



## Distribution of rhodolith beds and their functional biodiversity characterisation using ROV images in the western Mediterranean Sea

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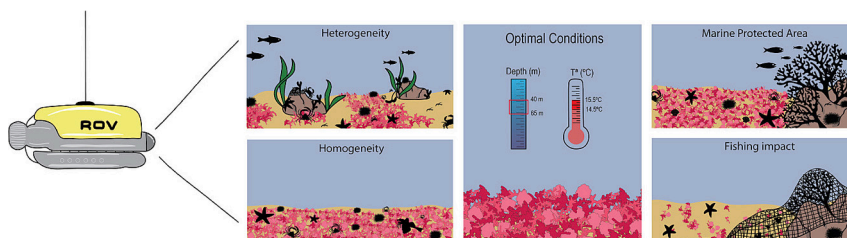
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### HIGHLIGHTS

- Video surveys showed that rhodoliths accumulate on coarse sediment bottoms.
- Relative abundance of rhodoliths was driven by depth and temperature.
- The optimal depth range for the occurrence of rhodoliths extended from 40 to 65 m while the temperature range was between 14.5 °C and 15.5 °C.
- Rhodolith beds on fishing grounds showed the lowest functional richness index.
- Functional richness was higher on heterogeneous sea-beds rather than on homogenous ones (higher  $\beta$ -diversity).

### GRAPHICAL ABSTRACT



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### ABSTRACT

Underwater biogenic habitats composed of unattached calcified red algae, named as rhodolith or maërl beds, may extant either alive or dead, over the seabed. The accumulation of rhodoliths constitute three-dimensional structured biogenic habitats that harbour high diversity of benthic organisms. In the Mediterranean Sea, rhodolith beds can be found between ca. 50 and 100 m, increasing diversity of the continental shelf habitats and their conservation value. Despite the remarkable relevance of these habitats, information regarding their spatial distribution in the western Mediterranean is scarce. In addition, these habitats are threatened by a range of anthropogenic activities and by climate-driven changes. In this study, we explored areas with rhodoliths' occurrence from the north to the south of the east coast of Spain. By feeding video recording data into a spatial distribution model, we assessed which biophysical drivers: (i) shape the spatial variation in the abundance of rhodoliths and (ii) define the assemblages of the biological traits and functional richness of the associated epibenthic fauna recorded by video. In addition, we examined the impact of fishing activities on these habitats. Our results evidenced that 'Depth' and 'Temperature' were important environmental factors explaining rhodoliths variation, and we defined their optimal distribution range in the western Mediterranean. The biological traits approach showed significant effects of the geographical location of rhodolith beds and their small-scale spatial heterogeneity on the functional richness index. Indeed, the lowest functional richness value was observed in the area closer to trawl fishing which could be related to habitat degradation due to trawling. This study contributes to the knowledge of deep-water rhodolith beds in the western Mediterranean and reinforce the importance of rhodolith beds in continental shelves as these constitute heterogeneous seabed habitats that harbour a high species and functional diversity.

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## 1. Introduction

Rhodolith beds are accumulations of living and dead unattached coralline algae that can cover large areas of the seafloor (Barberá et al., 2003; Neves et al., 2021). Also known as maërl beds (Foster, 2001), these complex habitats occur worldwide, from tropical to polar environments (Bosence, 1983; Foster, 2001). In European waters, they are found along the North-East Atlantic coast, from Svalbard to Portugal (Barberá et al., 2003; Peña et al., 2014) and in the Mediterranean Sea (Ballesteros, 1988). In the western Mediterranean, these beds occur from subtidal waters down to 100 m depth (Riosmena-Rodríguez et al., 2017), generally accumulating over soft sediments (de Juan et al., 2013).

Studies focused on the spatial distribution of rhodolith beds identify major environmental conditions which determine habitat structure, for instance, light, sedimentation, hydrodynamics (currents and wave turbulence) and temperature (Carvalho et al., 2020; Holz et al., 2020; Martín et al., 2014; Sañé et al., 2016; Sciberras et al., 2009; Wilson et al., 2004). In the European Atlantic waters, rhodolith beds occur from low intertidal waters down to 50 m depth in very clear waters (Peña et al., 2014). Nevertheless, in the oligotrophic Mediterranean Sea, the low terrestrial sediment input caused by the absence of large rivers allows sufficient light availability to reach greater depths (Ballesteros, 1989; Barberá et al., 2003; Barberá et al., 2012; Foster, 2001; Joher et al., 2016). In addition, the influence of hydrodynamics and sedimentation defines the occurrence and shape the structure of rhodoliths (Bracchi et al., 2019; Foster, 2001; Sañé et al., 2016; Sciberras et al., 2009). Water motion is key to prevent the smothering of rhodoliths by fine sediments (Joshi and Farrell, 2020; Marrack, 1999; Wilson et al., 2004). However, high water movement can translocate rhodoliths and break them up, thus constraining their distribution (Marrack, 1999; Otero-Ferrer et al., 2020). Temperature is also a key driver of the geographical distribution of rhodoliths by determining the species composition at large-scale (Wilson et al., 2004).

Rhodolith algae are widely acknowledged as ecosystem engineers and hotspots of marine life that provide structural and functional complexity and supply a variety of ecosystem functions (de Juan et al., 2023; Kamenos et al., 2004; Tuya et al., 2023). The characteristic three-dimensional hard structures of rhodoliths provide refuge and nursery for juveniles of commercial species (Costa et al., 2020; Ordines and Massutí, 2009) and create microhabitats providing shelter and food for a great diversity of macrofauna, such as molluscs, crustaceans and polychaetes (Barberá et al., 2003; Foster, 2001; Kamenos et al., 2004; Sciberras et al., 2009). Moreover, rhodolith beds, as biogenic calcareous habitats, could contribute to long-term carbon sequestration and, due to their global distribution, constitute one of the most important carbonate deposits of the world (Amado-Filho et al., 2012; Martín et al., 2005, 2007).

Despite rhodolith beds have a remarkable conservation value, numerous human activities, such as bottom trawling, effluent discharges or alien species, as well as climate change-driven impacts, threaten their ecological integrity (Barberá et al., 2017; Peña et al., 2014; Rindi et al., 2019; Riosmena-Rodríguez et al., 2017). Legislation measures have been proposed to increase their conservation status and implement fishery regulations by banning trawling activities on these habitats (i.e., Barcelona Convention Decision 1999/800/EC, and Mediterranean Fisheries Regulation EC no. 1967/2006, Order AAA/2808/2012) (Barberá et al., 2017). In addition, two maërl-forming species, that have been identified in the Mediterranean, *Phymatolithon calcareum* and *Lithothamnion corallioides*, are considered species of community interest included in Annex V of the EC Habitats Directive (Council Directive 92/43/EEC) (Wilson et al., 2004).

Shifting the focus to a regional perspective, in the western Mediterranean, the current spatial distribution and occurrence of rhodolith beds largely respond to historically fishing pressure and changes in environmental conditions (Barberá et al., 2012; de Juan et al., 2013; Wilson et al., 2004). However, the lack of current and past information about rhodolith beds distribution and small-scale heterogeneity makes the

assessment of their evolution in time difficult. Considering the scarce information available on western Mediterranean rhodolith beds, it is mandatory to define the limits of the parameters driving their distribution. Our working hypothesis is that the suitable area for rhodolith beds development over continental shelves is conditioned by a narrow range of variability of environmental factors. Therefore, the objective of the present study is to define which biophysical factors drive: (i) the abundance of rhodoliths and (ii) assemblages of the biological traits of the associated epibenthic biodiversity in rhodolith beds, as well as, their functional richness index in the east coast of Spain. In order to do so, soft bottoms with rhodoliths occurrence were explored using video recording, a non-intrusive technique that allows the acquisition of a diversity data in a continuous scale frame while minimizing habitat alteration (Bicknell et al., 2016; Hewitt et al., 2004).

