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# Coralligenous assemblages of continental shelf: Multiple spatial scale variability in the western Sardinia

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ABSTRACT

Mediterranean mesophotic hard bottoms are mostly characterized by coralligenous banks. Although investigations on this habitat have increased in the last years, knowledge about its structure and spatial variability is still very limited as most studies are focused on the description of assemblages of peculiar and small locations such as biodiversity hotspots. This study aimed at i) describing coralligenous megafauna on the western Sardinian continental shelf between 80 and 120 m of depth, ii) assessing the distribution of the dominant taxa, and iii) estimating patterns of spatial variability at different scales. The coralligenous banks were studied along five sectors of the western Sardinian continental shelf by means of Remote Operated Vehicles (ROVs) and images were analyzed to identify the main taxa or morphological groups and their abundance. Results highlighted several common patterns among sectors, with assemblages dominated by the gorgonians *Eunicella cavolini* and *Callogorgia verticillata*. On the other hand, some taxa (e.g. *Callogorgia verticillata*, *Paramuricea hirsuta, Antipathella subpinnata, Corallium rubrum Paramuricea clavata*, *Poecillastra compressa* and *Aplidium* spp.) mainly contribute to segregate the coralligenous assemblages within the considered sectors of this study. A high small-scale variability was also observed. The presence of extensive and well diversified mesophotic animal forests stresses the importance to improve the conservation of the western Sardinian continental shelf.

## 1. Introduction

Mesophotic environments are a major part of the continental shelves and represent a key transition zone between shallow and deep systems (Lesser et al., 2009). The assemblages distributed in the mesophotic zone are extremely rich and diverse, hosting complex three-dimensional organisms over biogenic and rocky reefs both in tropical (Lesser et al., 2009; Kahng and Kelley, 2007; Locker et al., 2010) and temperate environments (Sink et al., 2006; James et al., 2017). In the Mediterranean Sea, the mesophotic zone stands from the depth of 1% surface irradiance down to the deepest extent of benthic primary producers. Thus, while varying according to water transparency, the upper and the lower limits are commonly reported between 50-60 and 120–150 m of depth, respectively (Cerrano et al., 2019). Mediterranean mesophotic hard bottoms are characterized by coralligenous reefs, biocenotic complex habitats generating tridimensional biogenic structures, mainly produced by the accumulation of calcareous encrusting algae growing in reduced light conditions (Ballesteros, 2006). They are monumental bioconstruction of the Mediterranean Sea, contributing to seascape formation through geomorphological changes of the seafloor (Bracchi et al., 2017). Coralligenous reefs are one of the most relevant Mediterranean habitats for the wide distribution, biodiversity and role in carbonate production and balance of $CO_2$, and they are considered among the habitats of European Community interest, included in Barcelona Convention (against pollution in the Mediterranean Sea), in the Habitat Directive (E.C., 1992) and in the Marine Strategy Framework Directive (E.C., 2008).

Two main coralligenous types are known, cliffs and banks. The former develops in shallower waters (about 20–50 m) on vertical/subvertical rocky substrate and the latter is built over horizontal substrates below 40–50 m depth, also on detritic bottoms (Ballesteros, 2006). Most of the deep coralligenous habitats consist in banks (Ballesteros, 2006;

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Bracchi et al., 2015), which are widespread on large portions of the Mediterranean continental shelf (Cerrano et al., 2019). They are characterized by a high biodiversity, in some cases, dominated by large arborescent anthozoans building outstanding three-dimensional animal forests, called coral gardens, which host a rich invertebrate and fish fauna (Cerrano et al., 2010; Bo et al., 2014b; Grinyó et al., 2016; Gori et al., 2011, 2017).

The assemblages of coralligenous banks are composed by long-lived engineering species exhibiting slow growth rate and high sensitivity to environmental alterations (Cerrano et al., 2019), which make this habitat highly vulnerable (Angiolillo et al., 2015). The main threats for this habitat are the mechanical damages produced by trawling (Bo et al., 2014a; Ferrigno et al., 2018a, 2021; Enrichetti et al., 2019a), by increased sedimentation rates (Ferrigno et al., 2018a; Piazzi et al., 2019b), and by accumulation of solid waste and debris (Angiolillo et al., 2015; Casoli et al., 2017). Sediment resuspension caused by trawling can decrease light irradiance and cover sessile organisms (Althaus et al., 2009), threatening large banks in most of Mediterranean continental shelves (Ferrigno et al., 2018a).

