM), to produce predictive maps of various biological parameters (Franklin, 2010; Reiss et al., 2015). The benthic communities of the Atlantic and Mediterranean European continental shelves, have been studied since the early twentieth century, serving as baseline for posterior studies (among others, Ford, 1923; Stephen, 1923; Jones, 1950; Thorson, 1957; Pérès and Picard, 1964; Cabioch, 1968; Glémarec, 1973). SDM are based in the assumption that the species and such communities' distributions, used as response variables, are mainly driven by environmental factors (Guisan and Zimmermann, 2000), allowing the prediction of biological variables (number of species or species presence, abundance, or biomass), in areas from where only environmental data is available (Franklin, 2010). The selection of the environmental predictors is therefore very important in SDM, as these should be explicative of the species or community distributions (Mateo et al., 2011). Regarding marine benthic communities' distribution, this is strongly dictated by abiotic factors, such as sediment grain-size and organic matter (Ellingsen, 2002; Martins et al., 2013), depth (Gogina et al., 2010), energy at the bottom (Rosenberg, 1995), oxygen (Hill et al., 2002) and light reaching the seabed (Connor et al., 1997, 2004; Davies et al., 2004). However, due to the collinearity among these variables, the most sampled, grain-size and depth, are often used as surrogates to some

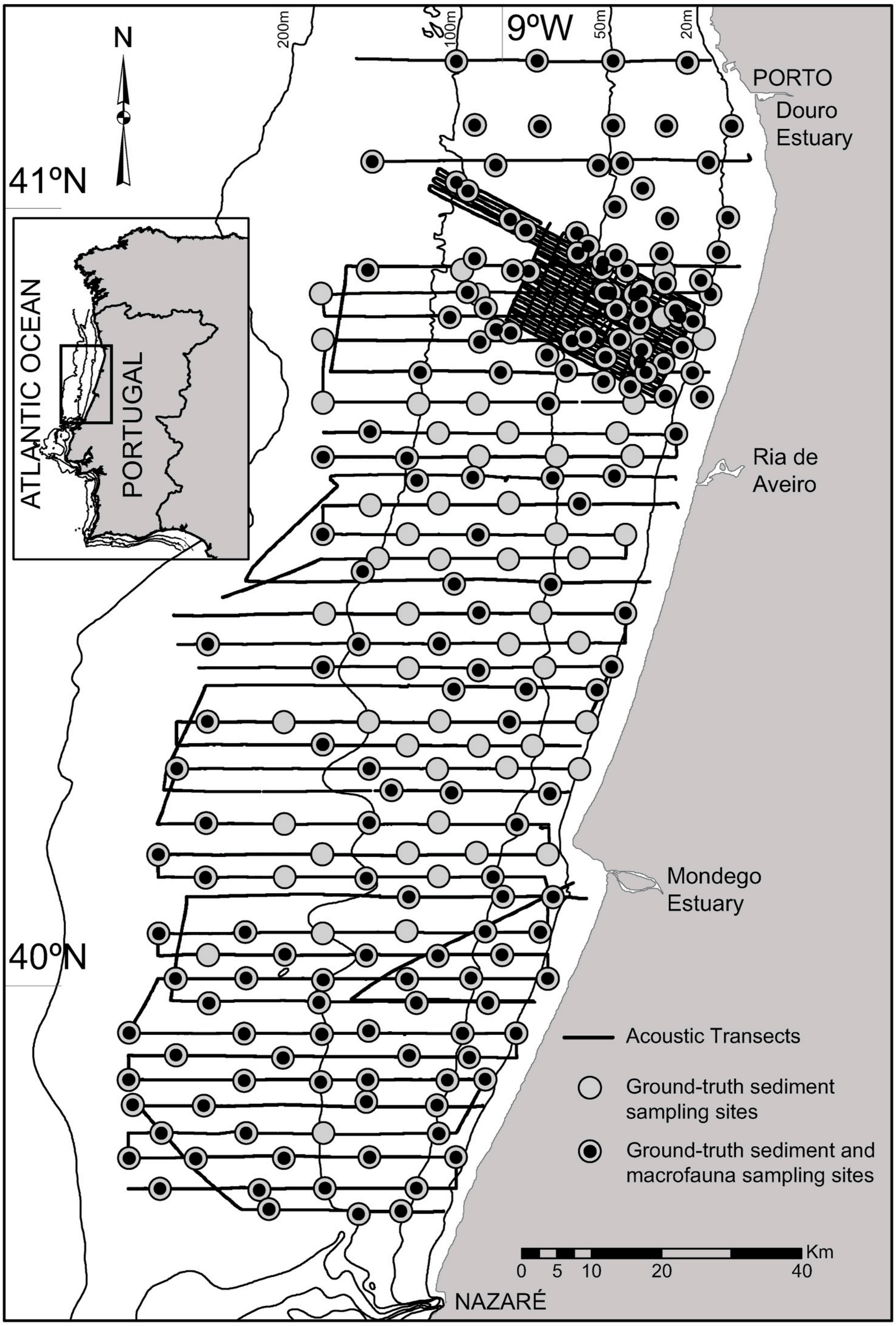

Fig. 1. Survey area showing the positioning of the acoustic transects for depth survey, the ground-truth sediment (grey circles) and the macrofauna sampling sites (black circles).

of the other (Austin, 2007; Gogina et al., 2010). Moreover, when aiming to find which environmental factors drive the biological response, it is very important to account for collinearity among the explanatory variables (Guisan and Zimmermann, 2000; Franklin, 2010; Zuur et al., 2010). SDM have been used in marine studies to predict the distribution of a wide range of marine biological entities and descriptors, such as cetaceans (Becker et al., 2019; Karamitros et al., 2020), macroalgae (Young et al., 2015), fish (Schmiing et al., 2013), fish larvae (Carassou et al., 2008), corals (Hu et al., 2020), polychaetes (Willems et al., 2008), macroinvertebrate benthic communities, using community distribution models (CDM) (Moritz et al., 2013) and their biological parameters, namely species richness, abundance or Shannon-Wiener diversity (Rosa-Filho et al., 2004). Regarding their applicability in the management of the marine ecosystems, SDM have been widely used, namely for studying the impact of climate change in species distributions (Weinert et al., 2016), risk assessment related to invasive species (Jones et al., 2013), selection of recovery areas for impacted habitats (Elsäßer et al., 2013) and conservation planning (Bajjouk et al., 2015).

The present study aimed to identify, characterize, model, and map the macroinvertebrate benthic communities from Portugal's shelf north of Nazaré Canyon, where previous studies reported some of the highest benthic invertebrate abundances in this continental shelf (Martins et al., 2013). Specifically, this study aimed to improve current knowledge of the continental shelf benthic habitats north of Nazaré Canyon by i) producing maps of environmental parameters, extrapolating from point sampling data; ii) develop CDM relating the presence/absence of the biological communities to environmental variables; iii) combine the previous two to produce maps with the distribution of the most probable benthic communities throughout the study area.