Ecological models were applied to identify biophysical drivers shaping the variation in the abundance of rhodoliths identified in areas of the seabed through video transects. We applied Species Distribution Models (SDM), a useful tool in Ecology to describe the complex, often non-linear, relationships between species and their environment and build predictors of species distribution at multiple spatio-temporal scales (Elith and Leathwick, 2009; Morán-Ordóñez et al., 2017). Video techniques have also proven to be a good mechanism to extract information on the biological traits of the observed organisms through taxonomical expert knowledge (de Juan et al., 2015). Analysis of biological traits is an approach widely used in marine ecological studies to assess changes in communities as a response to environmental conditions and human impacts (i.e., bottom trawling) (de Juan et al., 2007). Biological traits approach can also be applied to unravel ecosystem functions in order to understand the functional role of species' assemblages and the consequences of alterations in a community (Boyé et al., 2019; de Juan et al., 2022). In this study, a biological-traits approach was applied to the list of species identified in the video footage to be analysed as a proxy of functional diversity associated to rhodolith beds. Finally, we examined the impact of fisheries on these habitats in the western Mediterranean.

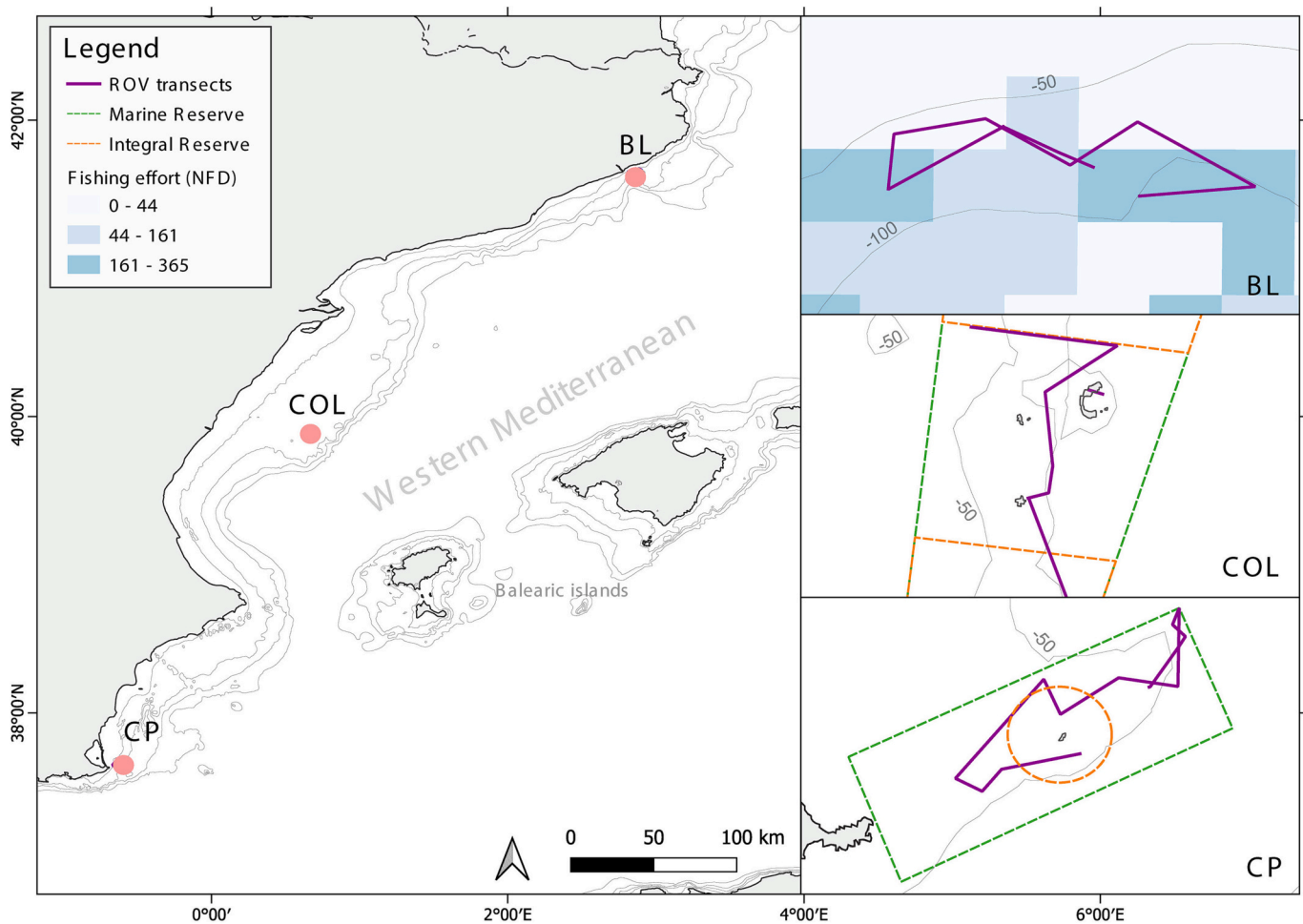
## 2. Material and methods

### 2.1. Study area

To explore the drivers of rhodoliths distribution over the western Mediterranean continental shelves, we selected three study areas located between 40 and 100 m depth, along the east coast of Spain (western Mediterranean), from north to south: Continental shelf off Blanes (BL), Columbretes Islands (COL) and Cabo de Palos e Islas Hormigas (CP) (Fig. 1). These areas were selected based on previous knowledge extracted from the research projects COMSOM, FORMED and MINOUW (de Juan et al., 2013; Demestre et al., 2017; García-de-Vinuesa et al., 2018). The study areas are in different environmental contexts along the Spanish coast, including differences in the geomorphology of the continental shelf and intensity of fishing activities. Each transect was defined according to previous knowledge from experts on potential areas of rhodoliths aggregations, besides Guillén et al. (2017) provides geomorphological information on our study areas.

The study area BL is located in the shallower area of a submarine canyon in front of the port of Blanes (Catalonia, Spain) (Fig. 1). The submarine canyon is surrounded by fishing grounds ranging from 50 m down to 800 m. Considering the wide depth range, the area has a high habitat heterogeneity, with the alternation of crinoid aggregation habitats, muddy bottoms and rhodolith beds (observations from MINOUW project). This area is a productive fishing ground, where bottom trawling is the main fishing technique (García-de-Vinuesa et al., 2018).

The study area COL is located offshore the coast of Castelló (Spain) and it is around a volcanic archipelago formed by a set of three groups of islets and one main island. This area is characterized by the presence of CO<sub>2</sub> vents between 35 and 50 m, which determines the composition of



**Fig. 1.** Map of the studied areas along the east coast of Spain in the western Mediterranean Sea. From north to south: BL: Continental shelf off Blanes; COL: Columbretes Islands and CP: Cabo de Palos. Purple line represents the transects recorded with the ROV. (BL): Fishing effort (Number of Fishing Days x boat) for the year 2018 is represented in blue. (COL) and (CP): Green and orange dotted lines delineate the marine and the integral areas of both Marine Reserve Areas, respectively.

benthic communities and habitats (Linares et al., 2015). The entire archipelago is a Marine Natural Park since 1990 (BOE n° 97, of 23rd April 1990), where no trawl fishing is allowed, but limited artisanal fishing is permitted.

