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Characterizing soft-bottom epibenthic megainvertebrate communities of the Mediterranean continental shelf: a biogeographic approach

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ABSTRACT

Partitioning of the Mediterranean basin has so far mainly focused on surface waters, relying on biogeochemical and hydrological data while the Mediterranean seafloor has received much less attention. Bioregions are essential units for conservation planning, as they provide a framework for designing representative networks of protected areas. Therefore, seafloor-specific bioregions are needed to support the management and conservation of benthic ecosystems. While benthic habitat mapping is generally based on macrofaunal patterns, we propose the first mesoscale partitioning of the Mediterranean seabed based on epibenthic megainvertebrate communities. Benthic records from the MEDITS programme (International Mediterranean Bottom Trawl Survey) were used to partition the Mediterranean soft bottoms. Using k-means clustering combined with Random Forest modelling, we grouped sites according to similarities in biotic composition and predicted their distribution in relation to environmental variables. The analysis was conducted independently across four sub-basins: the Western Mediterranean, the Central Mediterranean, the Adriatic Sea, and the Aegean Sea. This approach identified 16 distinct bioregions, each characterized by unique epibenthic megainvertebrate communities. The partitioning revealed a pronounced bathymetric gradient, with deep-sea bioregions showing a more homogeneous set of indicator taxa and greater similarity across regions compared to the more distinct communities found on the shelf and slope.

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These coherent bioregions can serve as spatial units to enhance the representativeness of conservation priority networks and provide a valuable complement to the existing EUNIS seabed habitat classification, which does not explicitly account for vulnerable epibenthic megainvertebrate communities.

1. Introduction

Benthic mapping is essential for assessing and reporting the ecological status of the seabed, as well as for supporting effective resource management and conservation planning (Lacharité and Brown, 2019; Lecours, 2017). The EUSeaMap program (Vasquez et al., 2023), supported by EMODnet, currently delivers the most comprehensive broad-scale seabed habitat maps for European waters. These maps are widely used in seabed management, conservation planning, and in the implementation of European policies such as the Habitats Directive and the Marine Strategy Framework Directive (Montefalcone et al., 2021). They are mainly derived from the European Nature Information System (EUNIS), a hierarchical classification built on environmental factors assumed to constrain benthic communities, including substrate type, energy levels, depth, and light penetration (Vasquez et al., 2023). While these standardized classifications facilitate habitat comparisons across regions, they integrate only limited biological data due to the scarcity of information on the distribution of biogenic habitats and benthic communities.

Bioregions are defined here as coherent geographical units characterized by relatively homogeneous and distinct biological communities and environmental conditions (Livingstone et al., 2018; Woolley et al., 2020). Bioregions are key units for ensuring the protection of ecologically unique areas and inform the designation of representative conservation networks (Lacharité and Brown, 2019; O'Brien et al., 2022). While early marine bioregionalizations were based on expert knowledge (Spalding et al., 2007), the development of remotely sensed data has enabled the delineation of bioregions based on environmental data (Roberson et al., 2017; Sayre et al., 2017). However, studies have shown that using true biological data leads to more ecologically meaningful bioregionalizations (Cooper et al., 2019; O'Brien et al., 2022; Woolley et al., 2020). Several statistical approaches can be adopted to delineate marine bioregions at a large scale (Deschamps et al., 2023; Hill et al., 2020). The “group-first-then-predict” strategy consists of clustering similar stations using methods such as k-means or hierarchical clustering, and then predicting their distribution by correlative modeling based on environmental preferences (Cooper et al., 2019). In contrast, the “predict-first-then-group” strategy relies on obtaining predictive distribution outputs and then identifying regions of similar profiles. Predictions can be obtained by single Species Distribution Models (Reygondeau et al., 2015), Joint Species Distribution Models, which account for species interactions (Murillo et al., 2024), as well as artificial neural networks (Bloomfield et al., 2018) or compositional turnover models including Generalized Dissimilarities Models (Lasram et al., 2015). Finally, recent one-stage approaches simultaneously cluster and predict biological data from environmental conditions in a single process (Foster et al., 2013). Despite the development of these new methodologies, the simpler and common techniques (e.g., k-means, hierarchical clustering, and machine learning) are still widely used to characterize distinct benthic assemblages because of their efficiency and user-friendly implementation (De la Torriente et al., 2019; Murillo et al., 2016; O'Brien et al., 2022; Outrequin et al., 2025; Serrano et al., 2017).

The Mediterranean continental shelves and slopes are shaped by diverse geomorphological features (e.g., submarine canyons, seamounts), surrounded by relatively homogeneous soft bottoms which support a vast diversity of demersal fishes and benthic invertebrates (Bianchi and Morri, 2000; Coll et al., 2010; Danovaro et al., 2010; Salomidi et al., 2022). Facing decades of anthropogenic pressure (Eigaard et al., 2017), the region hosts the second most disturbed seafloor in Europe, with 69% of its coastal and shelf areas affected (Korpinen et al., 2021). Physical disturbances are particularly damaging for epibenthic megainvertebrates (i.e., larger than 1 cm), which can form dense aggregations easily destroyed by bottom trawling activities. Following the United Nations resolutions 61/105 (UNGA, 2006) and 64/72 (UNGA, 2009), several sensitive taxa (e.g., cold-water corals, octocorals, sponges, crinoids) have been recognized as indicators of Vulnerable Marine Ecosystems (VMEs) by the General Fisheries Commission for the Mediterranean (GFCM) (FAO, 2009). Different multiannual management plans and measures have been applied in the Mediterranean, both from the GFCM and the European Union (e.g., Fisheries Restricted Areas, reduction of fishing effort, catch limits, creation of new MPAs). The designation of representative networks of protected areas, which encompasses the diversity in benthic communities, is now required to maximize the effectiveness and ecological coherence of seabed management in the Mediterranean (O'Brien et al., 2022).

Previously, the Mediterranean Sea has been partitioned into environmentally homogeneous bioregions based on hydrological and biogeochemical data, often representative of the surface waters (Berline et al., 2014; D’Ortenzio and Ribera d’Alcalà, 2009; Rossi et al., 2014). The Mediterranean seafloor has already been classified using a complex set of environmental variables (Reygondeau et al., 2017), demonstrating that the partitioning of surface layers cannot be directly projected on benthic environments, which are divided into a greater number of bioregions. Species community distributions are still rarely included in the benthic partitioning of the Mediterranean. While the current EUNIS typology accounts for macrofauna assemblages, epibenthic megainvertebrate communities remain largely overlooked and have only recently been described locally in the Mediterranean (De la Torriente et al., 2019; Dominguez-Carrió et al., 2022; Enrichetti et al., 2019; Fabri et al., 2014; Moccia et al., 2021). A comprehensive overview of the structure of epibenthic megainvertebrate communities is still needed to develop effective conservation management of this compartment, which is particularly impacted by bottom trawling pressure.

This study provides the first mesoscale bioregionalization of the Mediterranean Sea based on soft-bottom epibenthic megainvertebrate communities, mapping their spatial extent across regions down to 1000 m depth, the current trawling limit (Recommendation GFCM/29/2005/1). For this study, we used the largest standardized set of benthic data currently available in the Mediterranean Basin, collected under the MEDiterranean International Trawl Survey programme (MEDITS) (Spedicato et al., 2019). Soft-bottom communities from this survey are composed of epibenthic megainvertebrates (>1 cm), living on or above the seafloor, either sessile, burrowing, or with limited mobility. In particular, (1) we partitioned the Mediterranean trawlable soft bottoms into coherent bioregions representative of distinct epibenthic megainvertebrate communities using non-hierarchical k-means clustering; (2) provided a biological and environmental description of these bioregions; and (3) modelled and mapped the spatial distribution of these bioregions on Mediterranean bottoms through a machine learning approach.

2. Materials and methods

2.1. Study area

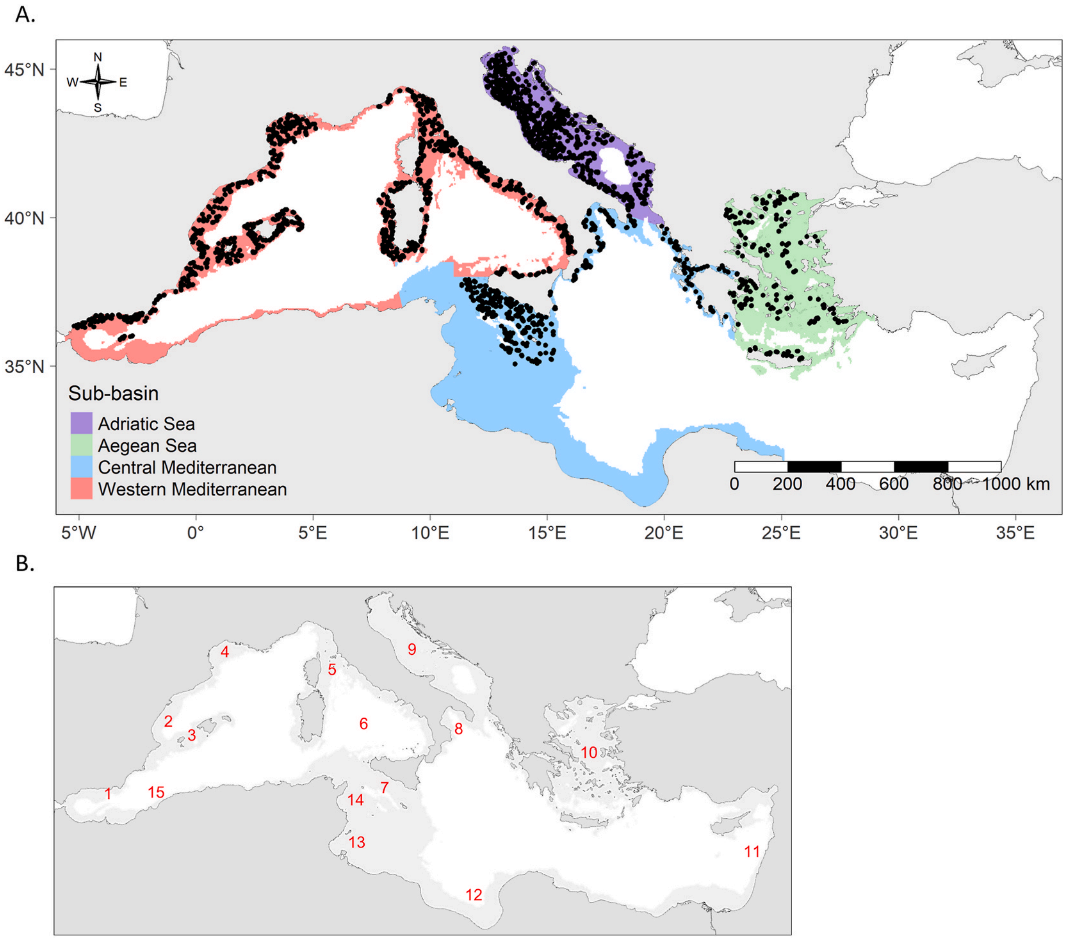
The study was performed on trawlable soft bottoms of the Mediterranean Basin from the continental shelf to the meso-bathyal plains (Emig, 1997) (<1000 m). Analyses were conducted independently within four sub-basins corresponding to the GFCM subregions (FAO, 2022): Western Mediterranean, Central Mediterranean, Adriatic Sea, and Aegean Sea (Fig. 1). Although MEDITS surveys provide an extensive and unique dataset of epibenthic megainvertebrate records, benthic sampling is not officially mandated, as the survey primarily targets the assessment of bentho-demersal commercial stocks. This subdivision was necessary due to decreasing taxonomic resolution and spatial coverage in the data from Western to Eastern European countries participating in the survey (Table S1.1 and Figure S1.1). Finally, the study area was extended to the southern parts of the Western, Central Mediterranean, and Aegean Seas through model extrapolation. However, the scarcity of observations in the Levantine Basin prevented robust clustering, and the environmental conditions in this sub-basin are highly unique (Coll et al., 2010), making it inappropriate to extrapolate bioregions from other sub-basins to this region.