2. Material and methods

2.1. Study area and samples collection

The study area corresponds to the Portuguese continental shelf from Nazaré to Porto, between 9- and 154-m depth, extending 165 Km along the north-south direction and covering and area of approximately 7000 Km^2 (Lat 39°42′20″N to 41°11′31″N, Fig. 1). This area offers special interest, as it is comprised in the NATURA 2000 network (NATURA, 2000 Network Viewer, 2021), the Portuguese continental shelf is the widest and characterized by a variety of soft sediments, including the most extent areas of coarser sediments, inhabited by a diverse and abundant macrofauna (Martins et al., 2012; Mamede et al., 2015).

A total of 226 sites were sampled, in three campaigns conducted in 2007, 2010 and 2011, for sediment grain-size analysis of which 169 were also used to study the macrofauna (Fig. 1). The samples were obtained using a 0.1 m^2 Smith-McIntyre grab, with the coordinates and depth of each sampling site being recorded. At each site, two grab samples were collected, one for the sediment grain-size analysis and the other for macrofauna. On board, the samples were submitted to a visual quality control and rejected for low quantity of sediment and when discrepancies between the samples were noticed. Concerning the grain-size analysis, a portion of the grab content was stored in 0.5L plastic boxes, whereas for the macrofauna the whole sediment collected in the grab was sieved on board over a 1 mm mesh size. The material retained was fixed in neutralized formalin (4%), stained with rose Bengal. A bathymetric dataset was recorded (Fig. 1) using the acoustic QTC VIEW Series IV and V systems, connected to a 50 kHz echosounder Hondex 7300II, with the transducer mounted on the side of the vessel. The acoustic system included a laptop for data acquisition, storage and visualization, and a Differential Global Position System (DGPS) to acquire the coordinates, which were continuously logged along with depth, permitting the post-processing of the acoustic data in a geographic information system (GIS). A total of 2514 Km of acoustic transects were undertaken, embracing 167945 data points between 8.9 and 154-m depth.

2.2. Laboratory analysis

A sediment grain-size analysis was performed by wet- and dry-sieving, through the steps described in Quintino et al. (1989). Further, the sediment macrofauna samples were individually washed in the laboratory over a 0.5 mm sieve. Hereafter, the specimens were hand sorted, separated by large macrofauna groups and stored in 70% ethylic alcohol. After sorting, the sediment was kept and checked for macrofauna specimens left behind by another team member. All samples were verified and double sorted. Using stereomicroscope and optical microscope, the macroinvertebrates were identified to species level, whenever possible, according to recommended bibliography. The identification quality was assessed by experienced colleagues and using the World Register of Marine Species (WoRMS Editorial Board, 2017), to obtain the species authority and currently accepted name.

2.3. Data analysis

2.3.1. Environmental data spatial interpolation

Using Gradistat (v4.0, Blott and Pye, 2001), several sediment parameters were calculated per sample: fines or mud (<0.063 mm), sand (0.063–2 mm) and gravel (>2 mm) contents (expressed in % of the total sediment dry weight); and kurtosis, determined using the method of moments described in Krumbein and Pettijohn (1938), calculated logarithmically. The sediment was classified using the median value, according to the Wentworth scale (Doeglas, 1968), their spatial distribution being given in Mamede et al. (2015).

Spatial interpolations of depth, kurtosis and fines and gravel fractions, were made using Empirical Bayesian Kriging (EBK) incorporated in ArcGIS 10.2, a straightforward and robust kriging method (Krivoruchko, 2012). In order to increase its accuracy, suitable transformations were made for each variable, namely: i) square root for bathymetry; ii) fourth root for sediment sample kurtosis; iii) additive log-ratio (alr) to fines, sand and gravel contents, as recommended for compositional data (Odeh et al., 2003), after adding a very small amount to fines and gravel contents, i.e. 0.0001, to account for zero values. Using the alr transformation, the combined values of composed data (fines, sand and gravel) sum up to 100% (Pawlowsky-Glahn and Egozcue, 2006), which would not occur if the kriging of these variables were performed independently.

For each variable, the EBK parameters were manipulated following the best interpolation using the results of a leave-one-out cross-validation analyzing the following parameters given automatically by EBK: i) Root Mean Square Error (RMSE), that measures the difference between the predicted and the measured values; ii) Average Standard Error (ASE), showing the average of the prediction standard errors; iii) Root Mean Square Standardized Error (RMSSE), corresponding to a ratio between the previously mentioned parameters, evaluating if the prediction standard errors are valid.

The spatial interpolation results were exported as raster surfaces with the resolution of 0.0027 decimal degrees (approximately 250m). Each variable was then back transformed to the original scale. The predicted values of bathymetry and kurtosis were back transformed by square (x^2) or raised to the fourth power (x^4), respectively, whilst in the case of the fines and gravel contents, the predictions were back transformed using the alr back transformation, subtracting 0.0001 to both grain-class contents.

For each environmental variable, the accuracy of the interpolation was evaluated visually and using the Pearson correlation coefficient between the observed and predicted values.

2.3.2. Macroinvertebrate multivariate data analysis

The macroinvertebrate abundance matrix was square root transformed to decrease the importance of the most abundant species, followed by the calculation of the Bray-Curtis similarity matrix among sites. This matrix was submitted to cluster and ordination analysis in the software PRIMER v6 (Clarke and Gorley, 2006), using hierarchical agglomerative clustering with the group-average algorithm (UPGMA), and Principal Coordinates Analysis (PCO). The aim was to find natural agglomerations of samples (i.e., benthic communities), meaning that, the samples within a group will be more similar among them, than with samples belonging to other groups. From the cluster analysis, three sampling sites appeared isolated and were excluded from the subsequent analysis. The macrofauna communities were characterized using environmental variables and mean values for a set of biological indices, namely abundance, alpha diversity, total species richness, number of exclusive species and their characteristic species. The most characteristic species were obtained using the product between the constancy and fidelity for each species in a community. Constancy corresponds to the frequency expressed as the percentage of a species presence in a community (Dajoz, 1996), while fidelity is the ratio between the constancy of a species in a community and the sum of that species constancy in all communities (Retière, 1979). For constancy, the species were classified as constant ($C > 50.0\%$), common ($50.0 \geq C > 25.0\%$), occasional ($25.0 \geq C > 12.5\%$) and rare ($C \leq 12.5\%$). For fidelity, as elective ($F > 90.0\%$), preferential ($90 \geq F \geq 66.6\%$), indifferent ($66.6 \geq F > 33.3\%$), accessory ($33.3 \geq F > 10\%$) and accidental ($F \leq 10\%$). The spatial distribution of the benthic communities was charted using ArcGIS (v10.2).

2.3.3. *Community distribution models (CDM)*

To relate environmental variables and macrofauna communities, the presence/absence of a given community per site was used as the response variable in binomial models. Fourth root transformations were applied to fines, gravel, and kurtosis. The transformed variables were renamed adding the subscript ‘4throot’ to each variable (e.g. fines $\%_{4throot}$). The correlations among explanatory variables were studied using the variance inflation factor (VIF) values, with a cut-off value of 3 previously chosen (Zuur et al., 2010). Fines$\%_{4throot}$ was retained as an explanatory variable, despite a VIF value of 3.1, given the borderline value and the well-documented influence of fines on benthic communities. Therefore, the explanatory variables used in the models were: fines$\%_{4throot}$, gravel$\%_{4throot}$, kurtosis$_{4throot}$ and depth.