The study area CP is located in the “Cabo de Palos e Islas Hormigas” Marine Reserve (Murcia, Spain). This area is found at depths between 40 and 50 m, and it is characterized by the presence of rhodolith, gravel, sands and mud (de Juan et al., 2013). The Marine Reserve was created in 1995 (BOE n° 161, of 7th July 1995), where bottom trawling is not permitted but limited artisanal fishing in the periphery of the Marine Protected Area (MPA) can be carried out. The study area encompassed the protected and nearby unprotected area around the reserve.

## 2.2. Video analysis for data acquisition

The study areas were surveyed in September 2020 using a Remotely Operated Vehicle equipped with video, ROV-LIROPUS, towed by the R/V “Sarmiento de Gamboa” along the three pre-defined transects (Fig. 1). Positioning of the ROV with respect to the sea-floor was ensured by differential Global Positioning System (GPS). The ROV was equipped with high-resolution cameras, which allowed us to record georeferenced video. It was also equipped with two lasers separated by a distance of 10 cm, that allowed the estimation of organism sizes, and with data-loggers for continuous recording of temperature (°C) and depth (m). This information allowed us to calculate slope (m/min, calculated as the depth

change per minute) and swept area per minute ( $m^2/min$ ). The ROV moved with an average speed of 0.5 knots and toured a mean of 11 km per transect, corresponding to an average of 16 h of video recording.

The video footage was visualized using the VLC media player, a free and open-source multimedia player and framework. The information of interest was the relative rhodolith coverage along the transect, the visible fauna (fishes and invertebrates) and flora (algae), and the physical characteristics of the seabed. For this purpose, two observers visualized the videos. When an organism was detected, the video was paused and the following information was annotated:

- (i) Identification and quantification of visible fauna and flora (minimum size 4 cm) at the lowest taxonomic level possible (species whenever possible).
- (ii) Estimation of rhodolith coverage: the percentage of coverage was visually determined by comparing the four levels defined. These levels were: 0 - rhodolith absence -, 1 - <25 %-, 2 -  $\geq 25 \leq 50$  %-, 3 - >50 %- (Fig. A.1).
- (iii) Description of biophysical parameters:

- **Substrate type:** Visual characterization of the sediment considering the categories: sandy, muddy sand, sandy mud, mud, mixed sediment (with the presence of gravel of different sizes and shells), coarse sediment (biogenic sand and

homogenous gravel), and rocky bottoms (rock or other hard substrata) (Fig. A.2).

- **Bottom relief:** Considered flat or with the presence of ripples (Fig. A.3).
- **Presence of rocky outcrops:** Considered when there were rocky outcrops with associated fauna or flora (Fig. A.4).
- **Presence of algal cover:** Filamentous algal covering substrate (Fig. A.4).
- **Presence of fisheries footprint,** such as lost or abandoned fishing nets or trawl tracks.

### 2.3. Data processing

The information gathered during the video visualization were grouped into 1 min interval. The quantitative variables (occurrences of each taxon) were calculated as the total sum, while for the qualitative variables such as rhodolith coverage and the biophysical parameters, the predominant category within the minute was noted. Based on this information, two data matrices were created:

#### (i) Environmental data

The environmental data matrix included the rhodolith coverage, the biophysical parameters described beforehand and the environmental variables such as depth and temperature. In this step, the substrate type variable was reduced to 4 levels -Mud, Mixed sediment, Coarse sediment and Rocky or other hard substrata-. Finally, the environmental data matrix was set up by adding a last variable:

- **Number of biotopes:** the number of biotopes that appeared when grouping observations into 1 min clusters was noted as a measure of small-scale heterogeneity. For this purpose, a biotope was counted whenever substrate composition, relief and/or rhodolith cover changed significantly.

#### (ii) Biological traits

A species density matrix was calculated for each minute as the sum of individuals per swept area ( $\text{ind}/\text{m}^2$ ). Each taxon identified in the video footage was then described considering the biological traits categories listed in Table 1. The biological traits included in the analysis were chosen for their suitability to inform on the sensitiveness of species to fishing and/or could be associated with ecosystem functions in soft bottoms (de Juan et al., 2015).

The biological traits assignment to each taxon was based on information extracted from different sources such as WoRMS (WoRMS editorial Board, 2023), Fishbase (Froese and Pauly, 2023), MarLIN (Marine Life Information Network, 2020) and its catalogue of biological traits information BIOTIC (MarLin, 2006), as well as from expert knowledge (e.g., de Juan et al., 2007; de Juan and Demestre, 2012). The

**Table 1**

List of biological traits and their levels considered to characterize large epibenthic fauna (after de Juan et al., 2015).

Biological traits	Levels
Size	Small (<1 cm), medium (1–5 cm), large (>5 cm)
Age	Annual, short, medium, long
Morphology	Arborescent, articulate, bivalved, crustose, cushion, flat, globose, stellate, turbinate, vermiform
Composition	Calcareous, chitinous, cuticle, none
Habitat	Attached, surface, subsurface
Mobility	Sessile, sedentary, crawler, swimmer
Feeding	Deposit feeder, suspension feeder, grazer, benthivorous, piscivorous, predatory opportunistic, planktivorous, primary producer

information was summarized using a binary code in a conversion matrix (i.e., trait absent or present). The taxon density matrix was multiplied by the conversion matrix to obtain the biological traits density matrix for its subsequent analysis.

Finally, the data from both matrices was assembled at 15 min intervals, considered the optimal time interval to have sufficient representativeness of taxa for statistical analysis. For each interval the mean was calculated for the numerical variables, while for categorical variables the most abundant characteristic was selected, with the exception of the variable 'Number of biotopes'. The information provided by this variable along the 15 min was classified within 3 categories: Homogeneous, a unique biotope typology within the 15 min; 2 Biotopes, – two different biotope typologies alternate in the 15 min (e.g., muddy sands and coarse sediment with <25 % rhodoliths); and, >2 Biotopes, >2 biotope typologies alternate or appear in the 15 min-.

A description of each study area was performed by calculating the percentage of area covered by substrate type and rhodolith abundance, in order to visually define the extension of substrate type and rhodolith coverage assemblages. Then, an estimation of taxonomic biodiversity was done through the quantification in percentage of the phyla and species in each area. In order to characterize the most abundant species in each area according to substrate type and rhodolith abundance, the percentages of the three species with higher density were represented.

### 2.4. Statistical analysis

#### 2.4.1. Environmental factors explaining rhodolith abundance

In order to identify the biophysical factors driving the distribution and abundance of rhodoliths over continental shelves in the study sites, we applied a species distribution model. SDMs use statistical algorithms that fit observations of species occurrence or abundance data to environmental conditions (Elith and Leathwick, 2009). The choice of statistical algorithms available to build SDMs is large, with differences in performance depending on the objective of the application (description vs prediction) (Derville et al., 2018). The model chosen was Boosted-Regression Tree (BRT) (Elith et al., 2008) a technique used to reveal important predictor variables and interactions between them (Elith and Franklin, 2017). BRT can be understood as an additive regression model in which simple tree models can be combined and fitted to provide improved predictive performance. BRTs: a) can handle different types of predictor variables (quantitative or qualitative) and accommodate missing data, and b) are able to fit complex non-linear relationships and identify interaction effects between predictors.