2.2. Data preparation

2.2.1. Biological data

Data on benthic invertebrates were extracted from the MEDITS database (Spedicato et al., 2019), provided by DG MARE (Commission's Directorate-General for Maritime Affairs and Fisheries). MEDITS is an annual bottom trawl survey conducted across eight EU Mediterranean member states (i.e., Croatia, Cyprus, France, Greece, Italy, Malta, Slovenia, and Spain), that aims to assess stocks of exploited demersal resources following a standardized protocol. The standard sampling gear used for MEDITS survey is the bottom trawl GOC 73 (Bertrand et al., 2002). Trawl stations, distributed across five bathymetric strata (officially 10–50, 51–100, 101–200, 201–500, 501–800 m, but up to 1000 m in some steep slope areas) and sampled using a random-stratified design, are repeated annually at the same locations each summer. The duration of the bottom trawl hauls is approximately 30 min on shallower bottoms (<200 m) and about 60 min in deeper areas where catches are less abundant, at a constant 3.5 kt speed using a 10 mm mesh size net in the cod end.

The MEDITS trawl is not specifically designed to sample benthic organisms and therefore does not capture a precise size range of individuals. Despite a codend mesh size of 10 mm, net obstruction may cause smaller individuals to be caught. Nevertheless, only individuals larger than 1 cm caught during the MEDITS survey are identified, wet-weighed, and counted on board following the latest version of the MEDITS Handbook (Spedicato et al., 2019). The term “megabenthic invertebrates” is commonly used to refer to epibenthic invertebrates that are vulnerable to bottom trawling (Dominguez-Carrió et al., 2022;



01. Alboran Sea	06. Tyrrhenian Sea	11. Levantine Sea
02. Catalan Sea	07. Strait of Sicily	12. Libyan Sea
03. Balearic Sea	08. Ionian Sea	13. Gulf of Gabes
04. Gulf of Lion	09. Adriatic Sea	14. Gulf of Hammamet
05. Ligurian Sea/Corsica	10. Aegean Sea	15. Algerian Sea

Fig. 1. Map of the study area restricted to 1000 m depth: (A) partitioning into four sub-basins, with black dots representing MEDITS trawl stations; (B) location of the main Mediterranean seas.

Enrichetti et al., 2019; Grinyó et al., 2018; Stamouli et al., 2022). The >1 cm size range for megabenthic invertebrates was also reported in a recent study in the Atlantic (Outrequin et al., 2025). Alternatively, since most of the trawl catches are composed of epifauna, and although infauna may also be observed as a result of the ploughing action of the trawl, Hiddink et al. (2026) simply referred to trawled invertebrates as epifauna. In the absence of a standardized and widely accepted term to specifically designate this biological compartment, the term “epibenthic megainvertebrates” was used in this study. Although MEDITS benthic data have been available since 2012, only records from 2016 to 2021 were retained in the Western and Central Mediterranean and in the Adriatic Sea to remove potential identification bias present in the first years due to limited taxonomic expertise (Table 1). Records from Malta were restricted to the period 2018-2021 as no earlier data were available (Table 1). Regarding the Greek surveys, data on epibenthic megainvertebrates have been systematically reported in the Southwestern Aegean (Argo-Saronic region) since 2019. In the Northern Aegean, benthic data are available at the class level, while in other regions of the basin, only crustaceans are reported. Consequently, only Greek records from 2019 to 2021 in GFCM Geographical Sub-Areas (GSA) 20 (Eastern Ionian Sea) and GSA 22 (Northern Aegean Sea and Argo-Saronic region) have been considered. Stations from the southern part of GSA 22 and from GSA 23 were excluded (Figure S1.2 and S1.3). The trawled for each trawl was computed using the trawled distance and net horizontal opening (measured with acoustic sensors (MEDITS, 2017)). The biomass of each taxon caught was then expressed in g/km^2 to standardize the effort unit. Epibenthic megainvertebrate records from phylum to genus level were retained, excluding pelagic taxa (such as jellyfish). Cephalopods, which may dominate the biomass in some stations, were also excluded since they cannot be considered strictly benthic.

Rare taxa may result from true biological scarcity in the environment or from varying levels of taxonomic expertise. To limit identification errors or bias due to the irregular presence of expert scientific staff, some taxa had to be aggregated at higher taxonomic levels. Therefore, it was necessary to standardize the taxonomic resolution across areas. Taxa were grouped at a higher taxonomic level if they were recorded in less than 60% of the years per GSA, or if they accounted for less than 5% of all stations per GSA and years.

2.2.2. *Environmental data*

Depth and substrate type are widely recognized as important drivers of benthic species distribution (Rex, 1981). A bathymetric raster layer (depth, m) was extracted from the EMODnet portal (https://emodnet.ec.europa.eu/en) at a resolution of 0.001° (i.e., approximately 0.1 km). Benthic terrain variables (i.e., slope and rugosity) were derived from the bathymetric layer (function *terra::terrain* in R). The European broad-scale seabed habitat map (EUSeaMap) (Vasquez et al., 2023) downloaded from EMODnet was used to compute the average grain size of the sediment (mm) (Millot and Vaz, 2024) using Folk's sediment fractions (Folk, 1954) and applying the equation from Renard et al. (1997). This equation calculates the mean grain size of a substrate as the average grain size of each sediment fraction (gravel, sand, mud), weighted by the proportion of that fraction within the substrate. The log-transformed version of this variable was used in this study. Additional environmental raster layers were extracted from the platform Bio-ORACLE (Assis et al., 2024), which uses monthly data of sea bottom variables from 2010 to 2020 to generate climatologies at a resolution of 0.05° (i.e., approximately 5 km). Average values from near-bottom water conditions, were extracted for nine variables: seawater temperature (°C), salinity (PSU), current speed (m.s^{-1}), pH, dissolved oxygen (mmol.m^{-3}), chlorophyll *a* (mmol.m^{-3}), silicate (mmol.m^{-3}), nitrate (mmol.m^{-3}), and phosphate (mmol.m^{-3}) concentrations. Details on environmental variables are summarized in Table S2.1.

Table 1

Number of MEDITS trawl stations per sub-basin. A map of GFCM Geographical Sub-Areas (GSA) is available in Figure S1.2.

Sub-basin	GSA	Period	Number of stations
Western Mediterranean	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12	2016-2021	3250
Central Mediterranean	13, 14, 16, 19, 21	2016-2021	1302
	15	2018-2021	
	20	2019-2021	
Adriatic Sea	17, 18	2016-2021	1465
Aegean Sea	22	2019-2021	232

When required, rasters were resampled (function *terra::resample* in R) to a resolution of 0.04° (i.e., approximately 4.5 km) to match the resolution of the biological data (average haul length of the MEDITS surveys). The midpoint coordinates of the MEDITS hauls were used to extract environmental values from the set of raster layers. Correlations among the different environmental predictors were calculated, and only one predictor per group of highly correlated variables (mean Spearman's rank coefficient >0.7) (Dormann et al., 2013) (function *stats::cor* in R) was retained according to ecological relevance. All records from the four sub-basins were considered to select a common set of predictors and facilitate the comparisons between environmental conditions.

2.3. *Identification of bioregions*

2.3.1. *Data transformation and K-means clustering*

Raw biological data were split by sub-basin and converted into “species × stations” matrices. The present study was based on standardized biomass associated with a strongly asymmetric distribution, including a few observations with high values and many with null or low values. Therefore, biomass values were log-transformed (log(x+1)) to avoid an over-weighting of abundant species, as the total biomass of each taxon acts as its weight in the following analysis (ter Braak and Smilauer, 2015). Logarithmic transformation is suitable for strongly right-skewed data with log-normal distribution (Legendre and Legendre, 2012). The Square root transformation was tested, but did not sufficiently correct the asymmetry. Each dataset was then standardized across stations using a Hellinger transformation (*vegan::decostand* in R (Legendre and Gallagher, 2001);), resulting in rooted relative abundances suitable for Euclidean-based community analyses. Finally, a Principal Component Analysis (PCA; *ade4::dudi.pca* in R) was applied. While PCA assumes linear gradients and may lead to a simplification of ecological patterns at broad spatial scales, this approximation was preferred because it reduces noise in large datasets and prevents assigning disproportionate weight to rare taxa. Transformation-based PCA approaches are widely used for the analysis of community data (Legendre and De Cáceres, 2013; Legendre and Gallagher, 2001). Axes that explained at least 2% of the total variance were retained. The combined use of log-transformation, Hellinger transformation, and PCA has been previously applied to pre-process data for community analyses (Receveur et al., 2024). Data were not aggregated by year across the time series.

The non-hierarchical clustering algorithm k-means (Macqueen, 1967) (function *stats::kmeans* in R), was applied to group similar stations in each sub-basin based on epibenthic megainvertebrate biomasses. The k-means algorithm was selected among other hierarchical clustering methodologies because it gave more spatially coherent groups of stations. MEDITS trawl stations were classified in *k* clusters, considering the minimum squared Euclidean distance between stations. Initial centers of the clusters were randomly selected, and 100 runs were computed to obtain a robust clustering result. For this study, the optimal number of clusters (Ikotun et al., 2023) was determined using the NbClustNbClust function in R (Charrad et al., 2014), which selects the best partition by consensus across thirty clustering validity indices including the silhouette value, gap statistic, and the Calinski–Harabasz and KL indices. In some cases (e.g., the Central Mediterranean and the Aegean Sea), the resulting classification contained clusters with less than 10 stations, which were discarded from the analysis due to their very divergent biotic composition. The PCA was then rerun, and both the number of retained axes and the optimal number of clusters were re-evaluated.