For each community, using the R built-in function (R Core Team, 2020), a binomial GLM for presence/absence was obtained assuming a clog-log link function. This function is advised, over the more commonly used logit-link function, when the response variable has considerably more zeros than ones (Zuur et al., 2009), as it is the case of the presence/absence of the benthic communities in the study area. A backward stepwise selection was followed, with only the significant terms ($p \leq 0.05$) retained in the final models. To validate the models, the spatial distribution of the residuals was evaluated using the p-value of the Moran’s I test under the null hypothesis that no spatial correlation was present among model residuals (Bivand, 2020; Zuur et al., 2007). Some of the models presented evidence of spatial correlation between the residuals ($p \leq 0.05$), namely the models for the communities identified as C, D, E and G. This was handled by adding a spatial correlation structure to the model through an autocovariate (range: −1 to 1), representing the correlation among nearby locations in space, calculated using the function autocov_dist of the R package ‘spdep’ (Bivand, 2020). For these models, the spatial autocorrelation of the residuals was again evaluated using the p-value of the Moran’s I test, after which non-significant p-values were obtained, revealing that the spatial autocorrelation among residuals could then be neglected for all situations encountered.

The percentage of occurrence of a given community was given by the expression:

$$P(C_i) = 1\text{-}exp(\text{-}exp(z)) \tag{1}$$

where $P(C_i)$ is the percentage of occurrence of a given community and z is the function of the explanatory variables.

Using the pROC package for R (Robin et al., 2020), the performance of the models was evaluated by the area under a ROC curve (AUC) (Hanley and McNeil, 1982). The AUC value represents the probability that a randomly chosen presence has a higher probability of occurrence than a randomly chosen absence. The accuracy of the models was evaluated as high ($AUC \geq 0.9$), moderate ($0.9 \geq AUC > 0.7$) and low ($0.7 \geq AUC > 0.5$) (Swets, 1988). The percentage of explained null deviance was also considered in the evaluation of the model performances (Guisan and Zimmermann, 2000).

Using the CDM expressions and the maps of the environmental variables, through the spatial analyst toolbox included in ArcGis 10.2, maps revealing the probability of presence of each macrofauna community were produced. The seven maps were then combined, achieving a unique map presenting the spatial distribution of the most probable community in the study area. The workflow to produce this map is shown in Fig. 2, detailing the four steps involved in their production. In brief: step 1. the seven maps where combined in one map presenting the highest value for each pixel; step 2. The pixel values of this map were subtracted to each of the seven maps, resulting in seven maps showing values of 0 where each community is the most probable; step 3. These new and intermediate seven maps were reclassified with $0 = 0$ and $>0 = 1$ to 7 (one different value per map); step 4. These maps were combined. The pixels of this map presented values 1 to 7, to which were assigned the letters of the respective macrofauna community (i.e., A to G).

The observed spatial distribution of the macrofauna communities, based on point samples, was superimposed to this predictive map, to assess the percentage of coincidence between the observed distribution and the most probable distribution of the macrofauna communities.

3. Results

3.1. *Environmental data layers*

The pattern shown by the layer of the predicted bathymetry presented a high concordance with the measured depth values. Both data sets show well the rock-outcrop of ‘Pedra da Galega’, revealed by the sudden change of bathymetry (Fig. 3A). This is also confirmed by the strong and positive Pearson correlation between the observed and predicted depth values ($r = 0.99$).

The values obtained from the interpolated layers for the fines fraction, gravel content and sediment kurtosis, presented a close agreement with the observed point samples values (Fig. 3B–D). This agreed with the strong relationships between the observed and predicted values for each variable revealed by the Pearson correlation coefficients, respectively 0.96 for fines, 0.74 for gravel and 0.92 for kurtosis. The measured fines sediment fraction ranged from 0 (in 10 sites) to 97.8% and for gravel from 0 (in 92 sites) to 86.3%. Kurtosis presented values between 1.1 and 54.3. The sediments with higher fines content were located beyond 100-m depth, manly in the northwest and southwestern parts of the study area, (Fig. 3B). Off Douro River, sediments with higher fines content were located at lower depth and closer to shore (Fig. 3B), revealing the export of fines to the continental shelf from this important river or northern Iberia Peninsula. Gravel was mainly present in two areas, the larger off Ria de Aveiro, between 20 and 100m deep, and the smaller off Mondego estuary close to the 50m isobath (Fig. 3C).

3.2. *Macroinvertebrate benthic communities’ distribution and characterization*

A total of 64485 specimens were sampled in this study, belonging to 708 taxa, distributed by 11 phyla (Table S1 in the supplementary material). The cluster analysis identified seven groups (hereafter designated as communities, Fig. S1 in the supplementary material), their spatial distribution in the study area and in axis 1-2 of a PCO ordination, comprising 30.1% of total variation, being presented in Fig. 4.

The summary statistics for each community, including the most characteristic species, are given in Table 1. Community A is settled in