In order to perform the BRT model, we set 'Rhodolith abundance' as the response variable (four levels – the different levels of coverage: 0, <25 %, <50 % and >50 %). The explanatory variables considered were three categorical variables: 'Location' (three levels – the surveyed localities: BL, COL, CP), 'Relief' (two levels: Flat or Ripples), 'Substrate' (four levels – different types of substrate with more than two observations: Mud, Mixed sediment, Coarse sediment and Rocky or other hard substrata), two logical variables: 'Rocky outcrops' and 'Fishing' (two levels: Presence or Absence) and four numerical variables with 'Depth (m)', 'Temperature (°C)', 'Slope (m/min)' and 'Area ( $\text{m}^2/\text{min}$ )' (Table 2).

The model was fitted to a Poisson distribution for the response variable, using the pooled data from the three localities. For our analysis, the initial tree complexity values were 3, 4, 5, 6, 7 with learning rates values of 0.0005, 0.001, 0.005, 0.01, 0.05. We selected the optimal settings of the model by means of the number of trees (minimum of 1500 trees) and the lowest deviance coefficient (for detailed methodology and model selection criteria, Elith et al., 2008). The outputs of the model showed the contribution of each environmental variable to the overall performance of the model and helped produce partial dependency plots for each predictor (Carvalho et al., 2020). BRT models were fit using the R package 'Dismo' (Hijmans et al., 2022).

**Table 2**

Explanatory variables used in the statistical analysis: BRT, multivariate model and GLM. The environmental variables were quantitative, all other variables were categorical.

Biophysical parameters	Levels			
Location	BL	COL	CP	
Rhodolith coverage	Absence	<25 %	≥25 ≤ 50 %	>50 %
Relief	Flat	Ripples		
Substrate	Mud	Mixed sediment	Coarse sediment	Rocky or other hard substrata
Number biotopes	Homogeneity	2 Biotopes	>2 Biotopes	
Algal cover	Presence or absence			
Rocky outcrops				
Fishing				
Environmental	Depth (m)	Temperature (°C)	Slope (m/min)	

## 2.4.2. Biological traits

**2.4.2.1. Multivariate model.** In order to visualize the important biophysical factors explaining the variability in biological traits composition in soft-bottoms associated with rhodoliths, the biological traits density matrix was displayed through a Canonical Correspondence Analysis (CCA), based on Jaccard Distance, from the R package ‘vegan’ (Oksanen et al., 2022). Moreover, a multivariate regression model was fit using the R package ‘mvabund’ (Wang et al., 2022).

For the multivariate regression model, the biological traits density was set as the response variable, while the explanatory variables were five categorical variables: ‘Location’ (three levels – the surveyed localities: BL, COL, CP), ‘Rhodolith abundance’ (four levels – the different levels of coverage: 0, <25 %, <50 %, >50 %), ‘Relief’ (two levels: Flat or Ripples), ‘Substrate’ (four levels – different types of substrate with more than two observations: Mud, Mixed sediment, Coarse sediment and Rocky or other hard substrata) and ‘Number biotopes’ (three levels – Homogeneity, 2 Biotopes or >2 Biotopes); three logical variables: ‘Algal cover’, ‘Rocky outcrops’ and ‘Fishing’ (two levels: Presence or Absence) and three numerical variables with ‘Depth (m)’, ‘Temperature (°C)’ and ‘Slope (m/min)’ (Table 2).

With the same biological traits matrix, a “fourth-corner” analysis (Brown et al., 2014; Warton et al., 2015) was performed to examine the influence of biological traits on the interaction between the abundance and environmental matrices. To determine which environmental and trait variables to include in the analysis, we followed the model-based approach described in Brown et al. (2014), using the method of least absolute shrinkage and selection operator (LASSO, Hastie et al., 2009) based on penalized likelihood. The analysis was conducted with the function *traitsglm* of the R package ‘mvabund’ (Wang et al., 2012), using the negative binomial as distribution function for the response matrix (taxon abundance).

**2.4.2.2. Functional richness.** The functional richness was calculated based on the matrix of biological traits density, for the species assemblages identified, using ‘*specnumber*’ function from package ‘vegan’ (Oksanen et al., 2022). This measure is a count of the number of different traits in a given sampling unit, in our case the functional richness index is representing only the biological traits diversity of visible benthic fauna identified in each 15 min video footage intervals.

We explored the effect of environmental variables on functional richness by performing a generalized linear model (GLM) from the R package ‘stats’ (R Core Team, 2022). The stepwise approach for the selection of the best model consisted in running a full GLM with ‘Richness index’ introduced as the response variable and including all biophysical parameters as the explanatory variables (Table 2). The model was fitted to a Poisson distribution. Removal of all non-significant factors was done with function ‘*stepAIC*’ from the R package ‘MASS’ (Venables and Ripley, 2002). We followed a backwards model selection based on the lowest AIC. The explanatory variables that remained, at the selected model, were ‘Location’ (three levels – the surveyed localities: BL, COL, CP), ‘Number biotopes’ (three levels – Homogeneity, 2 Biotopes or >2

Biotopes), ‘Algal cover’ and ‘Rocky outcrops’ (two levels: Presence or Absence) and ‘Depth (m)’. A posterior post-hoc analysis was performed with variable ‘Location’ from the R package ‘emmeans’ (Lenth, 2022).

All analyses were computed in R (R Core Team, 2020) under version 4.2.1.

## 3. Results

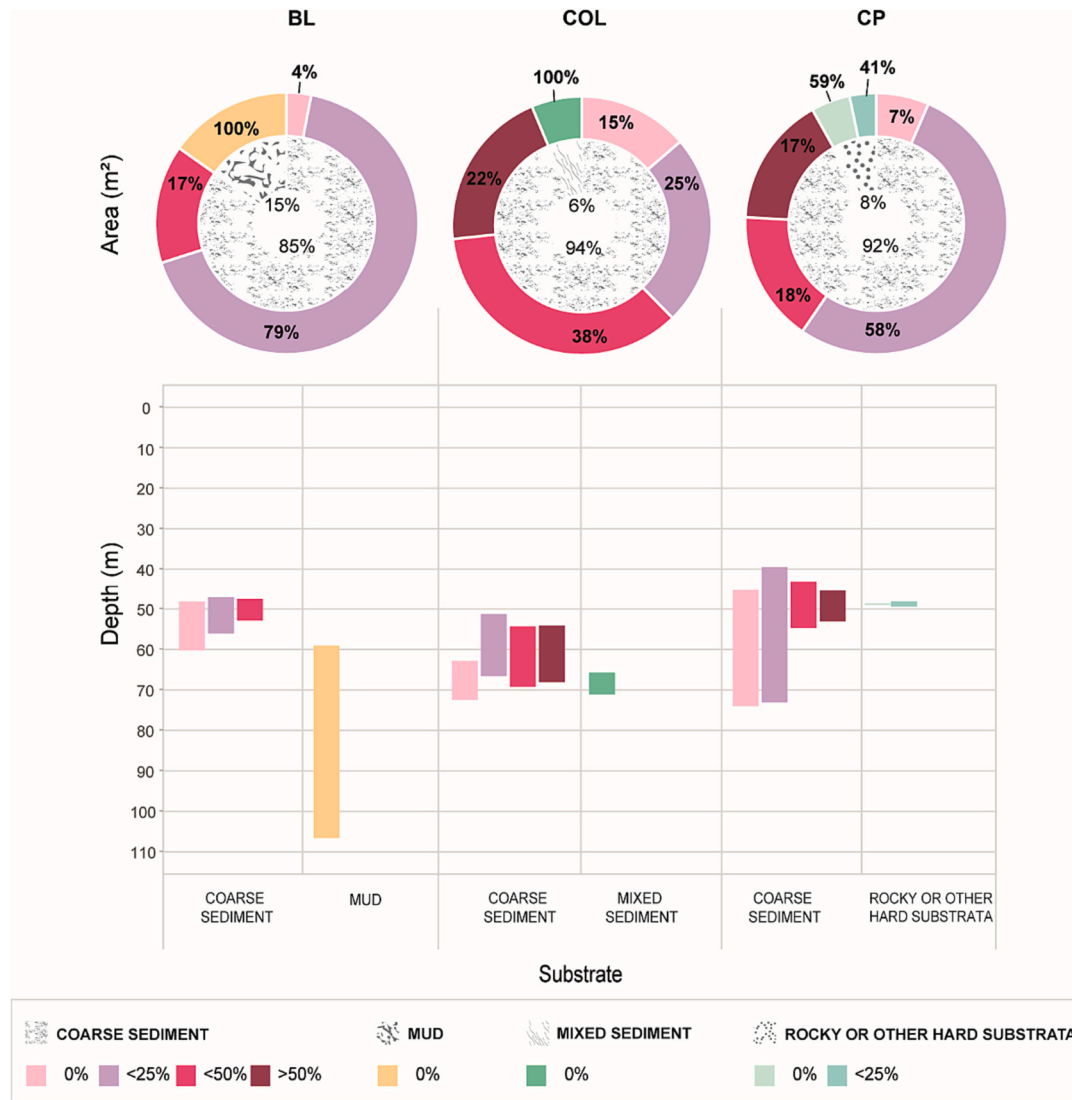
### 3.1. Physical and biological description of the sites