2.3.2. Ecological characterization of clusters

The ten main indicator taxa of each cluster were identified to validate their ecological relevance, as a bioregion must be characterized by a distinct set of indicator taxa to be considered a meaningful ecological entity (Carignan and Villard, 2002). An indicator value index (IndVal^g) was calculated on transformed data for each taxon using the function *indicspecies::multipatt* in R (Dufrene and Legendre, 1997). The IndVal^g index is computed as the product of specificity (the probability that a station where the taxon is present belongs to a given cluster) and fidelity (the probability of finding the taxon in stations assigned to that cluster). It measures the association between a taxon and a cluster, but does not reflect dominance. For each cluster, the ten taxa with the highest significant IndVal^g scores were retained as the top indicator taxa.

Additionally, taxonomic richness (S, the total number of taxa) and Pielou's evenness index (J′, Pielou, 1969) were calculated for each cluster to provide complementary information on community diversity and structure. Taxonomic richness reflects the number of taxa present, whereas Pielou's evenness informs on the structural dimension of the community by describing how biomass is distributed among taxa.

Finally, the environmental ranges (for the selected environmental predictors) across the stations within each cluster were calculated. Both these environmental ranges and the values of the diversity indices were visualized using radar plots to facilitate comparison of the overall characteristics of each cluster.

2.3.3. Machine learning predictions and performance assessment

A Random Forest (RF) algorithm was applied to each sub-basin dataset to predict the distribution of clusters in unsampled areas, following an approach similar to Species Distribution Modeling (Elith and Leathwick, 2009). Here, RF confronted a multi-class response variable (i.e., cluster) with environmental conditions, instead of presence-absence or abundance data. This common machine-learning algorithm (Breiman, 2001) was selected for its ability to predict factor-type response variables and for its robustness to noise and non-linear patterns in the data (Chaudhary et al., 2016; Rodriguez-Galiano et al., 2012). Initial datasets were randomly split into training data (80%) to calibrate the models and generate predictions, and testing data (20%) to assess the performance of the models. RFs were fitted by keeping the default number of trees ($n = 500$) and using the selected set of environmental predictors. Response curves for all selected environmental predictors and for all clusters were generated, and the contribution of each predictor to model performance was assessed using the Gini Index. The idea is that features that better split the data (reduce Gini impurity across all trees) are considered more important (Breiman et al., 1984). The probability of presence of each cluster was predicted across the study area using the function *RandomForest::predict* in R. To convert fuzzy probability outputs into a single cluster-assignment map, each pixel was assigned to the most probable cluster. Pixels corresponding to hard bottoms were excluded based on the average grain size raster layer.

Overall accuracy for each RF was assessed using the function *randomForest::confusionMatrix* in R, by comparing the classification obtained by clustering and by RF predictions on the testing dataset. To evaluate the ability of RFs to predict each cluster, three additional metrics were calculated: sensitivity (the proportion of stations correctly predicted as belonging to a specific cluster), specificity (the proportion of stations correctly predicted as not belonging to the cluster), and cluster-specific balanced accuracy (the average of sensitivity and specificity).

Predicted areas of cluster membership delineated by the RF models and characterized by distinct epibenthic megainvertebrate communities defined the bioregions of the study.

2.3.4. Uncertainty assessment

Model errors per bioregion were assessed by calculating the percentage of stations misclassified by the RFs compared to the k-means clustering classifications. In addition, the magnitude of the environmental extrapolation performed by the modeling process in unsampled areas was assessed across the whole study area. The Extrapolation Detection tool (*Exdet*) (Mesgaran et al., 2014), based on Euclidean and Mahalanobis distances, was used to quantify and map "univariate extrapolation", corresponding to environmental conditions outside the range of observed environmental data. The "analogous" spaces correspond to environmental conditions already observed in the calibrating data (Mesgaran et al., 2014).

2.4. Combining bioregions across the Mediterranean

The four sub-basin raster layers were combined to create a comprehensive bioregionalization map of the Mediterranean soft bottoms to 1000 m depth. A new color code was determined to represent the degree of similarity among bioregions from different sub-basins. A PCA was conducted on the full species community matrix (i.e., a station by species matrix including all available observations for the four sub-basins), which was both log-transformed and Hellinger-transformed as before. Passive projection into the PCA multidimensional space of the bioregion assignment vector (expressed as a categorical variable) of each station was then performed using the function *vegan::envfit* in R. Finally, the centroids of each bioregion were plotted on the ordination biplot, and the coordinates of the first and second PCA axes were used as a proxy for similarity between bioregions. A color palette was assigned to map bioregions across the Mediterranean, reflecting the similarity in the composition of their epibenthic megainvertebrate communities.

All statistical analyses were performed with the R software v 4.2.2. Specific R packages were used for this study, including *Nbclust* (Charrad et al., 2014), randomForest (Breiman et al., 1984), *indicspecies* (De Cáceres et al., 2010), and dsmextra (Mesgaran et al., 2014).

3. Results

3.1. Statistical diagnostics

The optimal number of clusters determined by the *NbClust* function was five for the Western Mediterranean and the Adriatic Sea, and three for the Central Mediterranean and the Aegean Sea (Figure S1.4). This classification was obtained after excluding 25 stations out of the 6250: 9 in the Central Basin and 16 in the Aegean Sea, due to their highly divergent community composition.

Seven environmental predictors were selected among the thirteen variables included in the correlation analysis to predict the distribution of the bioregions (Figure S1.5): depth (in m), average grain size of the sediment (in mm), mean bottom salinity (in PSU), mean bottom current speed (in m.s^{-1}), mean bottom temperature (in °C), mean bottom pH, and mean bottom concentration of Silicate (in mmol.m^{-3}) (Figure S1.6). The remaining variables were highly correlated to depth and, therefore, were excluded from further analyses.

Robust predictions were obtained from the four RF models with a global accuracy ranging from 0.82 to 0.89 (Evaluation metrics are detailed in Table S1.2). Depth was the most important contributor to the RF predictions, while the influence of average sediment grain size was minimal. Predictions were, secondly, mainly driven by pH and silicate concentrations in the Western Mediterranean, silicate, salinity, and temperature in the Central Mediterranean and the Adriatic Sea, and temperature and salinity in the Aegean Sea (Figure S1.7). The response curves of the clusters for each environmental predictor are presented in Figures S1.8, S1.9, and S1.11.

3.2. *Spatial distribution of bioregions and indicator taxa*

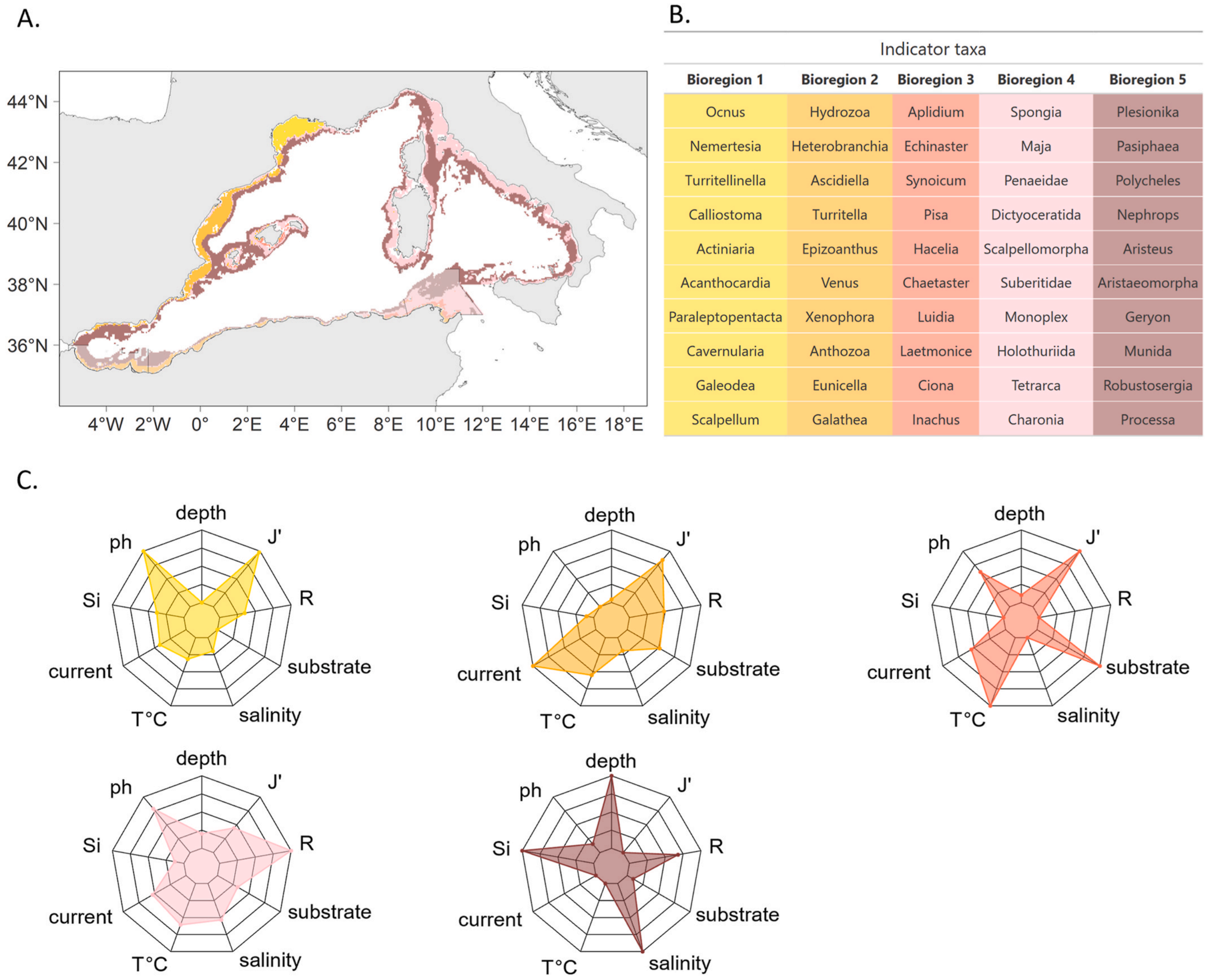
3.2.1. *The Western Mediterranean*

The Western Mediterranean was divided into five distinct bioregions (Fig. 2). Three were spatially isolated: the continental shelf of the Gulf of Lion (B1: Bioregion 1), the shelf of the Catalan Sea (B2), and the area around the Balearic Islands (B3) (Fig. 2A). The distribution of these bioregions was extrapolated to the Southern Mediterranean Sea (faded color shades), with B2 predicted along the Moroccan and Algerian shelves, and B3 predicted along the Northern Tunisian shelf. The remaining two bioregions were more broadly distributed, across the shelf break and slopes of the basin (B4) and the deep waters (B5) (Fig. 2A).