Coralligenous cliffs have been extensively investigated and information about biodiversity (Casas-Güell et al., 2015, 2016; Doxa et al., 2016), spatial variability (Piazzi et al., 2004, 2016) and effects of human pressure (Kipson et al., 2011; Piazzi et al., 2012, 2019a; Betti et al., 2020) are available. On the contrary, banks have received little attention, likely because they are less accessible (Gori et al., 2017). In recent years, the improvement of technical tools for inspection survey (e.g. acoustic devices and Remote Operated Vehicles) and the inclusion of coralligenous reefs within the European Directives (Cánovas-Molina et al., 2016; Ferrigno et al., 2017; Enrichetti et al., 2019b), have led to an increase of investigations focused on the biogenic banks of the continental shelf (Bo et al., 2011, 2015; Aguilar et al., 2018; Santín et al., 2018; Enrichetti et al., 2019c; Appolloni et al., 2020; Idan et al., 2021; Bialik et al., 2022). However, scientific knowledge is still limited, and banks distribution and assemblage structure are unknown for large areas of the Mediterranean Sea. Moreover, most of the studies have focused on assemblage descriptions within biodiversity hotspots, such as shoals and continental shelf edge (Bo et al., 2011, 2012; 2014b), while patterns of spatial variability at large scale of coralligenous banks are little known (Ferrigno et al., 2018b; Enrichetti et al., 2019c). Identifying relevant scale of assemblage structures' variations allows determination of an appropriate sampling spatial scale. This is crucial in monitoring programs and environmental impact studies, especially for priority habitats which need to be investigated within international legislations (Piazzi et al., 2016).

In Sardinia (Western Mediterranean Sea) coralligenous cliffs have been investigated in several coastal areas down to 40 m of depth (Bianchi et al., 2007; Ponti et al., 2014; Piazzi et al., 2018, 2021a; Canessa et al., 2020; Ceccherelli et al., 2020; Pinna et al., 2021) and assemblages of hard substrata on the continental margin, between 150 and 200 m, have been described (Bo et al., 2015; Cau et al., 2015, 2017a, b,c). The presence and distribution of coralligenous banks have been recently mapped on a large part of the continental shelf (De Falco et al., 2022). However, only little information is available about the assemblage structure of Sardinian mesophotic environments (Simeone et al., 2014).

This study aimed at contributing to the knowledge of coralligenous banks i) describing coralligenous megafauna on the western Sardinian continental shelf between 80 and 120 m depth, ii) assessing the distribution of the dominant taxa, and iii) estimating the patterns of spatial variability at different scales.

## 2. Material and methods

In the western Sardinia, mesophotic coralligenous banks develop on a surface of several hundreds of $km^2$ between 50 and 170 m of depth, mostly associated to rocky outcrops which, in turn, are related to the morpho-tectonic features of the continental shelf (De Falco et al., 2022). This study was focused on the 80–120 m deep banks of the western Sardinia where five sectors were selected: Bugerru (BUG), Catalano (CAT), Bosa (BOS), Alghero (ALG), and Asinara (ASI) (Fig. 1). Each sector corresponds to about 50 km of coastline. In each sector, three random sites corresponding to about 5 km of coastline were considered and in each site two transects 100 m long were sampled through Remote Operated Vehicles (ROVs). Overall, 30 transects for a total of 3000 m of seabed were surveyed. ROVs (Pollux 3 and Velociraptor) were equipped with a high-resolution camera and an acoustic positioning system for geo-localization of the video images. ROV moved along linear tracks, in