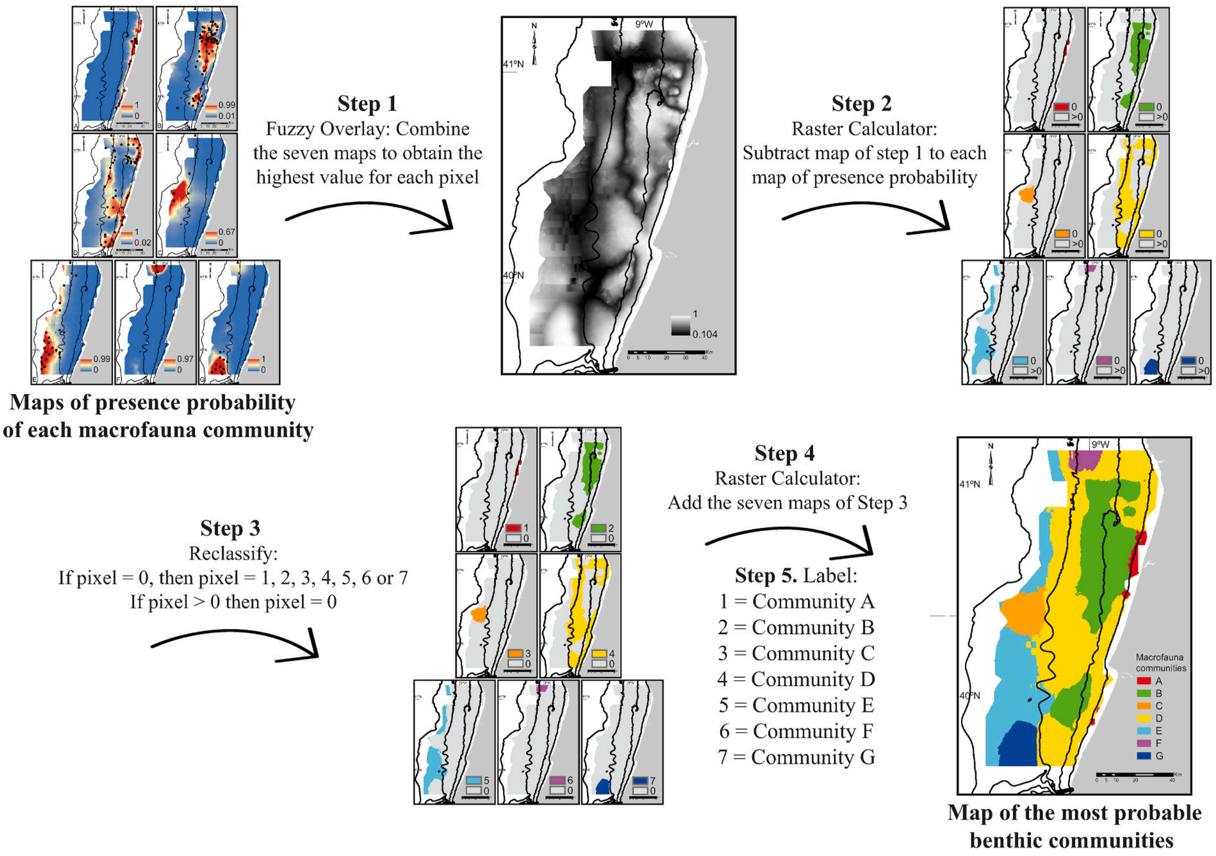

Fig. 2. Schematic representation of the workflow to produce the map presenting the most probable distribution of the macroinvertebrate communities in the study area.

clean medium and coarse sands near the coastline (<50-m depth) (Fig. 4 and Table 1). It presented the highest mean abundance (1013.9ind/0.1 m^2) and the lowest total species richness (92 spp., ex-aequo with community F) (Table 1). Community B is settled on coarse sediments, very coarse sand and fine gravel, up to 100-m depth, being distributed along almost the whole latitudinal range of the study area (Fig. 4 and Table 1). This community presented the highest values for alpha diversity (60.2 spp./0.1 m^2), total species richness (470 spp.) and exclusive species (147 spp.) (Table 1). Community C is settled on a confined area in the deep coarse sands, while community D is settled on fine sands up to 100-m depth along all the latitudinal gradient of the study area (Fig. 4 and Table 1). Community E is settled on deep (>100-m depth) very fine sands located mainly in the southwestern part of the study area, off the Mondego estuary (Fig. 4 and Table 1). Community F represents the mid-shelf muddy sediments off Douro estuary, in the northwestern part of the study area (Fig. 4 and Table 1). It presented the lowest values for total species richness (92 spp.) and exclusive species (2 spp.) (Table 1). Community G represents the deep (>100-m depth) muddy sediments in the south part of the study area, off the Mondego estuary (Fig. 4 and Table 1). The lowest mean abundance (122ind/0.1 m^2) and alpha diversity (21.3 spp./0.1 m^2) were registered here (Table 1).

3.3. Community distribution models (CDM)

According to the results presented in Table 2 and comparing the patterns shown by the environmental layers (Fig. 3) and the maps presenting the probability presence of the several biological communities (Fig. 5), the presence of each macrofauna community was best explained by different environmental variables. The mathematical sign (±) of each parameter coefficient reveals the tendency of the correlation, positive or negative. The accuracy performance of all models was high, with AUC values always above 0.9 (Table 2). The map showing the most probable community and its evaluation (Fig. 6 and Table 3), confirmed the high agreement between the distribution of the point samples representing each benthic community and the predicted distribution layers (overall concordance = 81%). The best agreement was obtained for the communities identified through the highest number of samples (>20 sites, i. e., B, D and E, cf. Table 3).

The spatial distribution of community A was significantly explained by fines%$_{4throot}$ and depth (Table 2), and negatively correlated with both variables. Visually, the probable distribution of this community coincided reasonably well with its real spatial distribution, closer to shore. However, the agreement distribution between the observed point samples and the expected layer occurred only for 33% of the cases (Figs. 5 and 6, and Table 3).

The spatial distribution of community B was significantly correlated with fines%$_{4throot}$ and gravel%$_{4throot}$ (Table 2), with negative and positive correlations, respectively. The patterns shown on the map of the expected communities (Fig. 6) and the coincidence value of 88.1% (Table 3), revealed the close match between the observed and the expected distribution of this community.

Regarding community C, the inclusion of an autocovariate in the model was required (Table 2). This CDM presented the lowest deviance explained (35.4%, Table 2) and depth was the single environmental variable significantly related to the spatial distribution of community C (Table 2), with a positive correlation. This was also the community with the lowest coincidence between the real and the predicted distribution (20%, Table 3).

The CDM for community D also required the inclusion of an autocovariate. The significant environmental variables contributing for the distribution of this community were gravel%$_{4throot}$ and kurtosis$_{4throot}$, both inversely related to the community distribution, and depth, directly