The Gulf of Lion epibenthic megainvertebrate community (B1) displayed a composition in mollusk genera, including *Turritellinella* (formally *Turritella communis*), *Calliostoma*, *Acanthocardia*, and *Galeodea*, along with the hydroid *Nemertesia* (Fig. 2B). The shelf of the Catalan Sea (B2) was represented by a diverse set of indicator taxa, including the classes Hydrozoa, Anthozoa, and the subclass Heterobranchia. Specific cnidarian genera also characterized the region, such as *Epizoanthus* and *Eunicella*, as well as gastropods such as *Turritella* (distinct from *Turritella communis*) and *Venus,* specific to the continental shelf. The Balearic Islands bioregion (B3) hosted taxa typical of shallow waters, including tunicates such as *Aplidium*, *Synoicum,* and *Ciona*. Coastal starfishes (*Echinaster*, *Hacelia*, *Chaetaster,* and *Luidia*), and crabs (*Pisa* and *Inachus*) were also indicative of this region. The shelf break and slope bioregion (B4) included a variety of indicator taxa, such as sponges of the genus *Spongia*, the order Dictyoceratida and the family Suberitidae, the shallow-water spider crab *Maja*, shrimp from the family *Penaeidae*, and barnacles from the order Scalpellomorpha. Lastly, the deepest bioregion (B5) was dominated by mobile decapod crustacean taxa, including *Plesionika*, *Pasiphaea*, *Polycheles*, *Nephrops*, *Aristeus*, *Aristaeomorpha,* and *Geryon* (Fig. 2B).

3.2.2. *The Central Mediterranean*

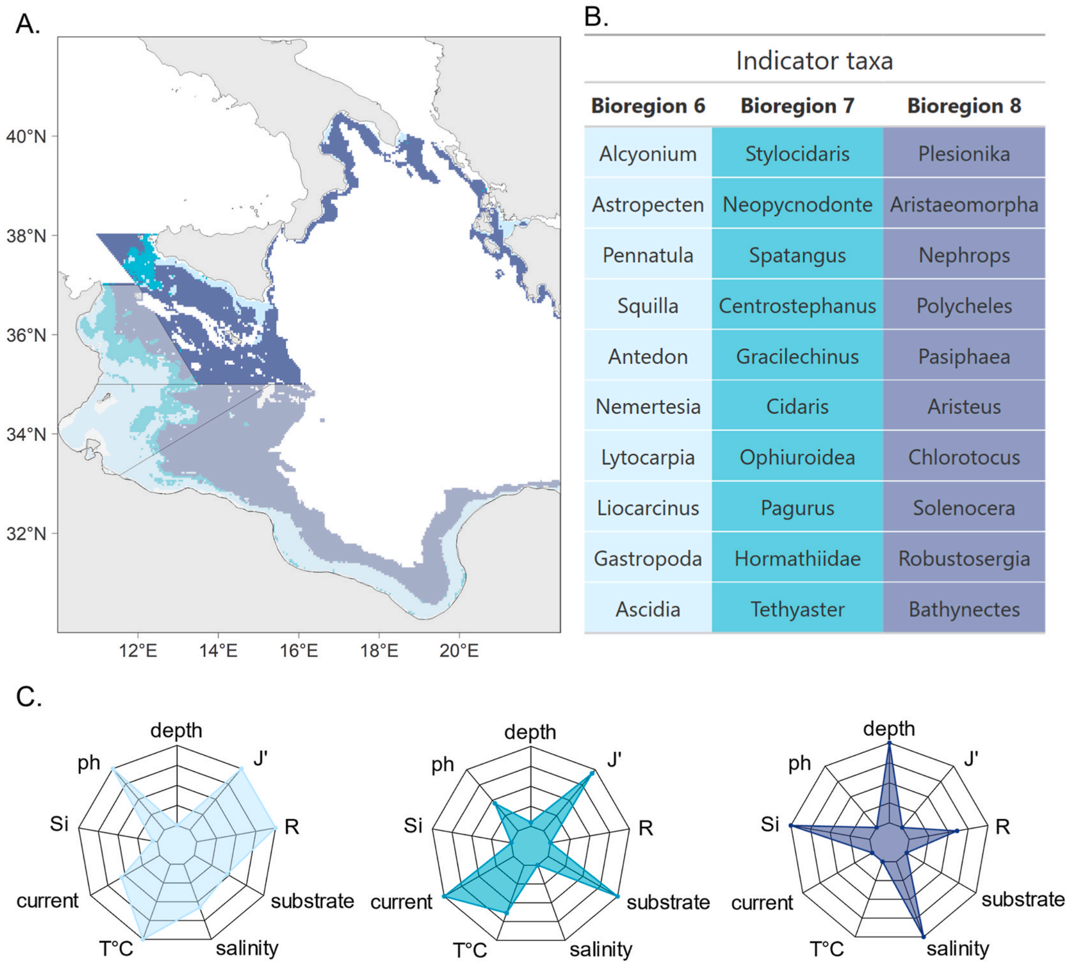
The Central Mediterranean included three distinct bioregions (Fig. 3): the Central Mediterranean continental shelves (B6), the Southwestern Sicilian region extending along the Tunisian upper slope (B7), and the Central Mediterranean deep waters (B8) (Fig. 3A). The



Indicator taxa

Bioregion 1	Bioregion 2	Bioregion 3	Bioregion 4	Bioregion 5
Ocnus	Hydrozoa	Aplidium	Spongia	Plesionika
Nemertesia	Heterobranchia	Echinaster	Maja	Pasiphaea
Turritellinella	Ascidiella	Synoicum	Penaeidae	Polycheles
Calliostoma	Turritella	Pisa	Dictyoceratida	Nephrops
Actiniaria	Epizoanthus	Hacelia	Scalpellomorpha	Aristeus
Acanthocardia	Venus	Chaetaster	Suberitidae	Aristaeomorpha
Paraleptopentacta	Xenophora	Luidia	Monoplex	Geryon
Cavernularia	Anthozoa	Laetmonice	Holothuriida	Munida
Galeodea	Eunicella	Ciona	Tetrarca	Robustosergia
Scalpellum	Galathea	Inachus	Charonia	Processa

Fig. 2. Partitioning of the Western Mediterranean in megabenthic invertebrate bioregions characterized by (A) their spatial distribution, (B) the 10 main indicator taxa, and (C) environmental and biological diversity ranges (J′, Pielou's evenness; R, taxa richness; T°C, seawater temperature; Current, current speed). Projections of bioregions in unsampled areas associated with higher uncertainty are shown with faded shading.



Indicator taxa

Bioregion 6	Bioregion 7	Bioregion 8
Alcyonium	Stylocidaris	Plesionika
Astropecten	Neopycnodonte	Aristaeomorpha
Pennatula	Spatangus	Nephrops
Squilla	Centrostephanus	Polycheles
Antedon	Gracilechinus	Pasiphaea
Nemertesia	Cidaris	Aristeus
Lytocarpia	Ophiuroidea	Chlorotocus
Liocarcinus	Pagurus	Solenocera
Gastropoda	Hormathiidae	Robustosergia
Ascidia	Tethyaster	Bathynectes

Fig. 3. Partitioning of the Central Mediterranean in megabenthic invertebrate bioregions characterized by (A) their spatial distribution, (B) the 10 main indicator taxa, and (C) environmental and biological diversity ranges (J′, Pielou's evenness; R, taxa richness; T°C, seawater temperature; Current, current speed). Projections of bioregions in unsampled areas associated with higher uncertainty are shown with faded shading.

distribution of these bioregions was extrapolated to the Southern Mediterranean Sea (faded color shades), with B6 predicted on the continental shelves of the Gulf of Hammamet and Gulf of Gabes (Tunisian waters) as well as along the Libyan continental shelves. B7 was predicted along the slopes of the Gulf of Hammamet and Gulf of Gabes, and B8 in the deeper waters of the Strait of Sicily and Libyan waters (Fig. 3A).

The shelf bioregion (B6) was characterized by sensitive species such as the soft coral *Alcyonium*, sea pens of the genus *Pennatula,* and the crinoid *Antedon,* as well as typical shallow-water taxa such as the crustaceans *Squilla* and *Liocarcinus,* and the sea star *Astropecten* (Fig. 3B). The intermediate bioregion (B7) was primarily represented by echinoderms, including sea urchins (*Stylocidaris*, *Spatangus*, *Centrostephanus*, *Gracilechinus,* and *Cidaris*) as well as the sensitive oyster *Neopycnodonte*. The Central Mediterranean deep waters (B8) were dominated by deep-sea crustaceans, including several indicator taxa similar to those found in the Western Mediterranean deep-water bioregion (B5) (Fig. 3B). Additionally, three crustacean indicator taxa, *Chlorotocus*, *Solenocera,* and *Bathynectes* were also important in this bioregion (Fig. 3B).