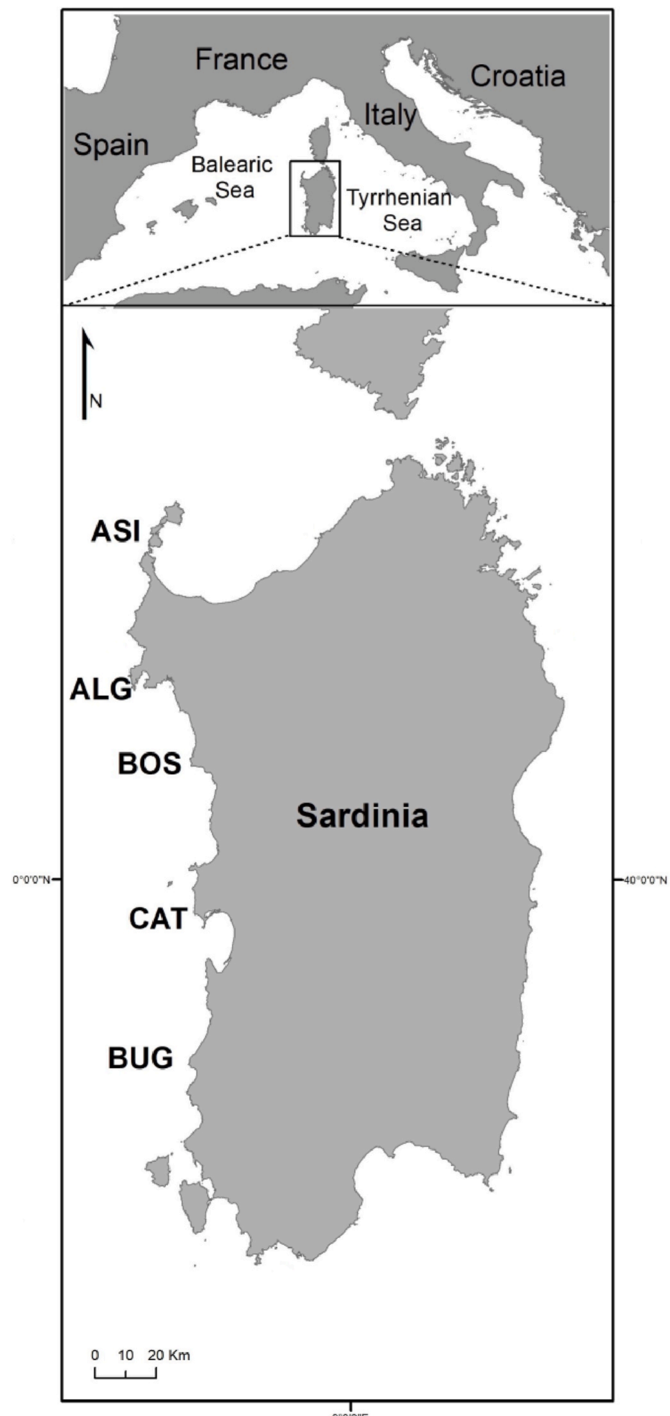


**Fig. 1.** Location of the study sectors of Sardinian continental shelf: Bugerru (BUG), Catalano (CAT), Bosa (BOS), Alghero (ALG), Asinara (ASI).