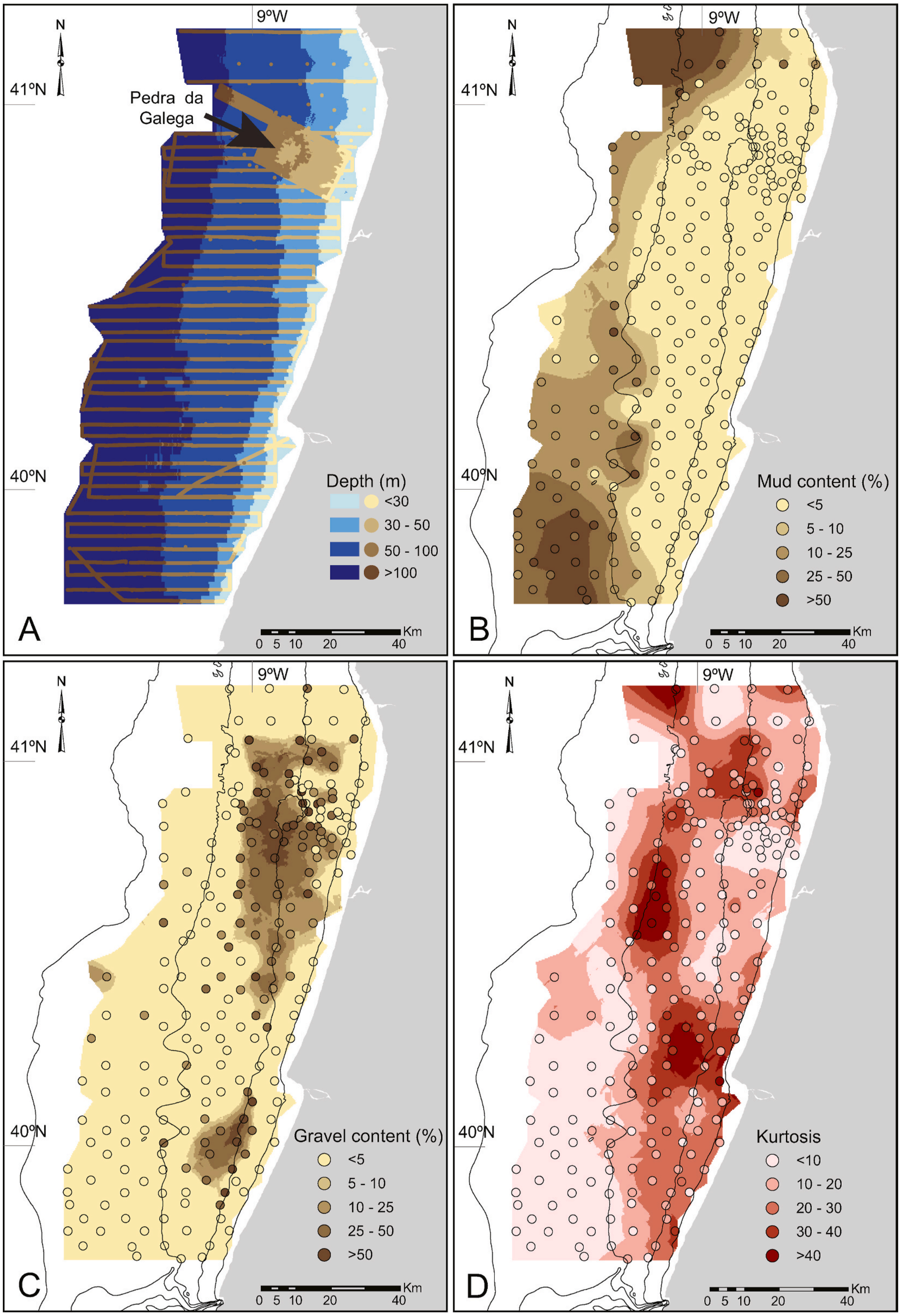

Fig. 3. Spatial distribution of the measured environmental data, shown as data points, and the respective interpolation layers, shown as surfaces, obtained through Empirical Bayesian Kriging (EBK): A – Bathymetry; B – Mud (particles <0.063 mm); C – Gravel (particles > 2 mm); D – Sediment Kurtosis.

related (cf. Table 2). Community D showed the highest agreement between the point samples and the layer representing the probability of occurrence of the community (90.6%, Figs. 5 and 6, and Table 3).

The CDM for the spatial distribution of community E also required the addition of an autocovariate and also included depth as a significant explanatory environmental variable, with a positive correlation (Table 2). The map in Fig. 5 revealed a high concordance between the predicted distribution of this community and its observed spatial distribution (83%, Table 3).

The spatial distribution of community F was significantly related with fines%$_{4\text{throot}}$ and depth, presenting respectively positive and negative correlations (Table 2). This CDM presented the highest

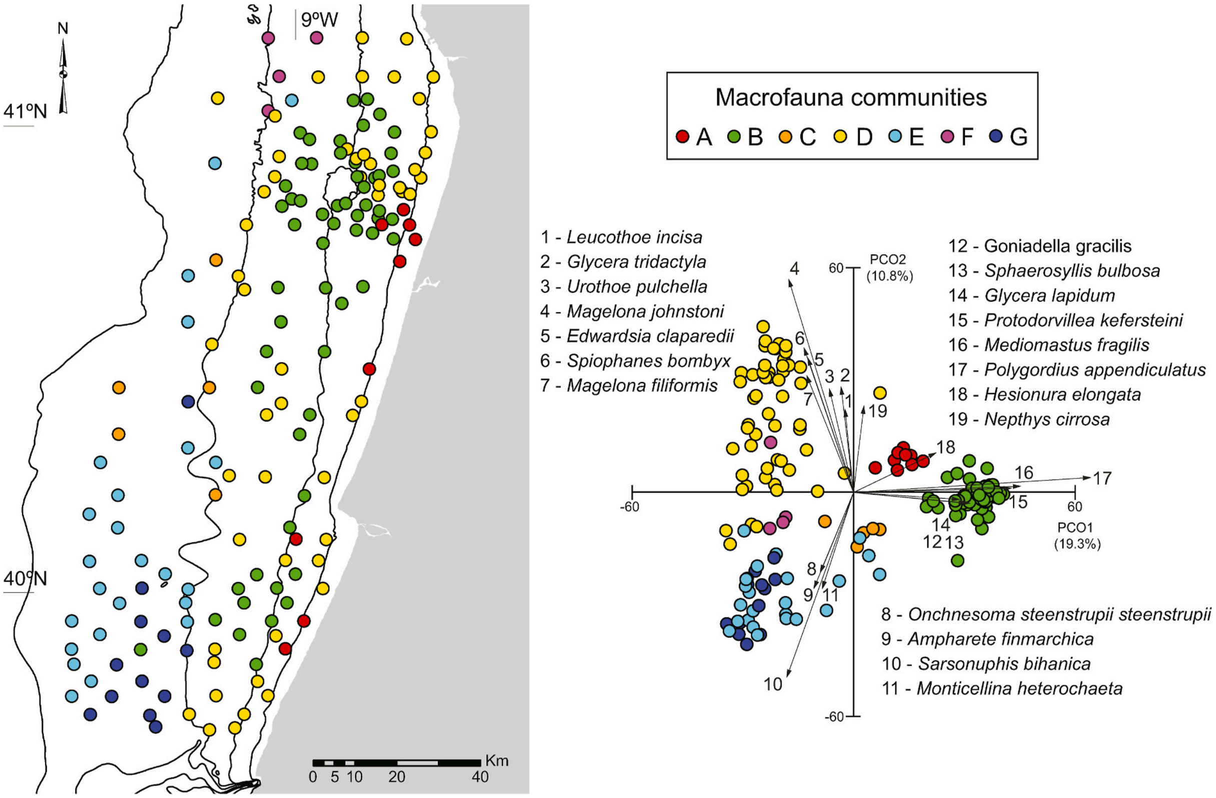

Fig. 4. Spatial distribution of the benthic macrofauna communities (A to G) in the study area and in axis 1-2 of a PCO ordination analysis, superimposed with the species vectors (multiple correlation >0.15). The vectors are scaled at 300% of the original size.

Table 1
Macrofauna communities summary characterization. Mean values are reported to the unit sample (0.1m2). Sediment types according to the Wentworth scale: G = gravel, VCS = very coarse sand, CS = coarse sand, MS = medium sand, FS = fine sand, VFS = very fine sand, M = mud (number of sediment samples in brackets); Constancy: Cn = constant, C = common, O = occasional; R = rare; Fidelity: E = elective, P = preferential, I = Indifferent, A = accessory; * = Exclusive species in each group.