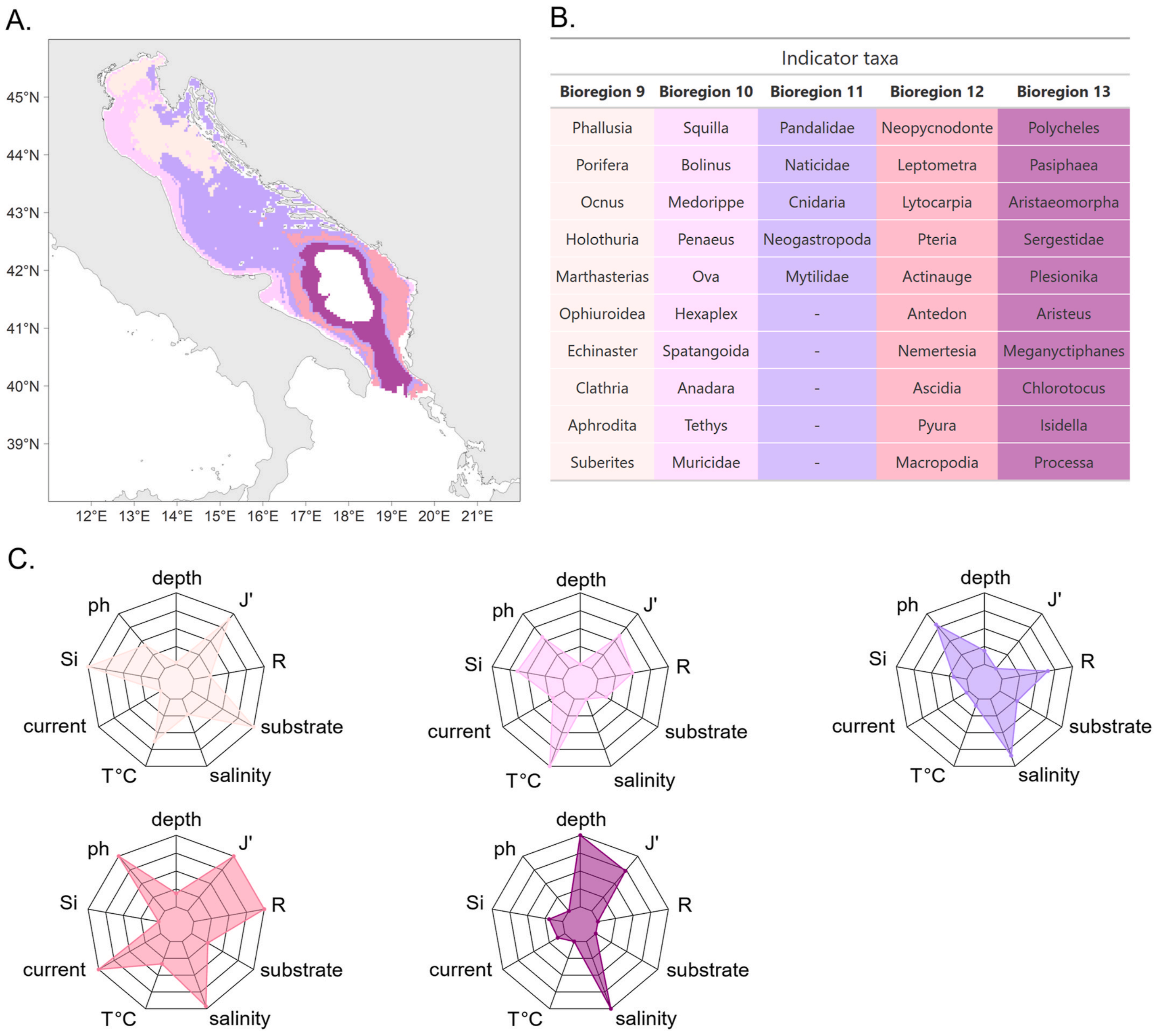
3.2.3. *The Adriatic Sea*

The Adriatic Sea was divided into five bioregions along a clear depth gradient (Fig. 4): the Northern Western Adriatic shelf (B9), the Northern Eastern Adriatic continental shelf (B10), the Central Adriatic shelf (B11), the Southern Adriatic slope (B12), and the deep waters of the Southern Adriatic (B13) (Fig. 4A).

The Northern Adriatic shelf (B9) was characterized by a diverse range of taxa, including the tunicate *Phallusia*, the sponges *Clathria* and *Suberites*, as well as echinoderms, including both the sea cucumbers *Ocnus* and *Holothuria* and the coastal sea stars *Marthasterias* and *Echinaster* (Fig. 4B). The western part of the Northern Adriatic shelf (B10) featured distinctive shallow-water species, including the mantis shrimp *Squilla,* gastropods such as *Bolinus*, and *Hexaplex,* and sea urchins such as *Ova* and other Spatangoida. The Central Adriatic shelf (B11) was distinguished by only five indicator taxa belonging to broader taxonomic levels: the families Pandalidae (shrimps), Naticidae (sea snails) and Mytilidae (bivalves), the order Neogastropoda, and the phylum Cnidaria. On the Southern Adriatic slope (B12), sensitive species were identified, including the oyster *Neopycnodonte*, the crinoids *Leptometra* and *Antedon*, as well as cnidarians such as the hydrozoans *Lytocarpia* and *Nemertesia* and the anemone *Actinauge*. Lastly, the Adriatic deep-water bioregion (B13) was characterized by specialized deep-sea crustaceans, including *Polycheles*, *Pasiphaea*, *Aristaeomorpha*, Sergestidae, *Plesionika*, and *Aristeus*, along with the vulnerable bamboo coral *Isidella* (Fig. 4B).

3.2.4. *The Aegean Sea*

The division of the Aegean Sea led to the identification of three distinct bioregions (Fig. 5): the shallow waters 0-200m depth (B14), a localized bioregion in the Argo-Saronic Gulf with patchy distribution in the Northern Eastern Aegean Sea (B15), and the deep waters 200-1,000m depth (B16) (Fig. 5A). The distribution of both shallow-water bioregion (B14) and deep-water bioregion (B15) were extrapolated in



Indicator taxa

Bioregion 9	Bioregion 10	Bioregion 11	Bioregion 12	Bioregion 13
Phallusia	Squilla	Pandalidae	Neopycnodonte	Polycheles
Porifera	Bolinus	Naticidae	Leptometra	Pasiphaea
Ocnus	Medorippe	Cnidaria	Lytocarpia	Aristaeomorpha
Holothuria	Penaeus	Neogastropoda	Pteria	Sergestidae
Marthasterias	Ova	Mytilidae	Actinauge	Plesionika
Ophiuroidea	Hexaplex	-	Antedon	Aristeus
Echinaster	Spatangoida	-	Nemertesia	Meganyctiphanes
Clathria	Anadara	-	Ascidia	Chlorotocus
Aphrodita	Tethys	-	Pyura	Isidella
Suberites	Muricidae	-	Macropodia	Processa

Fig. 4. Partitioning of the Adriatic Sea in megabenthic invertebrate bioregions characterized by (A) their spatial distribution, (B) the 10 main indicator taxa, and (C) environmental and biological diversity ranges (J′, Pielou's evenness; R, taxa richness; T°C, seawater temperature; Current, current speed).

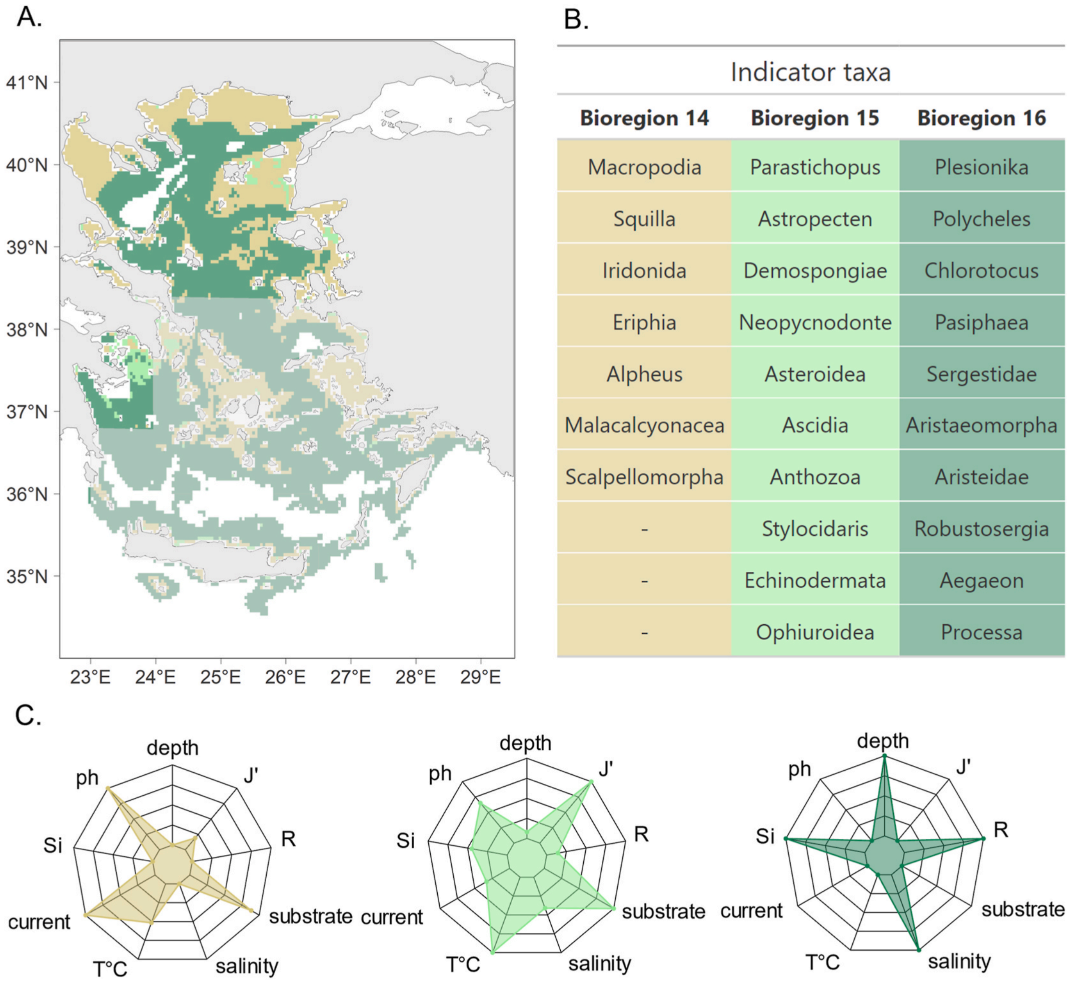
the Southern Aegean Sea (Fig. 5A).

Indicator species analyses revealed that the shallow-water bioregion (B14) was characterized by coastal crustaceans, including the spider crab *Macropodia*, the mantis shrimp *Squilla*, and the squat lobster *Iridonida* (Fig. 5B). The deep-water bioregion (B16) was defined by deep-sea crustaceans, similar to those in other basins, such as *Plesionika*, *Polycheles*, *Chlorotocus, Pasiphaea,* Sergestidae, and *Aristaeomorpha*. Lastly, the localized Argo-Saronic bioregion (B15) was distinguished by a high diversity of indicator taxa, including numerous echinoderms, such as the sea cucumber *Parastichopus*, the starfish *Astropecten,* and the sea urchin *Stylocidaris*, as well as the vulnerable oyster *Neopycnodonte.* The sponge class Demospongiae was also characteristic of this region (Fig. 5B).

3.3. *Ecological characterization of the bioregions*

In terms of environmental conditions, common oceanographic relationships can be identified among the different bioregions. For example, shelf bioregions were associated with the highest bottom temperature values (B3, B6, B10, B15) (Fig. 2C to 5C), while slope bioregions were often linked to the most intense bottom current velocities (B7, B12) (Fig. 3C to 5C). Deep-water bioregions exhibited the highest salinity values (B5, B8, B13, B16) and the highest bottom silicate concentrations (B5, B8, B16) (Fig. 2C, 3.C, 5.C), except in the Adriatic Sea, where the shelf was notably enriched (B9, B10) (Fig. 4C). In general, shelf and slope bioregions presented unique combinations of environmental conditions, whereas deep-water bioregions, particularly in the Western, Central, and Eastern Mediterranean Sea, shared more similar abiotic conditions.