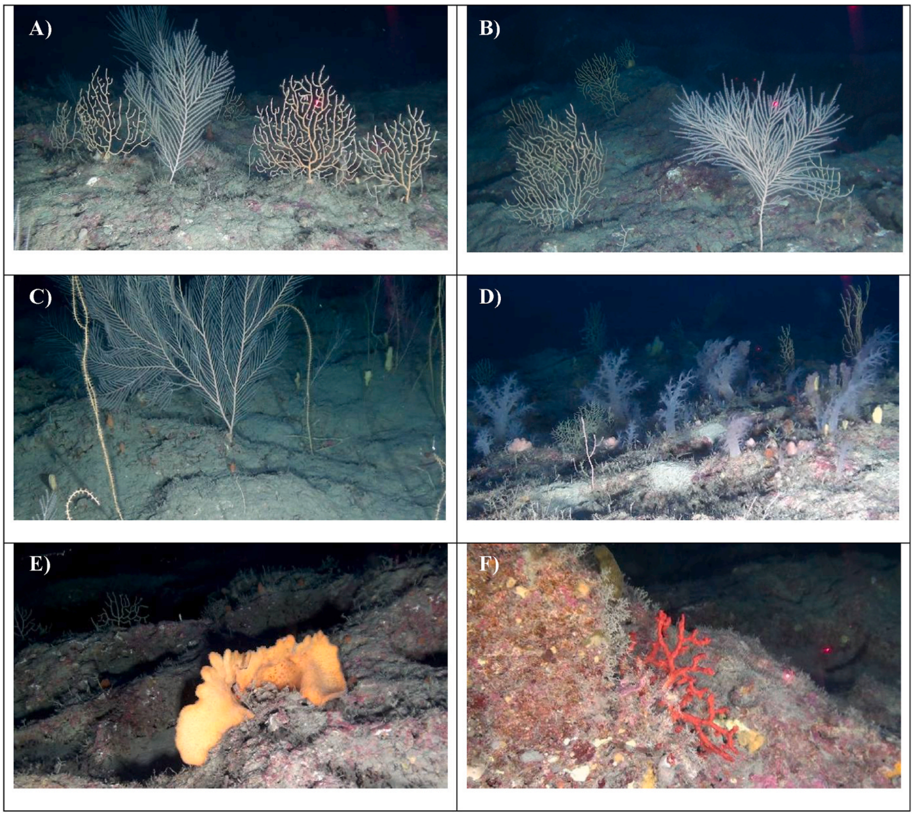


**Fig. 2.** Images of Sardinian coralligenous bank assemblages. A) and B) *Eunicella cavolini* and *Callogorgia verticillata*; C) *Callogorgia verticillata* and *Ellisella flagellum*; D) *Chironephthya mediterranea*; E) *Poecillastra compressa*; F) *Corallium rubrum*.

continuous recording mode, at constant slow speed (<0.3 ms$^{-1}$) and constant elevation from the seabottom (<1.5 m). Sampling was carried out during one oceanographic cruise on the R/V Minerva Uno of the Italian National Research Council in 2016 and other local surveys conducted between 2014 and 2019 (Table S1). From each video-transect, 10 images of the hard bottom were randomly selected (see Fig. 2).

Conspicuous organisms (large size organisms easily recognized in the images) were identified as distinct taxa, while those displaying similar morphological features were merged into morphological groups, following an approach already used for both shallower (Bianchi et al., 2004; Parravicini et al., 2009) and deeper (Ferrigno et al., 2017; Piazzi et al., 2021b) communities. The abundance of taxa/morphological groups was evaluated as percent cover, which is considered a main descriptor of the ecological status of coralligenous assemblages (Gatti et al., 2015; Montefalcone et al., 2017; Piazzi et al., 2021b). The percent cover of all sessile organisms was quantified in each image by superimposing a grid of 100 equal-sized squares (Dethier et al., 1993). For each image the percent cover was related to the total hard bottom surface, obtained by subtracting soft bottom zones or portions covered by motile organisms.

Spatial differences in the structure of assemblages (presence and abundance of taxa/groups) were analyzed by PERMANOVA based on Bray-Curtis resemblance matrix of untransformed data (Anderson, 2001). A 3-way model was used with Sector (five levels) as fixed factor, Site (three levels) as random factor nested in Sector and Transect (two levels) as random factor nested in Site, with images as samples ($n = 10$). Pair-wise test was used to discriminate between levels of significant fixed factors. Pseudo-variance components were also calculated for each spatial scale considered. A canonical analysis of principal coordinates (CAP, Anderson and Robinson, 2003) was performed in order to discriminate the main taxa/morphological groups contributing to dissimilarities among sectors. The taxa/morphological groups mostly contributing to the multivariate correlation (Pearson's $r > 0.5$) are reported in the CAP.

## 3. Results

A total of 25 taxa/morphological groups composed the assemblages in the western coralligenous banks of Sardinia (Table 1). The CAP analysis showed that the Anthozoans were the most common structural species (Figs. 2 and S1) and, among them, the gorgonians *Eunicella cavolini* and *Callogorgia verticillata* were dominant (Table 1, Fig. 3). *Paramuricea hirsuta* was also widespread, but with lower abundance, while *Ellisella flagellum, Parantipathes larix* and *Antipathella subpinnata* were only distributed in the southern sectors (Table 1). *Corallium rubrum* was more abundant in the Alghero sector and *Paramuricea clavata* was only found in the Asinara sector (Table 1, Figs. 3 and 4). Other species such as the sponges *Poecillastra compressa* and *Haliclona (Reniera) mediterranea* contributed to the structure of the assemblage especially at the Bugerru sector, while the ascidian *Aplidium* spp. was only found in the Bosa sector (Table 1, Fig. 4).