Communities	A	B	C	D	E	F	G
Number of sampling sites	9	59	5	53	24	4	12
Main sediment type	Medium sand	Very coarse sand	Coarse sand	Fine sand	Very fine sand	Mud	Mud
Sediment types (number of samples)	MS(5), CS(3), FG(1)	VCS(31), FG(19), CS (6), VFS(1), FS(1), MS(1),	CS(4), MS(1)	FS(42), VFS(4), VCS(4), Mud(1), MS(1), FG(1)	VFS(13), MS(3), FS (2), CS(2), VCS(2), FG(1), Mud(1)	Mud(4)	Mud(7), VFS (4), FS(1)
Fines content (mean, %)	0.10	1.30	1.92	5.90	23.59	78.64	55.56
Gravel content (mean, %)	10.23	41.94	8.30	3.58	8.19	0.04	0.04
Depth (mean, m)	25.4	57.1	120.5	56.5	126.8	90.2	122.0
Abundance (mean, ind./ 0.1m^2)	1013.9	629.1	156.4	248.5	128.5	128.8	51.7
Total species richness	92	470	115	386	327	92	112
Alpha diversity (mean, spp./0.1m^2)	23.0	60.2	42.6	39.0	45.7	34.3	21.3
Exclusive species	3	147	5	82	53	2	7
Characteristic Species (With Constancy and Fidelity indications)	*Gastrosaccus spinifer* (Cn/P) *Nephtys cirrosa* (Cn/I) *Pisione parapari* (Cn/I) *Nototropis falcatus* (Cn/P) *Hesionura elongata* (Cn/I)	*Gyptis propinqua* (Cn/E) *Malmgrenia ljungmani* (Cn/P) *Branchiostoma lanceolatum* (Cn/P) *Guernea (Guernea) coalita* (Cn/E) *Megamphopus cornutus* (Cn/E)	*Scalibregma celticum* (Cn/P) *Urothoe marina* (Cn/E) *Chaetozone carpenteri* (Cn/I) *Aricidea (Acmira) lopezi* (Cn/P) *Mesochaetopterus sagittarius* (Cn/I)	*Urothoe pulchella* (C/E)* *Glycera tridactyla* (C/E)* *Ampelisca brevicornis* (Cn/I) *Phoronida n.i.* (Cn/I) *Spiophanes bombyx* (Cn/I)	*Auchenoplax worsfoldi* (Cn/E) *Terebellides stroemii* (Cn/I) *Onchnesoma steenstrupii steenstrupii* (Cn/I) *Callianassa subterranea* (Cn/I) *Aricidea (Acmira) laubieri* (C/P)	*Tellina compressa* (Cn/P) *Thyasira* sp. (Cn/E) *Ampelisca spinimana* (Cn/P) *Thyasira flexuosa* (Cn/P) *Westwoodilla caecula* (C/E)	*Sarsonuphis bihanica* (Cn/I) *Nephtys incisa* (Cn/I) *Ampharete finmarchica* (Cn/A) *Labioleani-ra yhleni* (Cn/I) *Paralacydo-nia paradoxa* (Cn/I)

Table 2
Community distribution models (CDM), showing the expressions relating the explanatory variables (z, see Eq. (1)) to each benthic community, A to G; $F\%_{4thrt}$ = $Fines\%_{4thrt}$; $G\%_{4thrt}$ = $Gravel\%_{4thrt}$; K_{4thrt} = $Kurtosis\%_{4thrt}$; A_C, A_D, A_E and A_G = Spatial autocovariates of the respective models; AUC = Area under the ROC curve.

Community	CDM expressions	AUC	Explained Deviance (%)
A	$5.28–2.52F\%_{4thrt} – 0.183Depth$	0.971	56.6
B	$−2.00 - 1.03F\%_{4thrt} +1.30G\%_{4thrt}$	0.945	58.1
C	$−8.69 + 0.0327Depth + 40.4A_C$	0.929	35.4
D	$−2.39 - 1.10G\%_{4thrt} + 1.45K_{4thrt} – 0.0121Depth + 1.69A_D$	0.913	46.6
E	$−8.61 + 0.0575Depth + 12.7A_E$	0.960	56.8
F	$−19.9 + 8.96F\%_{4thrt} - 0.07365Depth$	0.997	74.8
G	$−8.95 + 2.46F\%_{4thrt} + 4.83A_G$	0.973	61.4

deviance explained (74.8%, Table 2). Its point sample spatial distribution was well captured by the binomial model, revealed by the high agreement between the observed and the expected distributions (Figs. 5 and 6), with a relative high coincidence (75%, Table 3), despite the low number of point samples that defined this community.

Concerning community G, the respective CDM required the inclusion of an autocovariate and retained the explanatory variable $fines\%_{4throot}$, with a positive correlation (Table 2). Despite the map of the most probable community presenting a similar distribution to the observed community point samples (Fig. 6), the resulting coincidence was not the highest (58.3%, Table 3).

4. Discussion

This study produced maps of environmental variables, and the habitat suitability for the seven benthic macroinvertebrate communities identified in the study area was modelled, by linking their point spatial distribution to spatial environmental data.

For the data interpolation of sediment parameters and depth, transformations were used to produce more accurate layers and to match the characteristics of the data (skewness and/or compositional type) (Krivoruchko, 2012). Besides the non-linear transformations applied to data with skewed distributions, the compositional sedimentary parameters (i.e. fines, sand and gravel contents) were specifically submitted to an additive log transformation, recommended for this type of data (Aitchison, 1982).

The unconstrained multivariate analysis allowed to describe seven benthic macrofauna communities distributed according to two main driving forces, sediment types and depth. In this same area, Martins et al. (2013) previously described only four communities. As the study area is homogeneous regarding some environmental parameters (e.g., salinity) and presumably presents high temporal stability regarding other environmental parameters (e.g., sediments, depth, oxygen at the bottom), the higher number of communities now described resulted from the higher sampling effort, which increased resolution, and not as consequence of temporal changes in the environmental parameters. The communities identified in this study have their analogue in other Europeans continental shelves, from the North Sea to the Mediterranean (Thorson, 1934, 1957; Spärck, 1935; Jones, 1950; Pérès and Picard, 1964; Glémarec, 1973; Cornet et al., 1983; Eleftheriou and Basford, 1989; Basford et al., 1990), as summarized in Table 4, also mentioning