Diversity indices can be compared between shelf, slope, and deep-water bioregions within a same sub-basin. In the Western Mediterranean and Adriatic Sea, slope bioregions were associated with the highest taxa richness (respectively B4 and B12) (Fig. 2C, 4.C). In the Central Mediterranean, the shelf bioregion (B6) showed the highest number of taxa, while it was the deep bioregion (B16) in the Aegean Sea (Fig. 3C, 5.C). Although the shelf bioregions of the Western Mediterranean (B1, B2,



Indicator taxa

Bioregion 14	Bioregion 15	Bioregion 16
Macropodia	Parastichopus	Plesionika
Squilla	Astropecten	Polycheles
Iridonida	Demospongiae	Chlorotocus
Eriphia	Neopycnodonte	Pasiphaea
Alpheus	Asteroidea	Sergestidae
Malacalcyonacea	Ascidia	Aristaeomorpha
Scalpellomorpha	Anthozoa	Aristeidae
-	Stylocidaris	Robustosergia
-	Echinodermata	Aegaeon
-	Ophiuroidea	Processa

Fig. 5. Partitioning of the Aegean Sea in megabenthic invertebrate bioregions characterized by (A) their spatial distribution, (B) the 10 main indicator taxa, and (C) environmental and biological diversity ranges (J′, Pielou's evenness; R, taxa richness; T°C, seawater temperature; Current, current speed). Projections of bioregions in unsampled areas associated with higher uncertainty are shown with faded shading.

B3) had lower taxa richness than the deep-water bioregion (B5), they exhibited a higher J' (Pielou index), indicating a more even distribution of biomass among taxa (Fig. 2C). In the Central Mediterranean and Aegean Sea, shelf communities (B6, B14, B15) were also more even than deep-water communities (B8, B16) (Fig. 3C, 5.C). In the Adriatic Sea, the slope bioregion (B12) exhibited the highest J' values, followed by the coastal shelf bioregion (B9), while the large shelf bioregion of the Central Adriatic exhibited the lowest (Fig. 4C). The absolute values of both diversity indices are presented in Table S1.3. Comparison in diversity indices cannot be made between bioregions from different sub-basins due to potential changes in taxa resolution across GSAs.

3.4. Combining bioregions across the Mediterranean

The relationship between the PCA axes and the bioregion assignment vector was highly significant ($p < 0.001$), indicating that the bioregion pattern aligned with the gradients captured by the ordination of all benthic observations.

The ordination revealed a clear distinction in epibenthic megainvertebrate communities along the first PCA axis, with deep-water bioregions (B16, B8, B5, B13) positioned on the left side, separated from the continental shelf and shelf-break/slope bioregions on the right side (Fig. 6A). This result illustrated the clear differences in benthic community composition along the depth gradient. However, within the continental shelf and slope groups, each bioregion was characterized by distinct communities, without clear bathymetric structuring. For example, the slopes of the Western Basin (B4) and Adriatic Sea (B12) exhibited similar communities, yet they were more closely associated with shelf bioregions (B6, B14) than with the Central Basin slope (B7). The gradient along the second PCA axis was more difficult to interpret in terms of environmental gradient but reflected differences in community composition specific to each bioregion, regardless of bathymetric level. Finally, the Central Adriatic shelf (B11) displayed uniquely distinct epibenthic megainvertebrate communities compared to all other bioregions (Fig. 6).

3.5. Quantifying uncertainties

RF predictions showed a low model error rate, with the percentage of correctly classified trawl stations per bioregion ranging from 74% to 98% (Figure S1.12). The degree and extent of environmental extrapolation varied across the sub-basins (Fig. 7). Despite the lack of observations along the African coasts, most of the Western Mediterranean exhibited environmental conditions similar to those in the calibration data (Fig. 7A). Larger environmental extrapolation was observed in the Southern Central Mediterranean, with univariate environmental extrapolation levels around -1.5 along the Tunisian and Libyan shelves (Fig. 7B). Moderate extrapolation levels were found in the deep waters of the Adriatic Sea (univariate extrapolation index from -0.5 to -2) (Fig. 7C), while a higher degree of extrapolation was detected in limited areas of the Aegean Sea (univariate extrapolation index from -2 to -8) (Fig. 7D).

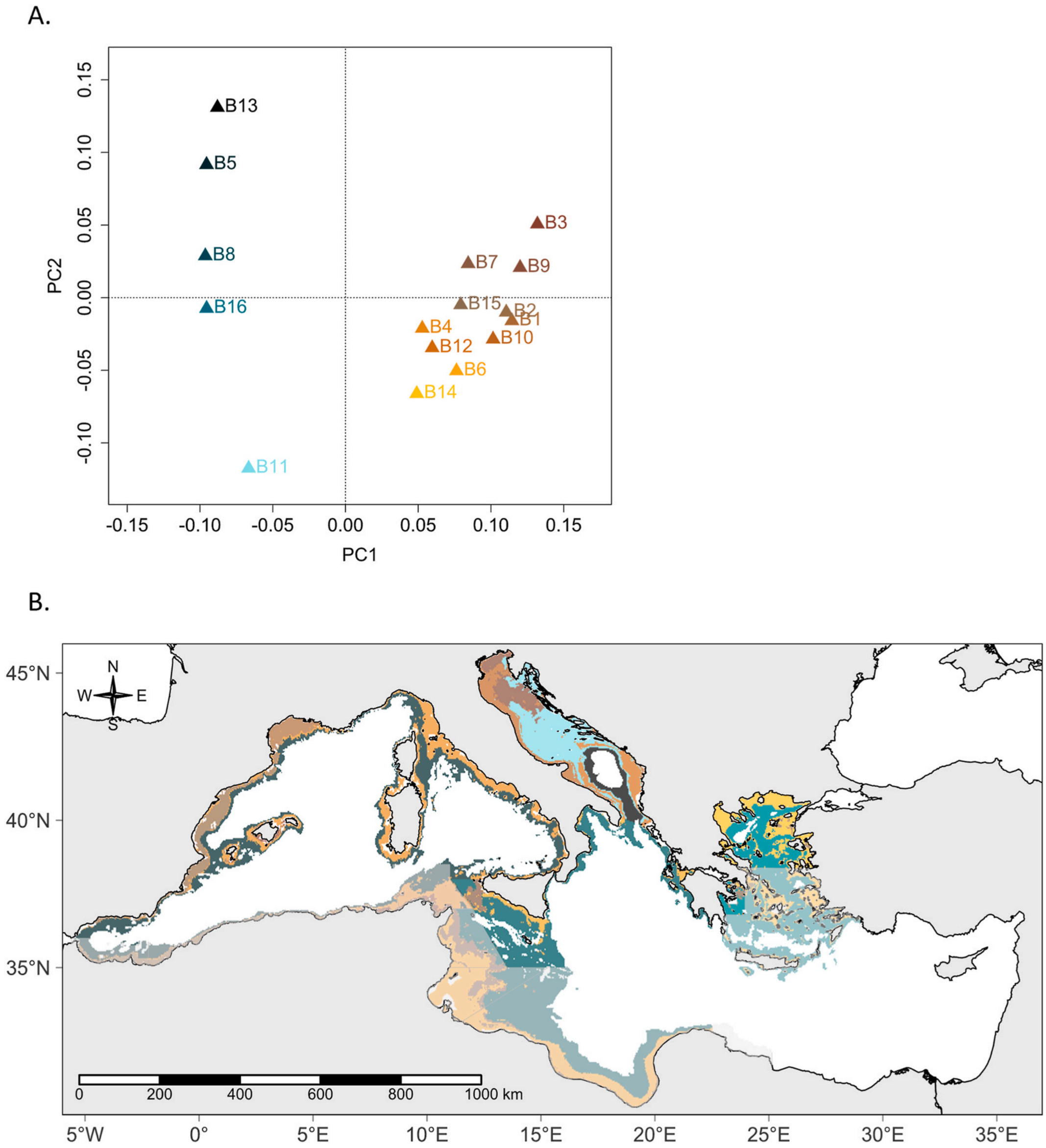


Fig. 6. Representation of (A) the position of the 16 cluster centroids associated with each bioregion along the two PCA axes, reflecting similarities in taxonomic composition, (B) the spatial distribution of Mediterranean bioregions, colored according to centroid position. More similar color tones indicate greater similarities in taxonomic composition. Projections of bioregions in unsampled areas are associated with higher uncertainty and are shown with faded shading. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

4. Discussion

This study proposes a mesoscale partition of the Mediterranean trawlable soft bottoms (above 1000 m), based on the composition of epibenthic megainvertebrate communities. It relied on an extensive dataset provided by the benthic by-catch of MEDITS trawl surveys. Sixteen clusters of distinct epibenthic megainvertebrate communities have been identified, resulting in biologically meaningful and spatially well-delineated bioregions. A strong bathymetric gradient structured epibenthic megainvertebrate communities across the four Mediterranean sub-basins, with clear differentiation between continental shelf (approximately areas <200m deep), slope (approximately between 200 and 400m deep), and deep (approximately >400m deep) bioregions. While a coast-to-offshore pattern of benthic communities has already been widely described in the Mediterranean (Pérès and Picard, 1964; Colloca et al., 2003; Tecchio et al., 2011), this study demonstrated for the first time this partitioning at the scale of the Mediterranean Sea for the poorly documented biotic compartment of epibenthic megainvertebrate communities, living on the most trawling grounds of the Mediterranean (Eigaard et al., 2017).

4.1. *Biological communities across bioregions as a function of the environment*

The spatial distribution of epibenthic megainvertebrate communities was strongly influenced by depth across the four Mediterranean sub-basins, showing a clear continental shelf-to-offshore structuration. Additional environmental parameters (e.g., temperature, salinity, pH, or silicate concentrations), also contributed to the predictions, although depth remained the main driver. The very low influence of substrate type was not expected because commonly identified as a main environmental forcing of benthic communities (Tecchio et al., 2011; Outrequin et al., 2025). Most of the MEDITS observations were made on mud or fine sand sediment, which are the main sediment type at the basin scale. Only a small portion of Mediterranean soft-bottoms consists of mixed or coarse sediments and hard substrates are not trawlable