The PERMANOVA analysis showed that in the western Sardinia continental shelf, the coralligenous bank assemblages were significantly different among sectors and transects, while variability among sites was not significant (Table 2). The pair wise test indicated significant differences between all the sector pairs (Table 2), with the northern and the southern Sardinian sectors having the most similar assemblages, while the Bosa sector was the most dissimilar from all the others (Fig. 4). Furthermore, the pseudo-variance components showed the highest variability among samples (73.6) and the lowest among sites (5.2, Fig. 5).

## 4. Discussion

This study described the variability at multiple spatial scales of mesophotic assemblages on hard substrata in the continental shelf of

 

**Table 1**
Percent cover (mean) of all taxa/morphological groups in each sector. Bugerru (BUG), Catalano (CAT), Bosa (BOS), Alghero (ALG), Asinara (ASI).

| TAXA | BUG | CAT | BOS | ALG | ASI |
|---|---|---|---|---|---|
| **Alcyonacea** | | | | | |
| *Alcyonium coralloides* (Pallas, 1766) | 0.00 | 0.00 | 0.00 | 0.00 | 0.10 |
| *Callogorgia verticillata* (Pallas, 1766) | 6.83 | 2.43 | 1.73 | 7.63 | 6.32 |
| *Chironephthya mediterranea* López-González, Grinyó & Gili, 2014 | 0.00 | 0.00 | 0.00 | 0.17 | 0.00 |
| *Corallium rubrum* (Linnaeus, 1758) | 0.00 | 0.02 | 0.00 | 0.73 | 0.42 |
| *Ellisella flagellum* (Johnson, 1863) | 0.28 | 1.35 | 0.00 | 0.00 | 0.00 |
| *Eunicella cavolini* (Koch, 1887) | 7.37 | 4.72 | 1.12 | 2.48 | 2.58 |
| *Paramuricea clavata* (Risso, 1826) | 0.00 | 0.00 | 0.00 | 0.00 | 1.94 |
| *Paramuricea hirsuta* (Gray, 1857) | 0.52 | 0.25 | 0.00 | 0.00 | 0.16 |
| **Antipatharia** | | | | | |
| *Antipathella subpinnata* (Ellis & Solander, 1786) | 0.00 | 1.33 | 0.00 | 0.00 | 0.00 |
| *Parantipathes larix* (Esper, 1788) | 0.00 | 0.85 | 0.00 | 0.00 | 0.00 |
| **Scleractinia** | | | | | |
| *Dendrophyllia cornigera* (Lamark, 1816) | 0.00 | 0.00 | 0.00 | 0.00 | 0.81 |
| *Dendrophyllia ramea* (Linnaeus, 1758) | 0.00 | 0.03 | 0.00 | 0.00 | 0.00 |
| **Hydrozoa** | | | | | |
| Large unidentified hydrozoans | 0.28 | 0.00 | 0.00 | 0.53 | 0.35 |
| **Porifera** | | | | | |
| *Agelas oroides* (Schmidt, 1864) | 0.00 | 0.00 | 0.07 | 0.00 | 0.00 |
| *Aplysina* spp. | 0.00 | 0.00 | 0.03 | 0.00 | 1.81 |
| *Axinella* spp. | 0.48 | 0.00 | 0.17 | 0.13 | 0.00 |
| *Haliclona (Reniera) mediterranea* Griessinger, 1971 | 0.43 | 0.00 | 0.13 | 0.23 | 0.00 |
| *Poecillastra compressa* (Bowerbank, 1866) | 0.92 | 0.00 | 0.00 | 0.08 | 0.00 |
| *Suberites* spp. | 0.13 | 0.00 | 0.17 | 0.23 | 0.00 |
| encrusting sponges | 0.42 | 0.52 | 0.47 | 0.47 | 0.58 |
| massive sponges | 0.88 | 0.55 | 0.55 | 0.78 | 2.00 |
| **Annelida** | | | | | |
| *Filograna-Salmacina* complex | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Bryozoa** | | | | | |
| *Reteporella* spp. | 0.03 | 0.03 | 0.00 | 0.17 | 0.00 |
| *Smittina cervicornis* (Pallas, 1766) | 0.03 | 0.00 | 0.00 | 0.00 | 0.03 |
| **Ascidiacea** | | | | | |
| *Aplidium* spp. | 0.00 | 0.00 | 0.15 | 0.00 | 0.00 |