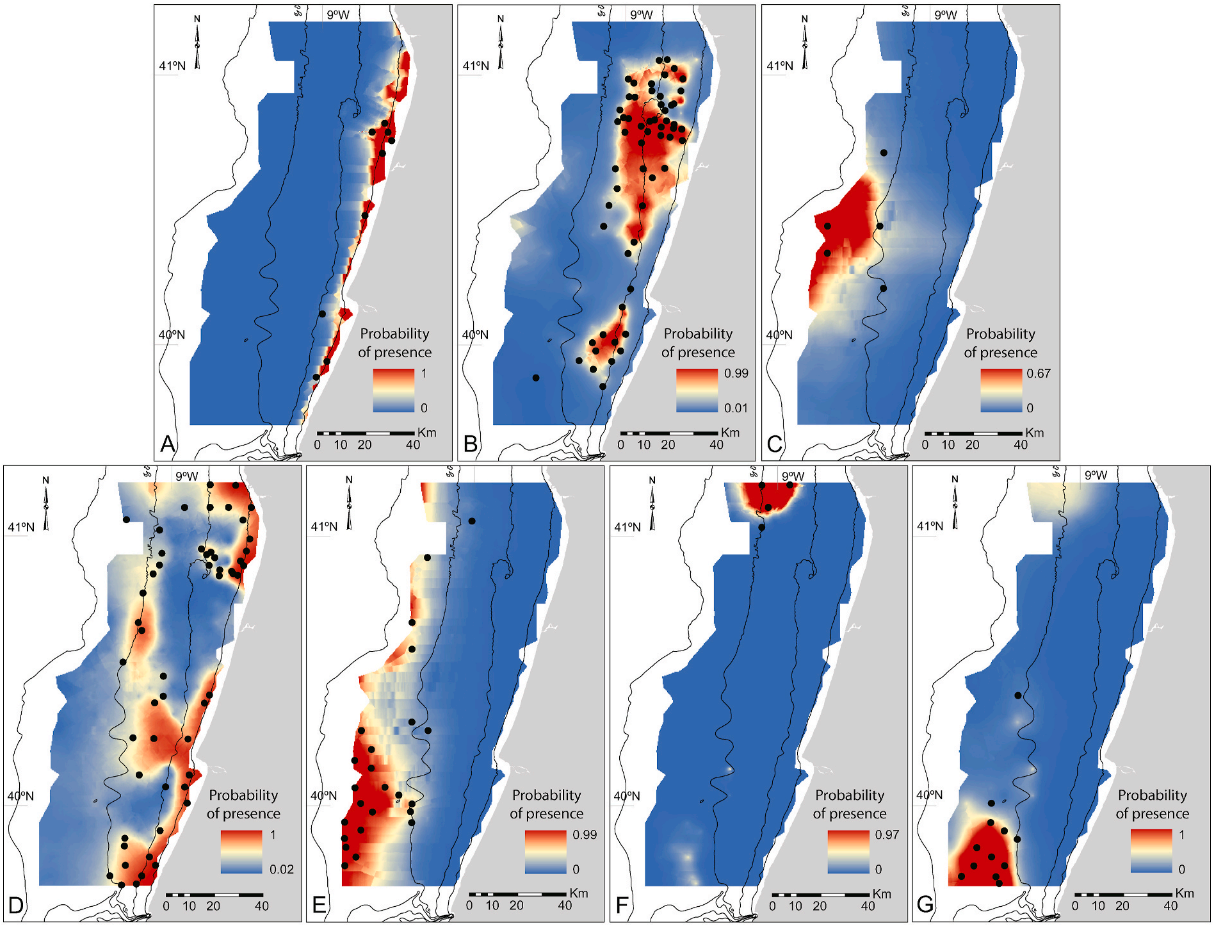

Fig. 5. Maps representing the presence probability of each of the seven macrofauna communities, A to G, in the study area. The dots represent the observed point sample distribution of the respective community.

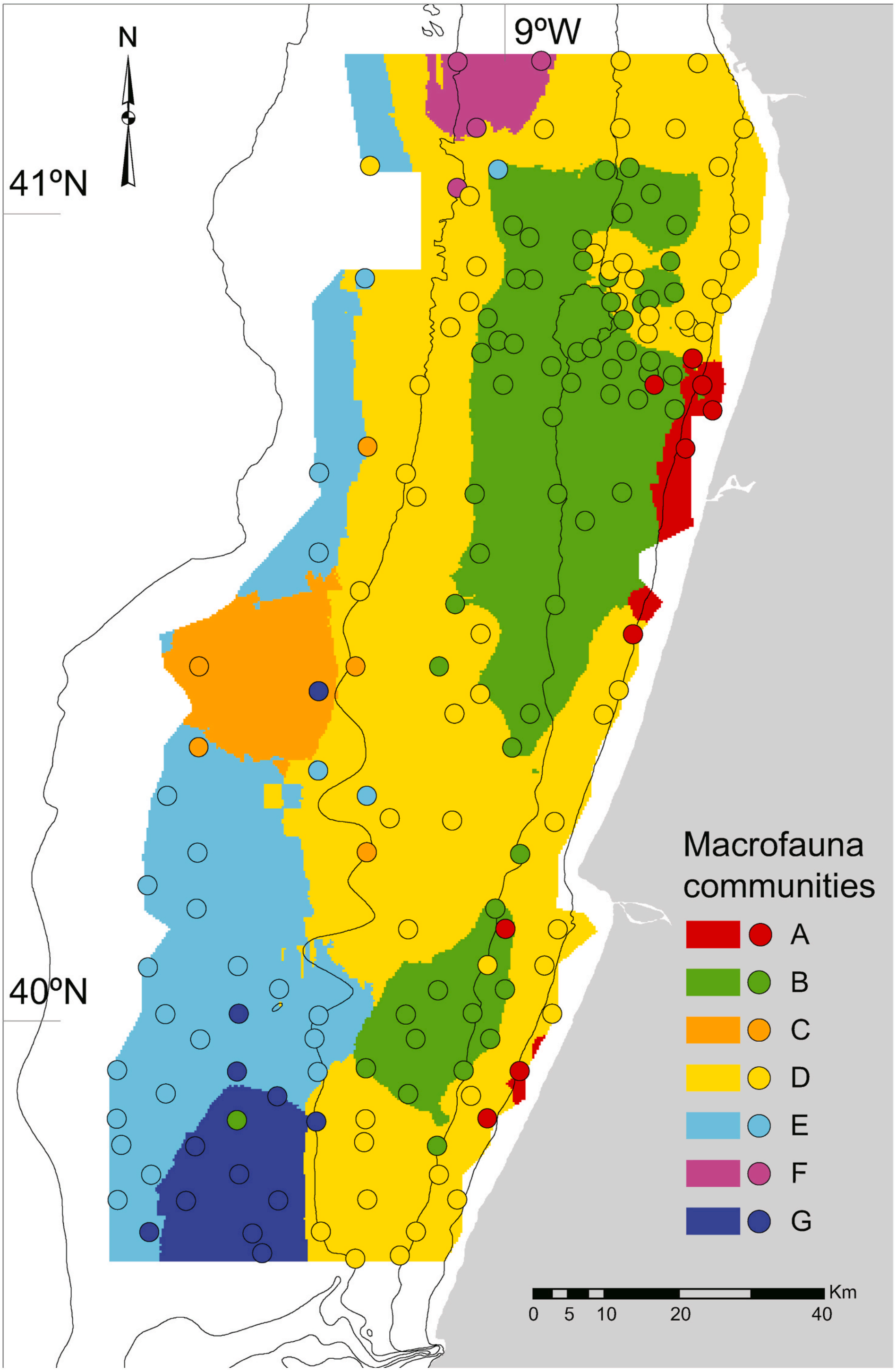

Fig. 6. Map presenting the observed and the most probable distribution of the macrofauna communities in the study area. The circles represent the observed spatial distribution of the communities, and the continuous layer represents the prediction of the most probable community.

which communities were not previously reported for this section of Portugal's continental shelf. Six of the seven communities presented in this study were previously known to occur along the Portuguese continental shelf (Marques, 1987; Freitas et al., 2003; Martins et al., 2013; Henriques et al., 2015). The novelty concerns the community here identified as community F, settled on muddy bottoms off Douro estuary, in the northern part of the study area. This community corresponds well to the *Thyasira* community accompanied by foraminifera reported from Northern Europe, namely by Stephen (1923) and by Thorson (1934, 1957), but never from Portugal. High abundances of foraminifera were confirmed through visual examination of this community sediments. Glémarec (1973) believed that this community did not have an equivalent in Southern European continental shelves. Martins et al. (2014) found high abundances of *T. flexuosa* north of the Douro estuary, which combined with the map of the Douro River mud patch (Dias et al., 2002), suggests that the present work identified the southernmost section of this Northern European muddy bottom macrofauna community. The present results contribute to increase the knowledge of the benthic communities of the Portuguese continental shelf (Northeast Atlantic), as performed in other European shelves, such as the Baltic Sea (Gogina

Table 3
Agreement between the distribution of the point samples representing the macrofauna communities, A to G and the modelled layers representing the expected distributions, as shown in Fig. 5; Figures in bold correspond to the quantity of point samples placed inside the layer representing the expected distribution of the community. Overall = total correctly classified samples/total samples.