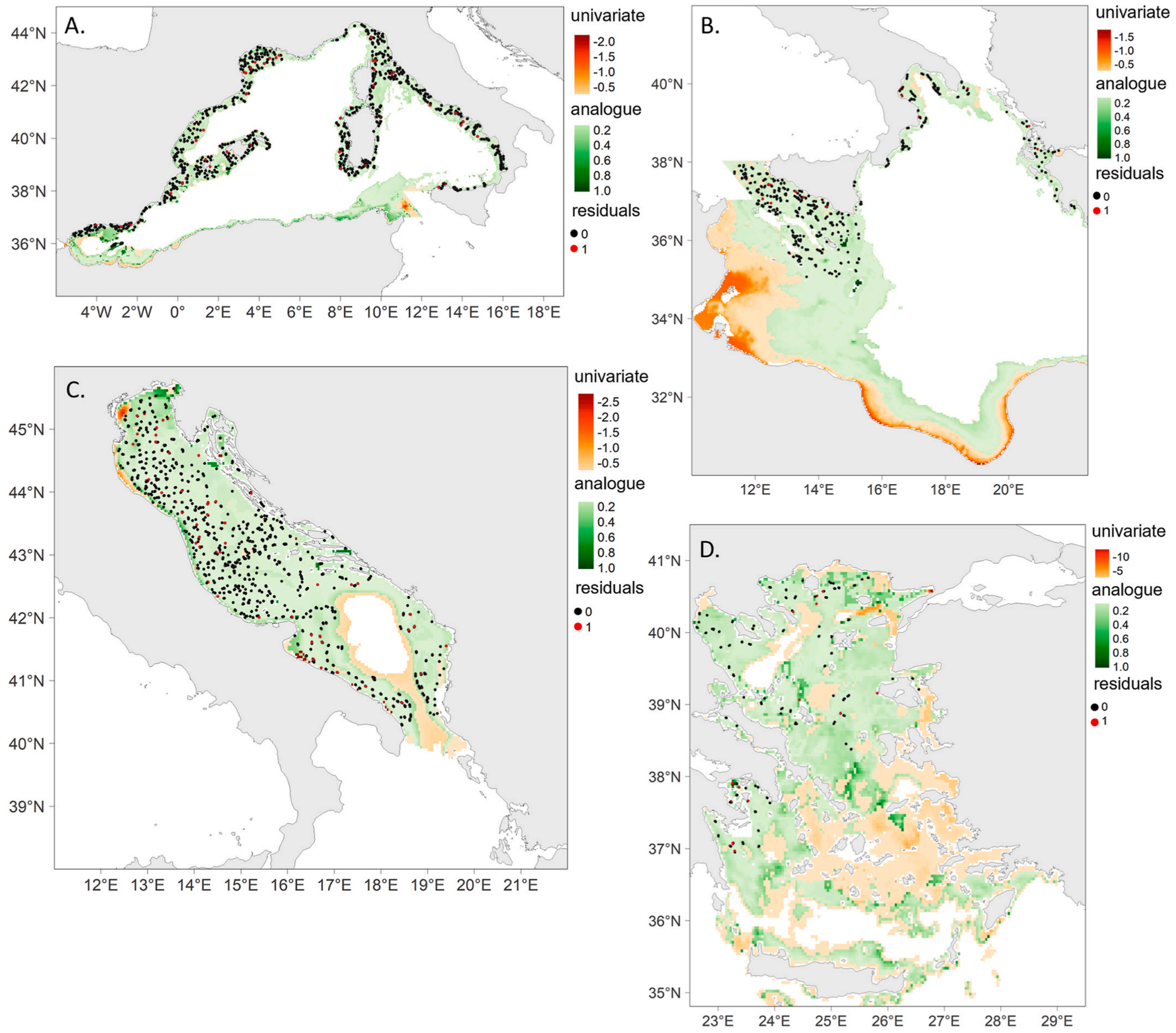


Fig. 7. Maps of univariate extrapolation (i.e., projections outside the range of the environmental space of calibrating data for at least one predictor) in orange and analogous conditions (i.e., projection in environmental conditions already known by calibrating data) in green for (A) the Western Mediterranean, (B) the Central Mediterranean, (C) the Adriatic Sea, and (D) the Aegean Sea. Correctly assigned observations are shown in black, and misclassified observations are in red. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

(Millot and Vaz, 2024). This may explain why sediment, here expressed by average grain size derived from Emodnet seabed habitat type, explained little of the variability observed in the biological data. Moreover, sediments may play a role at finer spatial scales than those captured by our observations (approximately 5 km).

The analysis of similarities among bioregions across the four sub-basins revealed a clear distinction between deep-water bioregions compared to shelf and slope bioregions, in epibenthic megainvertebrate composition. These results are in line with those of Terribile et al. (2016), who observed that differences in community composition in bioregions belonging to the deep strata (>400 m) were less marked than between shallower bioregions around the Maltese Islands. While very distinct communities characterized shelf and slope bioregions, a common set of deep-sea crustaceans was shared by deep-water bioregions (e.g., *Plesionika, Polycheles, Pasiphaea, Nephrops, Aristaeomorpha, Aristeus*). Nevertheless, these bioregions remained unique given the presence of specific indicator taxa, such as *Munida* in the Western Basin and the vulnerable bamboo coral *Isidella elongata* in the deep Adriatic Sea. Biogeographic patterns described in this study largely matched bottom depth categories, but not exclusively. In the Western Mediterranean, the two bioregions of the Gulf of Lion and the Catalan Sea exhibited distinct sets of indicator taxa despite sharing similar depth ranges. A similar pattern was observed for the three bioregions identified on the continental shelf of the Adriatic Sea, which also differed in their community composition despite comparable bathymetric conditions. These results indicated that, although depth is a major driver of epibenthic megainvertebrates communities, additional environmental and regional factors also play a key role in shaping the spatial structure of communities across the Mediterranean soft bottoms.

4.2. Comparison with other Mediterranean regionalizations

Regionalizations of the Mediterranean Basin have largely focused on epipelagic waters, based on satellite-derived chlorophyll data

(D'Orentzio & Ribera d'Alcalà, 2009; Palmiéri, 2014; Munoz et al., 2015; Mayot et al., 2016, Ciavatta et al., 2018; Basterretxea et al., 2018; El Hourany et al., 2021), as well as on biogeochemical parameters (Nieblas et al., 2014) and ocean circulation patterns (Berline et al., 2014; Rossi et al., 2014). Consensus regions (Ayata et al., 2018) were mainly located in the oceanic domain, and therefore did not overlap our bioregions restricted to the continental shelves and slopes. Reygondeau et al. (2017) proposed a unique vertical regionalization of Mediterranean waters, including a partition of the seabed. A key outcome of this work was that surface-water regionalizations cannot be extrapolated to the seafloor, as different drivers are involved. This supports the mismatch between our results and surface-based Mediterranean regionalizations. Based on a set of environmental parameters, they obtained much patchier regions compared to our larger but more spatially coherent bioregions. While physical and biogeochemical conditions seemed to capture fine-scale local variability, they did not attest to the ecological meaning of these regions, which must be justified by indicator taxa. In contrast, epibenthic megainvertebrates communities depicted mesoscale patterns, matching the spatial resolution required for systematic conservation planning, which relies on ecologically meaningful and spatially continuous regions to ensure adequate representation of communities within conservation networks (Combes et al., 2021; O'Brien et al., 2022; Roberson et al., 2017).

While no basin-scale partitioning of Mediterranean epibenthic megainvertebrates exists, a similar exercise has been conducted in North Atlantic waters (Outrequin et al., 2025). A strong coast-to-offshore gradient has also been shown to structure these communities. In contrast with our study, communities were associated with specific substrate types, from finer to coarser sediments. The predominance of mud and fine sand sediments on trawlable soft bottoms in the Mediterranean did not provide a sufficient gradient to establish such a distinction.

A strong bathymetric gradient has also been observed to drive coastal fish assemblages in the Mediterranean with a clear separation between inshore and offshore assemblages. Yet, only six compartments were identified by Hattab et al. (2015), compared to sixteen in our study, further demonstrating that benthic environments appear to be associated with a greater number of distinct assemblages. The pronounced north-south separation described for coastal fish assemblages could not be reproduced in our bioregionalization for which the southern coast structuration had to be extrapolated from the northern observations. Nevertheless, the latitudinal gradient, mainly driven by surface temperature, is expected to be less pronounced in the relatively homeothermic bottom waters of the Mediterranean continental margins (Cartes et al., 2004).

Some local comparisons can be made with regional partitioning of epibenthic megainvertebrate communities along the Mediterranean continental margins. Bioregional patterns studied along the Iberian Peninsula, using MEDITS crustacean data, revealed a clear distinction between the communities of the Catalan Sea and those of the Alboran Sea (Abelló et al., 2002). In the present study, while the communities of the Catalan shelf were specific to a unique bioregion (B2), the Alboran communities were separated but associated with the widespread deep-sea bioregion of the Western Basin (B5). In line with their study, deep-sea crustaceans such as *Geryon* characterized this region, but the biogeographic isolation of the Alboran Sea from the rest of the Western Basin was less clear in our results. Regarding French waters, a similar partition of the Gulf of Lion compared to our study was revealed by a seasonal bottom trawl survey (Vaz et al., 2023) with distinct shelf communities compared to those of the slope and deep waters. Some similar indicator taxa in both studies were found on the shelf, such as *Acanthocardia*, along with deep-sea crustacean indicators of deeper environments. However, while slopes were typically associated with filter-feeding and suspension-feeding organisms in local descriptions of the Western Basin (La Rivière et al., 2021), the bioregion corresponding to this depth strata (100-200 m) (B4) was characterized by sponge and crustacean taxa (e.g., *Spongia*, *Maja*, Penaeidae, Dictyoceratida). Nevertheless, these suspension feeder communities were indicators of the Adriatic slopes (B12), including *Leptometra*, *Antedon*, and *Nemertesia*. The broad spatial scale of the Western Basin may not have allowed the precise delineation of slope communities, but rather more general intermediate waters communities. Bioregional patterns in the other Mediterranean sub-basins were less documented, limiting relevant comparison.

4.3. *Comparison with marine benthic habitat classifications*

The Benthic Broad Habitat Types of the Marine Strategy Framework Directive (MSFD) (available at https://emodnet.ec.europa.eu/geonetwork/static/api/records/0a1cb988-22de-48b2-8cda-d90947ef77d1) primarily categorize habitats based on depth, light penetration, energy zones, and sediment types, with minimal reference to biological zones. However, our results suggest a low correlation between epibenthic megainvertebrate communities and mean grain size in soft sediment habitats, questioning the applicability of current European classifications for Mediterranean epibenthic megainvertebrate communities.

Constant revisions of the EUNIS classification have led to significant progress in the marine section of EUNIS 2019, which was furthered by the EUSeaMap project and the seabed map produced in 2023 (Vasquez et al., 2023). Nevertheless, distribution maps of the highest levels of EUNIS classification often result from local studies on macrobenthic endofauna and/or predictive mapping, which strongly rely on local abiotic conditions, generally resulting in a much finer partitioning. For instance, some deep bioregions (B5, B13) align with two EUNIS habitats (Mediterranean bathyal sand and lower bathyal mud), as well as our partitioning of the Adriatic shelf, which shared similar patterns (B9, B10, B11). However, the shelves of the Catalan Sea (B2) and the Central Mediterranean (B6, B7) overlapped more than five distinct EUNIS habitat types, from muddy detritic bottoms to coarse sediment. Therefore, both abiotic and biotic partitioning appear to be complementary for identifying relevant entities that should be represented in future conservation plans to ensure the protection of benthic communities.

The recent CodeMap program (Grande et al., 2025) offers a fine-resolution habitat classification for the Mediterranean and Black Seas based primarily on physical attributes and specific habitat-forming taxa. However, it is limited to discrete areas, whereas our basin-scale bioregionalization uses broad biological community data to define mesoscale patterns. Nevertheless, while differing in scale and methodology, the two approaches are locally complementary.