The video transects in the three study sites resulted in 53 h – 17 h in BC and COL and 19 h in CP- of footage over ca. 39,780 m<sup>2</sup> of survey, of which around 13 % were coralligenous rocks. This substrate was removed from the dataset as it is characterized by coralline crustose algae, not the objective of our study. Considering the remaining video footage, a total of 34,215 m<sup>2</sup>–12,580 m<sup>2</sup> in BC, 12,321 m<sup>2</sup> in CP and 9314 m<sup>2</sup> in COL-, we identified a total of 119 different organisms, belonging to eight phyla (Annelida, Arthropoda, Bryozoa, Chordata, Cnidaria, Echinodermata, Mollusca and Porifera), of which around 60 % were identified to species level. In terms of abundance, the phylum most represented in the total video footage were echinoderms with *Spatangus purpureus* (36.2 %) and *Echinaster sepositus* (13.7 %).

The site BL is characterized by biogenic sand and gravel, which represents 85 % of the area explored. About 25 % of this area, restricted to 46–56 m depth, had scattered rhodoliths (Fig. 2). Another important substrate identified in BL were muddy areas deeper than 60 m, with no evidence of rhodoliths. The most abundant species in this study area were the starfish *Echinaster sepositus* (32 %), and aggregated sponges (Porifera) (22 %), particularly found at low (<25 %) or null rhodoliths coverage in coarse sediment (Fig. 3).

The main substrate covering COL is biogenic sand and gravel with a 93 % of coverage; the remaining 7 % is covered by mixed sediments without the presence of rhodoliths (Fig. 2). Rhodolith beds were observed in the 52–68 m depth range within coarse sediment areas. In COL there was a larger extension of rhodoliths, with an abundance over 50 % detected in 22 % of the area. Considering the species’ densities, the dominant species along the transect was the echinoid *Echinaster sepositus* (23 %) and species from the phylum Porifera (17 %) (Fig. 3). Crinoids are characteristic of muddy bottoms, they represented 19 % of the density, in coarse sediment with rhodoliths coverage <50 %. Finally, it is worth to highlight the specific diversity found associated with mixed sediments without rhodoliths: fish density (6.23 %) and the presence of sessile cnidaria e.g., *Pennatula phosphorea* and *Veretillum cynomorium*.

The site CP is covered in 92 % of the area by biogenic sand and gravel, whereas the remaining 8 % is characterized by the presence of rocks and other hard substrata (Fig. 2). In this rocky substrate the presence of rhodoliths is scarce, representing <25 % of the coverage. However, in coarse sediments from 40 m to 73 m depth, there is a notorious presence of rhodoliths, with variable abundance from 0 % to >50 %. In this area, a high density of rhodoliths (>50 %) is present in 17 % of the surveyed area. Considering the species densities in CP we highlight important aggregations of the sea urchin *Spatangus purpureus*



**Fig. 2.** Characterization of the substrate types and rhodolith abundance for each studied area. Top: Pie charts represent the percentage of area (%) covered by different levels of rhodolith coverage (outer donut) according to the predominant substrate type (inner donut) at each study site. Bottom: Depth (m) range occupied by different levels of rhodolith coverage according to the predominant substrate type at each study site. From left to right: BL. Continental shelf off Blanes; COL. Columbretes Islands; CP. Cabo de Palos.

(49 %) at sites with rhodoliths presence (<25 % to >50 %), followed by lower densities of the starfish *Echinaster sepositus* (8 %) (Fig. 3). At sites with low or null rhodolith coverage and in rocky substrates, the predominant species belonged to Porifera. Furthermore, in rocky outcrops, we highlight the presence of demersal fish (2.76 %) and the hydrozoan *Nemertesia antennina* (1.62 %).

A completed list of the organisms identified is provided in Appendices (Table A.1), as well as a set of ROV images (Fig. A.5).

### 3.2. Environmental factors explaining rhodolith abundance

According to the BRT model (with a tree complexity equal to 6 and a learning rate of 0.001), the two main environmental factors explaining rhodolith abundance were ‘Depth’ and ‘Temperature’, explaining 24 % and 23 % abundance variation, respectively (Fig. 4). The other biophysical parameters considered (e.g., Location, relief, substrate) contributed less to the variation explained. ‘Location’ explained 9 % of the variation, and represented the highest contribution of a categorical variables.