Benthic community	Expected distribution							Total samples	Agreement (%)
	A	B	C	D	E	F	G		
A	**3**	2	0	4	0	0	0	9	33.3
B	0	**52**	0	6	0	0	1	59	88.1
C	0	0	**1**	2	2	0	0	5	20.0
D	0	4	0	**48**	1	0	0	53	90.6
E	0	1	0	3	**20**	0	0	24	83.3
F	0	0	0	1	0	**3**	0	4	75.0
G	0	0	1	1	3	0	**7**	12	58.3
Overall	3	52	1	48	20	3	7	166	80.7

Table 4
Macrofauna benthic communities described in this study and analogue communities in Europeans continental shelves. * Communities A and B share characteristics described in Pérès and Picard (1964) for the same community; ** Communities C, E and F were not previously reported for this section of Portugal's continental shelf.

This study	Northeast Atlantic	Mediterranean
A	Coarse sands of *Echinocyamus pusillus-Tellina pygmaea* (Glémarec, 1973) *Tellina tenuis* community (Spärck, 1935) The boreal Lusitanian *Tellina* community (*T. Tenuis* – *T. fabula*) (Thorson, 1957) Boreal shallow sand association of Jones (1950)	Offshore sands and gravels under swell influence (Pérès and Picard, 1964)*
B	Coastal gravels of *Branchiostoma lanceolatum* – *Venus fasciata* community (Thorson, 1957; Glemarec, 1973) Boreal offshore gravel association (Jones, 1950)	Offshore sands and gravels under swell influence (Pérès and Picard, 1964)*
C**	Coarse sand community (Eleftheriou and Basford, 1989)	Biocenosis of the offshore detritic bottoms (>80m, often named offshore sands and gravels) (Pérès and Picard, 1964)
D	*Venus gallina* community (Thorson, 1957) Coastal fine sands of *Venus gallina* – *Dosinia lupina* (Glémarec, 1973) Boreal offshore sand association (Jones, 1950)	Well sorted fine sands biocenosis (Pérès and Picard, 1964)
E**	Muddy sands of *Onuphis lepta* – *Auchenoplax crinita* (Glémarec, 1973; Cornet et al., 1983) Boreal offshore muddy sand association (Jones, 1950) As a modification of the shallower *Syndosmya* (now *Abra*) *alba* community (Thorson, 1957)	A suitable analogue was not found
F**	*Thyasira* community accompanied by foraminifera (Stephen, 1923; Thorson, 1934, 1957)	A suitable analogue was not found
G	Boreal offshore mud association (Jones, 1950) Offshore muds of *Ninoe armoricana* – *Sternaspis scutata* (Glémarec, 1973)	Terrigenous mud association (Pérès and Picard, 1964)

et al., 2016 and references therein).

The independent building of several CDM showed the relationship between the spatial distribution of each macrofauna community and baseline environmental variables. This is not possible when building the models simultaneously, as those developed by Degraer et al. (2008), because the model functions then derived are dependent of each other. However, the independent development of CDM for each community can produce areas where a community that presented high occurrence probabilities can be exceeded by others in the map combining the seven communities, which occurred in our study, for instance, between the maps of the E and G communities (cf. Fig. 5). Other studies have highlighted the relationship between benthic communities and the sediment fines fraction (among others, Ellingsen, 2002; Henkel and Politano, 2017), gravel content (among others, Seiderer and Newell, 1999; Carvalho et al., 2017), sediment kurtosis (among others, Cisneros et al., 2011; Yu et al., 2012) and depth (among others, Ellingsen, 2002; Dolbeth et al., 2007; Gogina et al., 2010). Although sediment kurtosis was found significant in one of the models here presented, it is difficult to conceptualize its role in benthic macroinvertebrate community structure, which could justify why this variable is so seldom used in benthic macrofauna studies (Cisneros et al., 2011). However, as kurtosis is a measure of the concentration of the grains relative to the average of the sediment grain-size (Blott and Pye, 2001), its significant relation with community D, suggests that the characteristic species of this community are well adapted to sediments presenting a high degree of grains with the same dimension. The environmental variable most often included in the models was depth (5 of the 7 models), probably due to its correlation with other environmental drivers, not included in the models (Austin, 2007; Gogina et al., 2010). In fact, this is the case of layers of environmental variables that are available for the study area (e.g., light (PAR) at the seabed or kinetic energy at the seafloor) (Vasquez et al., 2015; MARETEC, 2018), but because they were found highly correlated with depth in the study area, their inclusion in the models seemed useless. The mathematical signs of the coefficients of the environmental variables in the final models were in line with the expected by the environmental characterization of the macrofauna communities (see Table 1). As an example, if depth was kept in the final model for the shallower community (A), its coefficient presented a negative sign, implying a negative correlation. The same was shown by the sediment grain-size classes, with, for example, the CDM of the gravel (B) and muddy sediment (F and G) communities, showing significant positive correlation to gravel%$_{4throot}$ and fines%$_{4throot}$, respectively. For some models, an autocovariate had to be included, to fix the problem of the spatial autocorrelation of the residuals (Dormann et al., 2007). According to Austin (2002), if an autocovariate needs to be introduced in a model, it may indicate either a model misspecification, the missing of important environmental explanatory variables or unaccounted biological processes (e.g., species dispersal ability or physiological tolerances), responsible for the species dispersion. In this work, apart the model misspecification, it is difficult to know which of the other reasons (missing an important explanatory variable or unaccounted biological process) might have caused the spatial dependence of the model residuals, eventually both.

Comparing models from different benthic studies is delicate, due to the influence of the data traits on the model outcome, with emphasis on the sampling density and response prevalence for the case of presence/absence models (Bučas et al., 2013). The deviance explained by the CDM here developed (between 35% and 75%) is in the range of that presented by Moritz et al. (2013) (between 42% and 80%), who also developed distribution models for benthic communities, in the Gulf of Saint Lawrence, Canada.

Although the CDM showed a coherent picture of the communities' distribution, future collection of data, namely from the communities characterized by fewer sampling sites, should allow to develop more accurate and robust models, also allowing to have training and test datasets. Future work should focus on the integration of the maps here generated to be used as biological layers in the classification of these habitats according to the European Nature Information System (EUNIS) up to level 5 and, hereafter, apply them within the Marine Strategy Framework Directive, namely in the context of descriptor 6, seafloor integrity or the calculation of the Marine Biological Value used to evaluate the ecological status for descriptor 1, biological diversity (Derous, 2007; European Commission, 2008a).

Statement of informed consent, human/animal rights

No conflicts, informed consent, or human or animal rights are applicable to this study.

CRediT authorship contribution statement

Renato Mamede: Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Conceptualization. **Leandro Sampaio:** Writing – review & editing, Investigation. **Fernando Ricardo:** Writing – review & editing, Investigation. **Luísa Magalhães:** Writing – review & editing, Investigation. **Marta Lopes:** Writing – review & editing, Investigation. **Roberto Martins:** Writing – review & editing, Investigation. **Ana Maria Rodrigues:** Writing – review & editing, Project administration, Conceptualization. **Rosa Freitas:** Writing – review & editing, Supervision, Project administration, Conceptualization. **Victor Quintino:** Writing – review & editing, Supervision, Project administration, Formal analysis, Conceptualization.

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.

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Appendix A. Supplementary data

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