4.4. *Limitations and caveats*

4.4.1. *Quality of the MEDITS dataset*

In the absence of dedicated surveys to monitor benthic taxa, the bycatch of the MEDITS trawl survey represents, to our knowledge, the most comprehensive dataset to study epibenthic megainvertebrate communities living on the most trawled Mediterranean grounds (Terribile et al., 2016; Eigaard et al., 2017). It may be acknowledged that MEDITS trawl nets are not specifically designed for quantitative benthic faunal sampling and are limited to accessible flat and soft bottoms, excluding near-shore (<10 m) and very deep environments (>1000 m). However, the large swept area of the MEDITS bottom trawl allows for a high spatial coverage, not achieved by any other techniques such as grabs, beam trawls, or non-invasive video tools (Carbonara et al., 2020; Georges et al., 2024). It enables a better sampling of low-abundant epibenthic megainvertebrates, which can be easily overlooked by other methods (Farriols et al., 2024).

Despite a standardized MEDITS protocol implemented across the eight countries involved in the data collection, inter-regional comparisons of epibenthic megainvertebrate communities may nevertheless remain challenging due to uneven sampling in space and time. Although benthic sampling has been recommended since 2012, it is still not mandatory (MEDITS, 2017), resulting in variable survey periods across GSAs, both in terms of temporal coverage and seasonal timing of sampling. Nevertheless, by restricting the analysis to surveys conducted between 2016 and 2021, and pooling data across this time range, we ensured a relatively homogeneous sampling effort across most GSAs. We assumed that the relative temporal stability of hydrodynamic conditions at the seabed along Mediterranean continental margins (Cartes et al., 2004), compared to the high variability of surface waters driven by large-scale atmospheric oscillations and interannual hydrographic variability, allows us to disregard the temporal dimension of the data without introducing substantial bias. Moreover, low seasonal and interannual variability in epibenthic megainvertebrate communities has previously been reported in the Mediterranean Sea (Sardà et al., 1994; Vaz et al., 2023). Malta and Greece, where benthic sampling was initiated more recently, remained associated with lower sampling effort, and predictions in these areas should therefore be interpreted with greater caution. The sub-basin partitioning further allows the isolation of regions affected by stronger sampling bias (e.g., the Aegean Sea), where comparison with other sub-basins remained difficult to interpret. It is also still important to note that observations from 2016 to 2021, were not representative of the pristine state of the Mediterranean bottom habitats due to several decades of intense bottom trawling fisheries (Russo et al., 2019; Smith et al., 2023), which have already strongly impacted the epibenthic megainvertebrate community structure and composition.

Taxonomic resolution of the benthic dataset also varied by GSA, reflecting the expertise of each scientific group on board. The species richness in epibenthic megainvertebrates is positively correlated with research effort in the Mediterranean (Stamouli et al., 2022). Unequal taxonomic expertise is particularly marked in the Aegean Sea, where three different scientific teams are involved in conducting the survey. To overcome this problem, stations where only crustaceans have been sampled were not used in this study, although the dataset still remained unbalanced. Benthic taxa are recorded at the class level in the Northern Aegean Sea, while in the Argo-Saronic region, the survey benefits from specialized benthic staff. This difference may partly explain the isolation of this region into bioregion B15, characterized by a huge diversity of indicator taxa, including echinoderms (*Parastichopus*, *Astropecten*, *Stylocidaris*), sponges (Demospongiae), and bivalves (*Neopycnodonte*). In contrast, while the deep-water bioregion characterized by deep-sea crustaceans (B16) was in line with findings from other sub-basins, the exclusive set of crustaceans as indicators for shallower waters may misrepresent the true composition in epibenthic megainvertebrate communities. A more comprehensive and balanced dataset may possibly result in different geographic delineations of these bioregions and most certainly in a different set of indicator taxa.

4.4.2. Statistical limits

This study adopted a “group-first-then-predict " strategy, using k-means clustering to identify distinct epibenthic megainvertebrate communities, followed by Random Forest predictions (Breiman, 2001) to map their distribution. Despite robust outputs (accuracy above 0.82), the process remained sensitive to several user choices, including the type of clustering method or the number of optimal clusters (Ikotun et al., 2023). Choices can be supported by statistical criteria, but more pragmatically, must be validated according to ecological coherence. This k-means classification allowed the identification of spatially coherent groups of stations, characterized by many benthic taxa, including those with weak responses to environmental variables that are difficult to predict individually. Indeed, a “predict-first-then-group " approach using Generalized Dissimilarity Modeling (Mokany et al., 2022) was tested, but the observed environmental gradients failed to explain changes in biodiversity over space. This study adopted a well-established classification strategy whose effectiveness has been proven in recent studies describing benthic habitats (Livingstone et al., 2018; O'Brien et al., 2022; Serrano et al., 2017) despite the emergence of more holistic techniques that are more challenging to implement (Hill et al., 2020; Murillo et al., 2024).

Many ecologically meaningful environmental predictors have been included in the modeling process in order to explain a maximum of variability in epibenthic megainvertebrate observations. Adding key proxies of benthic food availability, such as Total Organic Carbon (TOC), could potentially improve model predictions. However, this parameter was not available for bottom conditions at the Mediterranean scale. Indirect proxies, including chlorophyll *a* concentration and primary productivity, were not included due to their strong correlation with depth. Nevertheless, given the low error rates of our models, additional predictors would not significantly improve our model's performance and may instead increase the risk of overfitting. Anthropogenic pressures were not considered as predictors in our study. Land-based pollution (e.g., nutrients input, organic matter) is largely restricted to coastal areas (Korpinen et al., 2021) and is not expected to have significant effects at the mesoscale in the basin. Similarly, eutrophication is rare in the Mediterranean due to the oligotrophic nature of the basin (Colella et al., 2016). In any case, such explanatory variables were not available on the seabed at the Mediterranean Basin scale. On the contrary, we believe that including bottom trawling activities, should have enhance the reliability of our predictions, given their structuring impact on epibenthic communities (Clark et al., 2016; Smith et al., 2023). However, data from tracking systems such as the European Vessel Monitoring System (VMS) are difficult to access, and Automatic Identification System (AIS) data significantly underestimate the fishing effort in the Mediterranean, especially in southern regions (Taconet et al., 2019). We encourage the inclusion of this factor in future work, now that promising studies have recently been developed using satellite tracking (Synthetic Aperture Radar, SAR), to provide accurate bottom trawling estimates in the Mediterranean (Marsaglia et al., 2024). Finally, due to the correlative nature of our models, we cannot fully elucidate causal relationships between each environmental predictor and biological communities (Shmueli, 2010). While it was not the focus of the present study, other types of approach may help understand these relationships such as Bayesian Models (Gelman and Shalizi, 2013) or Structural Equation Models (Lefcheck, 2016).

4.4.3. Extrapolation and uncertainties of the predictions

Predicting the distribution of bioregions using environmental variables can result in uncertain outputs when performed in areas where no biological observations were available (Araújo and Guisan, 2006). While the error rate of our models was very low (value observed vs predicted), the projections in the south of each sub-basin involved significant environmental extrapolations (i.e., areas of environmental conditions not known by the models). This was particularly the case for the southern shelf of the Central Mediterranean and the Central and Southern Aegean Sea. On the Tunisian shelf, the accuracy of those predictions may be ensured by the strong structuring effect of the bathymetry on epibenthic megainvertebrate communities, and aligned with benthic patterns identified in this region (Lasram et al., 2015). However, the significant environmental extrapolations in the Central and Southern Aegean Sea may lack accuracy. Indeed, the Cyclades plateau, a mostly coarse biogenic sand area between 50 and 110m depth, partly predicted as belonging to the B14 region in our study and only characterized by coastal crustaceans, is described in other studies as supporting nursery areas for soft clams, sea urchins and starfish species (Georgiadis et al., 2009) as well as important sponge abundance (Stamouli et al., 2023). Mapping the degree of environmental extrapolation is a way to ensure transparency about projections in areas of higher uncertainty, while also highlighting regions where acquiring new data remains essential to improve the reliability of the projections.

5. Conclusion

The trawlable soft bottoms of the Mediterranean Sea host a large diversity of epibenthic megainvertebrates, including vulnerable taxa highly sensitive to bottom trawling. A better characterization of epibenthic megainvertebrate communities and their bioregional patterns was necessary to improve the efficiency of existing protection measures, such as the Fisheries Restricted Area in force deeper than 1000 m in the Mediterranean. The present study proposed a partition of the Mediterranean soft bottoms (above 1000 m) into 16 bioregions of distinct epibenthic megainvertebrate communities. A strong bathymetric gradient revealed distinct shelf and slope communities, while deep-sea communities were more similar across the sub-basins. This first attempt of epibenthic megainvertebrate bioregion mapping provided a biologically meaningful partition of the Mediterranean soft bottoms, complementing the largely used EUSeaMap habitat maps for implementing European policies. In a conservation planning context, these bioregions can support the design of representative protected area networks by ensuring a balanced distribution of conservation targets across all types of epibenthic megainvertebrate communities (Combes et al., 2021; O'Brien et al., 2022; Roberson et al., 2017). This study shows that MEDITS data can be used to obtain accurate predictions of the distribution of epibenthic megainvertebrate communities in the absence of dedicated scientific benthic surveys. However, greater sampling effort and enhanced benthic expertise on board are still required to strengthen the ecosystemic dimension of these surveys. We also emphasize the need to enhance collaboration with Southern and Eastern Mediterranean countries to achieve a truly reliable bioregionalization at the basin scale.

CRediT authorship contribution statement

Jade Millot: Writing – original draft, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Sandrine Vaz:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization. **Tarek Hattab:** Writing – review & editing. **Christopher J. Smith:** Writing – review & editing. **Carlos Dominguez-Carrió:** Writing – review & editing. **Beatriz Guijarro:** Writing – review & editing. **Grégoire Certain:** Writing – review & editing. **Vasilis Gerovasileiou:** Writing – review & editing. **Vincent Georges:** Writing – review & editing. **Caterina Stamouli:** Writing – review & editing. **Michele Casini:** Writing – review & editing. **Chiara Manfredi:** Writing - review & editing. **Emanuela Fanelli:** Writing – review & editing. **Germana Garofalo:** Writing – review & editing. **Marie-Claire Fabri:** Writing – review & editing. **Daniela Massi:** Writing – review & editing. **Angélique Jadaud:** Writing – review & editing. **Adriana Profeta:** Writing – review & editing. **Pierluigi Carbonara:** Writing – review & editing. **Evgenia Lefkaditou:** Writing – review & editing. **Slavica Petović:** Writing – review & editing. **Athanasios Evangelopoulos:** Writing – review & editing. **Nikolaos Kamidis:** Writing – review & editing. **Ioannis Thasitis:** Writing – review & editing. **Jurgen Mifsud:** Writing – review & editing. **Kelly Camilleri:** Writing – review & editing. **Valentina Lauria:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Funding acquisition, 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

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2026.107951.

Data availability

Data will be made available on request.

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