The normalized partial response of rhodolith abundance for the

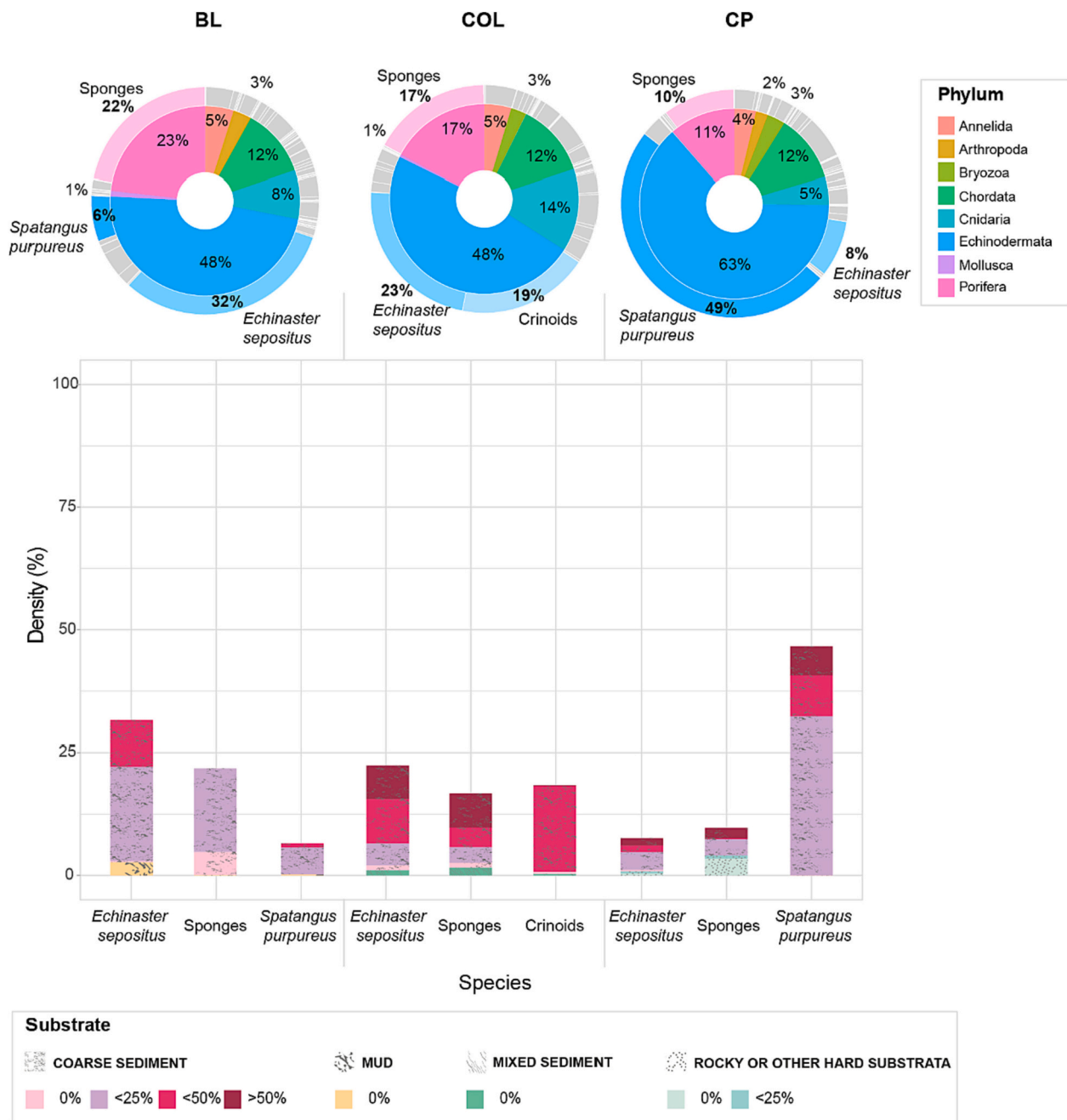
quantitative variables with highest contribution (depth, slope and temperature) indicated the optimal ranges for rhodolith cover in terms of relative abundances (Fig. 4). Across the three study sites, the relative rhodolith abundance was higher at depths between 40 and 65 m, while at deeper sites its abundance was drastically reduced. Higher rhodolith cover was found around slope values of 0 to 0.35 (m/min), i.e., rhodoliths tend to accumulate in flat places. Finally, temperatures around 14.5 °C were linked to a rapid increase in relative abundance of rhodoliths, but its abundance started to decrease after 15.5 °C.

Considering the categorical variables ‘Location’ and ‘Substrate’, with an explained variation of 9 % and 6 % respectively, the highest relative abundance of rhodoliths was found in COL and on bottoms dominated by coarse sediment. The lower relative rhodolith abundance was found in BL and, for ‘Substrate’, in muddy bottoms (Fig. 4).

### 3.3. Biological traits

#### 3.3.1. Multivariate model

The CCA biplot (Fig. 5), explained about 30 % of the variance of the assemblage structure. The main variables expressed in the CCA were

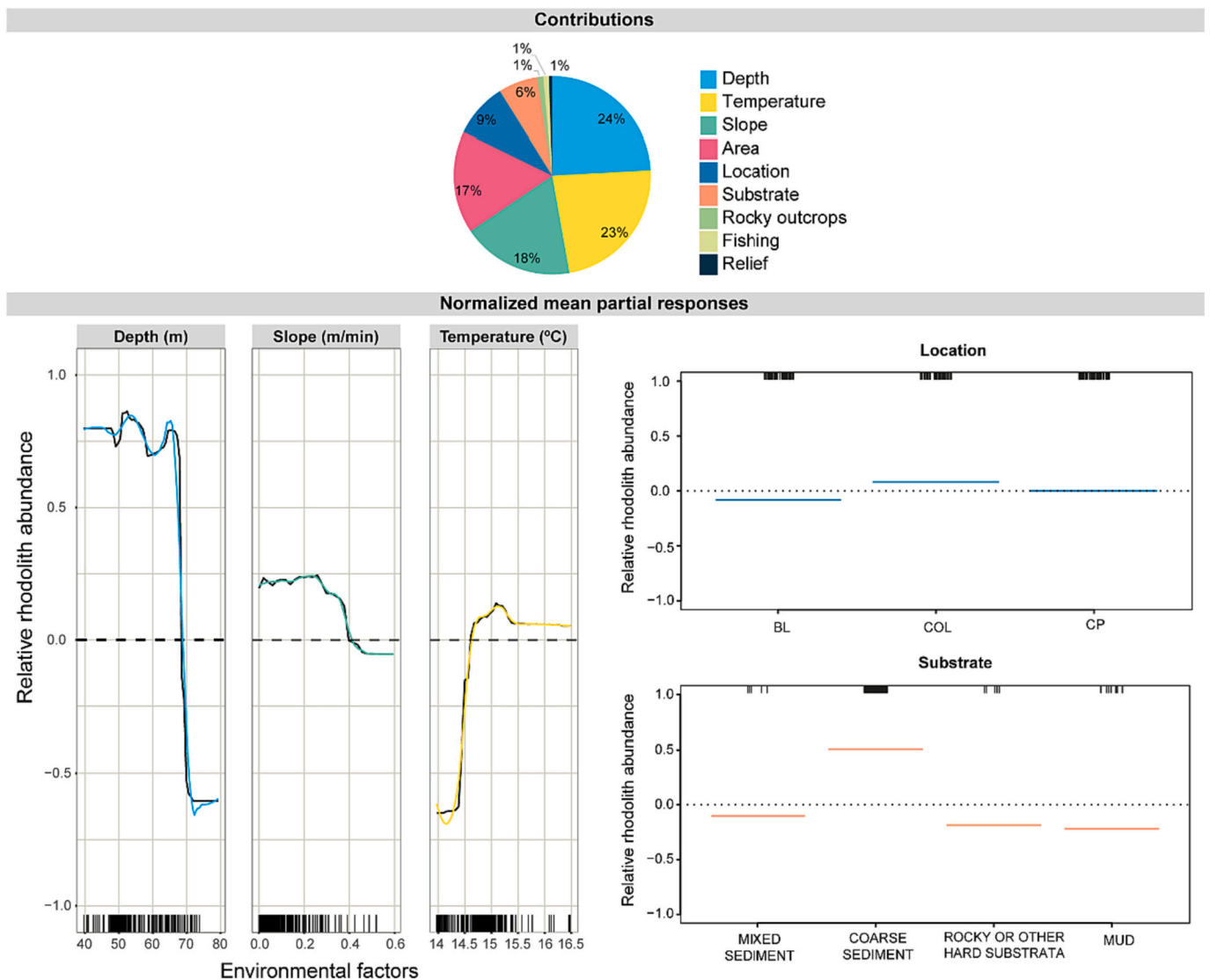


**Fig. 3.** Species composition according to substrate type and rhodolith abundance for each studied area. Top: Pie charts represent the percentage (%) of each phylum (inner donut) and the 3 species with higher density (outer donut) at each study site. Bottom: Bar plot represent the densities of the three most abundant species found at different levels of rhodolith coverage according to substrate type at each study site. From left to right: BL. Continental shelf off Blanes; COL. Columbretes Islands; CP. Cabo de Palos.

‘Location’, ‘Algal cover’, ‘Rocky outcrops’ and ‘Depth’, which defined some ecological groups according to biological traits distribution. Globose morphologies with grazing as a feeding strategy (e.g., represented by a grazing sea urchin), were aligned with CP station where algal cover was the highest. In addition, cushion and arborescent morphologies that live attached on the substrate, and characterized by suspension feeding strategy (e.g., from sponges or gorgonians), overlapped with the presence of rocky outcrops and hard substrate.

In the multivariate regression model the biophysical parameters explained 43 % of the biological traits’ composition. The variables that had a significant explanatory power were: ‘Location’, ‘Rhodolith abundance’, ‘Temperature’, ‘Algal cover’, ‘Fishing’, ‘Substrate’, ‘Rocky outcrops’ and ‘Number biotopes’ (Table 3). In addition, the multivariate

model of the interaction between species’ traits and environmental variables fit with the LASSO algorithm converged after 25 iterations (AIC = -4874.12), compared to the null model of no interaction (AIC = -4775.33). This result suggests that the species variability as response to environmental factors was significantly mediated by trait variables. Similar to the CCA results, the environmental factors selected were ‘Location’, ‘Algal cover’, ‘Rocky outcrops’ and ‘Depth’. The scaled coefficients of the species traits and environment interactions (Fig. A.6) show that most functional traits had relatively low influence on the power of environmental traits to explain the abundance of taxa. “Sessile” organisms were overrepresented in Rocky outcrops, while “crawlers” increased with depth and was less frequent in one of the sites, CP. The habitat trait “attached” was more prevalent in BL, area characterized by



**Fig. 4.** Results of the selected *Boosted Regression tree* model. Top: Variance contribution of the explanatory variables in the abundance of rhodoliths. Bottom: Plots of the normalized partial responses of the relative abundance as a function of the quantitative variables of Depth (m), Slope (m/min), Temperature (°C) and the two main qualitative variables: Location and Substrate. Mean relative abundance of rhodoliths is represented by 0. Higher values represent relative abundances higher than the mean and lower values represent lower relative abundances than the mean. *Black line*: BRT result; *colored line*: smothered BRT result to facilitate visualization.

the presence of sponges and gorgonians, than in COL and neutral in CP. However, “attached” tended to be underrepresented in areas with presence of rocky outcrops, due to presence of *Calliactis parasitica* and *Suberites domuncula* in BL, which are organisms attached to hermit crabs (Fig. A.6). Long-lived organisms were more common in sites with high algal cover, whereas larger organisms were more common in the shallower site CP and decrease their presence with depth.

### 3.3.2. Functional diversity

The most parsimonious GLM included the following biophysical factors: ‘Location’, ‘Depth’, ‘Algal cover’, ‘Rocky outcrops’ and ‘Number biotopes’, which explained 34 % of the variance of the functional richness index (Table 3). The most significant factors were ‘Location’ and ‘Number biotopes’. Functional richness values from CP were higher than in COL and BL, i.e., there was a higher number of different traits in CP. Nevertheless, the post-hoc analysis revealed non-significant differences between functional richness values in the two protected study sites (CP vs COL) or between COL and BL, while there were significant differences between CP and BL (Fig. A.7). Regarding the effect of ‘Number biotopes’

as an approximation of small spatial heterogeneity, an increase in the functional richness index was observed from one to two biotopes. However, when the number of biotopes was higher than 2, the functional richness value decreased (Fig. A.7).

## 4. Discussion

Our results show that, in agreement with other studies (Carvalho et al., 2020; Fragkopoulou et al., 2021), the relative abundance of rhodoliths is driven by depth and temperature. Depth, which directly conditions light availability, determines the presence and abundance of red algae and the rhodoliths forming species. In the North Atlantic, rhodolith beds have been identified from the intertidal down to 60 m depth (Hernandez-Kantun et al., 2017; Otero-Ferrer et al., 2020; Peña et al., 2014), while in the oligotrophic Mediterranean waters they can reach 100 m (Ballesteros, 1989; Basso et al., 1996). In our study site, a higher abundance of rhodoliths was observed in a narrow temperature range, 14.5–15.5 °C, decreasing rhodolith abundance at higher temperature. These results correspond to the upper temperature range

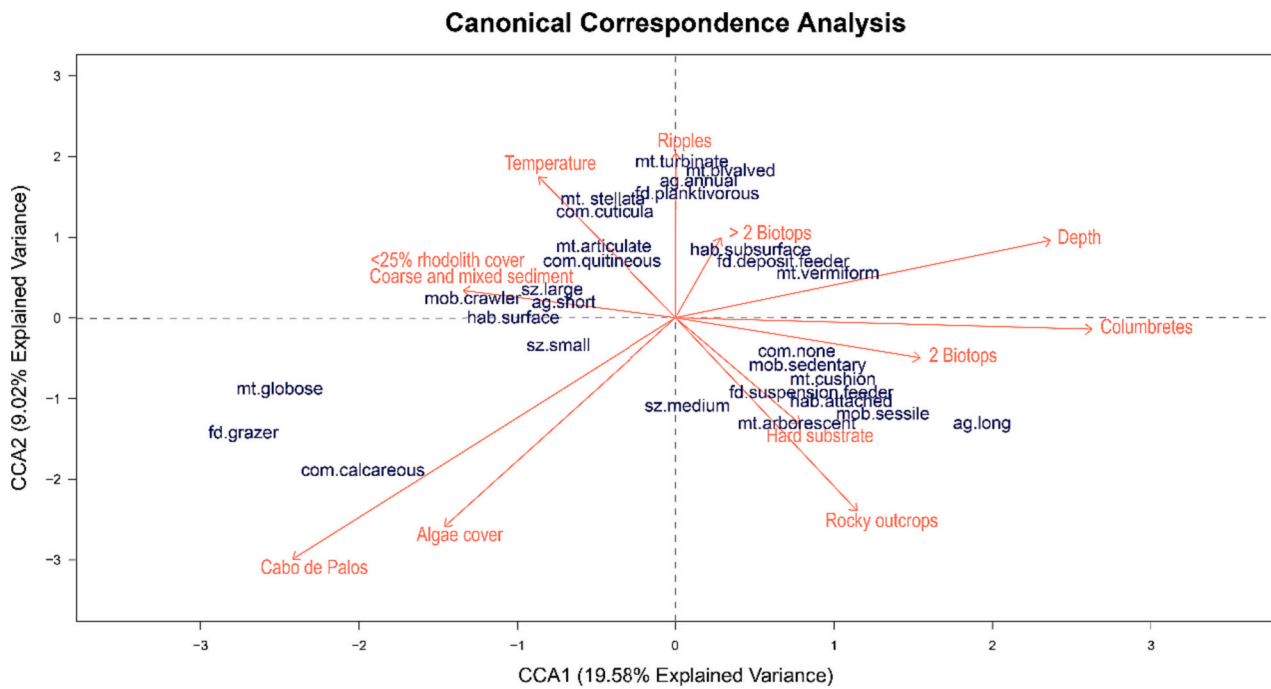


Fig. 5. Canonical Correspondence Analysis showing the position of different biological traits (blue) according to different biophysical parameters and Location (red arrows).

Table 3

Results of the statistical models applied to the multivariate biological traits matrix (top) and to functional richness index (bottom).

Model	Response variable	Explanatory variable	Df	F-value	P-values
Many LM	Biological traits	Location	2	802.2	<0.01
		Rhodolith coverage	3	138.8	<0.01
		Temperature	1	134.6	<0.01
		Depth	1	51.7	0.152
		Slope	1	53.0	>0.05
		Algal cover	1	150.8	<0.01
		Relief	1	28.8	>0.05
		Fishing	1	136.3	<0.01
		Substrate	3	180.9	<0.01
		Rocky outcrops	1	318.9	<0.01
		Number biotopes	2	110.5	<0.01
GLM	Functional richness index	Location	2	150.18	<0.001
		Depth	1	149.18	>0.05
		Algal cover	1	147.76	>0.05
		Rocky outcrops	1	143.06	<0.05
		Number biotopes	2	133.29	<0.01

observed in North Atlantic waters, with similar species composition distributed in shallower waters (9.6–17.6 °C, Martin et al., 2007). Nevertheless, a study in the Mediterranean reported shallow water rhodolith beds, exposed to seasonal warm temperatures as high as 25 °C (del Río et al., 2022).

On the other hand, substrate composition had relatively lower importance in the BRT analysis. However, it might be an important factor at a small spatial scale. Sediments composed of sand and coarse fractions favor the development of extensive rhodolith beds with higher coverage, often interspersed with patches of lower abundance. This patchy habitat supports higher diversity than a homogenous high rhodolith coverage (Boyé et al., 2019; de Juan et al., 2023). On the other hand, the presence of fine sediments, i.e., mud or muddy sands, restricts

the occurrence of rhodoliths. In fine sediments the burial of red calcareous algae due to sediment resuspension leads to the death of the specimens; this is a consequence to the lack of light irradiance and a reduction of the water movement around rhodoliths that could reduce gaseous exchange (Wilson et al., 2004). Accordingly, hydrodynamics arises as a determinant factor for rhodoliths establishment. Currents must be intense enough to prevent the burial of rhodoliths by fine particles (Tauran et al., 2020), thus avoiding suffocation of rhodoliths. Conversely, areas with high hydrodynamics are not suitable for the settlement of rhodoliths, because wave-induced turbulence breaks rhodoliths up or sweep them outside suitable areas for rhodolith beds development (Marrack, 1999; Foster, 2001). Therefore, a delicate balance of water movement is required for the correct development of areas with a high abundance of rhodoliths (Joshi and Farrell, 2020).

Our study evidenced, that the role of fisheries footprint, e.g., trawl tracks or lost fishing gear, was apparently minor in driving rhodoliths abundance. However, when comparing rhodoliths relative abundance across the three study sites, BL was the site with lower overall rhodolith abundance, which is currently subjected to commercial trawling activities. Cabanellas-Reboredo et al. (2017) and Barberá et al. (2017) reported that off Columbretes islands (close to our COL study site) a 6-year trawl ban resulted in different morphologies and sizes of two rhodolith forming algae. However, their results did not provide evident signs of enhanced rhodolith coverage compared with adjacent areas under a longer (25 year) fish ban. Similarly, Farriols et al. (2022) discussed that recovery of rhodolith beds from trawl impact may not be evident after a 3-year ban. These results are not surprising considering the slow growth of rhodolith-forming species (ca. 1 mm per year) (Blake et al., 2007). A study previously conducted in the CP site observed a high rhodolith coverage within no-trawling areas compared to open areas (de Juan et al., 2013). Furthermore, the biodiversity associated to rhodolith beds can also be affected by trawling and dredging, resulting in changes in species composition, dominance patterns and abundance of more sensitive species (Mangano et al., 2013; Ordines et al., 2007; Tauran et al., 2020).

Rhodoliths provide shelter for small organisms within its structure, especially the branched forms, and serve as fixation points for epiphytic

algae and epibenthos, harbouring a rich microbiome (Carvalho et al., 2020; Cavalcanti et al., 2018; Fredericq et al., 2019). For instance, Boyé et al. (2019) showed that in well-preserved rhodolith beds in the Brittany coast niche diversity and functional redundancy is promoted. Indeed, alternation of biogenic and sand habitats promotes a high species diversity at the seascape, including habitat-generalists and habitat-specialist species (de Juan et al., 2023). In our study, we focused on functional richness, which links species composition with the potential ecological functions associated to rhodolith beds (de Juan et al., 2022), and observed significantly higher functional richness in the two protected study sites (CP and COL). However, functional richness was highest in patchy biotopes consisting in two types of substrates. This result reinforces the ecological notion that heterogeneous seabed habitats might harbour higher diversity ( $\beta$ -diversity) than purely homogeneous habitats (de Juan et al., 2013).

The two MPAs (CP and COL) had distinctive ecological groups with different functional roles (Fig. 5). The CP MPA was characterized by species with a high bioturbation capacity that may contribute to rhodolith mixing in the surface sediment while feeding on other benthic organisms like abundant algal cover (Sciberras et al., 2009). In the other hand, COL MPA had a high presence of sessile suspension feeders that increase the three-dimensional habitat complexity, providing refuge for benthic species and fish juveniles.

Notwithstanding the importance of video surveys to investigate deep-water habitats at small scale (Kuhnz et al., 2022), we acknowledge important limitations of the technique.

The taxonomic inventory reported by visual censuses based on data from remote video observation was inevitably biased towards larger specimens of those conspicuous species. For instance, we obtained high density values for echinoderms (*Spatangus purpureus* and *Echinaster sepositus*) and sponges, similar to those species found in another deep-water rhodolith bed in the Mediterranean Sea (Barberá et al., 2012; Bracchi et al., 2019). In contrast to low density values for other epifaunal invertebrates (e.g., *Pennatula phosphorea*, *Veretillum cynomorium*, *Nemertesia antennina*), fishes and practically no representation of crustaceans. Therefore, it is important to complement visual censuses with other non-intrusive sampling techniques, such as eDNA (Boulanger et al., 2021), which may help providing a more complete view of the biodiversity present on rhodolith beds.

## 5. Conclusions

The present study is an important contribution that generates baseline knowledge on deep-water rhodolith beds in the western Mediterranean Sea. The continuous non-intrusive video survey of the seafloor was essential to characterize the small-scale heterogeneity of rhodolith beds and their associated functional biodiversity. This study reinforces the link between rhodolith occurrence and abiotic drivers, such as depth and temperature and proposed an optimal environmental range for rhodoliths' occurrence in the east coast of Spain. In this area, rhodolith beds extend from 40 to 65 m depth, are more common on thick substrates and in a temperature range between 14.5 °C and 15.5 °C. Fishing activity limits the extent of these bottoms. However, there are potentially key factors in the distribution of rhodoliths, such as bottom current or suspended sediment, which were not taken into account in this study, reflected by the percentage of variance not explained by our models. Other external factors such as nutrient inputs, invasive species, or limitations in ecological connectivity between seafloor areas may also limit whether or not rhodolith extension is possible. These current gaps in the knowledge of Mediterranean maërl bed occurrence encourages scientific efforts to understand the ecological and functional importance of these habitats in the region.

## CRedit authorship contribution statement

**Laia Illa-López:** Conceptualization, Methodology, Formal analysis,

Writing – original draft, Writing – review & editing, Visualization. **Andrea Cabrito:** Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing, Visualization. **Silvia de Juan:** Conceptualization, Writing – review & editing. **Francesc Maynou:** Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing. **Montserrat Demestre:** Conceptualization, Methodology, Writing – review & editing, Funding acquisition.

## 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.

## Data availability

Data will be made available on request.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.167270>.

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