western Sardinia. Results highlighted significant variability at both small and geographic sector scales considered in the study; on the other hand, several common patterns characterizing the assemblage were highlighted.

The high variability at small spatial scale highlighted by pseudo-variance components is a common pattern for biogenic habitats. It has already been described for shallower coralligenous assemblages (Piazzi et al., 2004, 2016) and is related to the heterogeneity of substrate and the biotic interactions (Ballesteros, 2006). Indeed, in stable conditions, such as those characterizing mesophotic systems, competitive mechanisms may be crucial in regulating the distribution of organisms (Grinyó et al., 2016). Moreover, the topographical heterogeneity of biogenic substrate may contribute to the patchy distribution of sessile species, influencing recruitment and offering a multitude of microhabitats with different physical conditions (Cocito, 2004). Also, anthropogenic disturbance due to fishing activities may contribute to enhance the heterogeneity of assemblages (Appolloni et al., 2020).

The pseudo-variance components also showed more homogenous assemblages at larger spatial scales. In fact, the gorgonians *Eunicella cavolini* and *Callogorgia verticillata* are dominant in all the investigated sectors and have a common pattern to that already described for the mesophotic habitats of south-western Sardinia (Cau et al., 2015). The relative homogeneity on a large spatial scale does not match the spatial patterns observed along the Sardinian coasts for shallower coralligenous assemblages. For the latter, different biogeographic patterns have been described (Piazzi et al., 2021a) and partially correlated to variations of water temperature which, on the contrary, is stable in deeper systems. On the other hand, other factors, such as substrate morphology and slope, sedimentation rates and deep bottom currents, could contribute to create physical gradients in mesophotic habitats (Bo et al., 2015; Grinyó et al., 2018, 2020). These factors may have a key role in shaping the structure of coralligenous assemblages (Enrichetti et al., 2019c). In fact, normally, continental shelves are mostly characterized by soft bottoms that may be interrupted by rocky shoals or outcrops (Bo et al., 2012; Ferrigno et al., 2018b; Grinyó et al., 2018); the extent of soft bottoms creates a major barrier to the dispersion of hard bottom benthic organisms inhabiting rocky shoals and outcrops, favoring the existence of peculiar assemblages (Bo et al., 2012). On the contrary, the western Sardinia continental shelf is characterized by extensive hard substrata (Simeone et al., 2014; De Falco et al., 2022), allowing the development of similar assemblages across hundreds of kilometers.

On the other hand, some locally distributed taxa contribute to distinguish the geographic sectors considered in this study such as highlighted by Pair-wise tests. Abundant colonies of *Corallium rubrum* were found only in the Alghero sector, although this species has been widely reported for other Sardinian mesophotic habitats (Cau et al., 2016). This finding confirms a pattern already highlighted for shallower coralligenous assemblages of western Sardinia, as this cnidarian was only reported along the Alghero coasts (Piazzi et al., 2021a). The gorgonian *Paramuricea clavata* was only found in the Asinara sector although this species is widely reported for Mediterranean mesophotic assemblages (Gori et al., 2017). In Sardinia, this species is abundant along the eastern coast, while has never been reported in the western coralligenous cliffs (Piazzi et al., 2021a); thus, results of the present study corroborate this pattern. The Anthipataria *Anthipathella subpinnata* and *Parantipathes larix* were found only in the Catalano sector. Both species are described to have a patchy distribution typical of all arborescent anthozoans characterized by a limited larval dispersion (Bo et al., 2014b; 2015).

Coralligenous bank assemblages of Sardinian continental shelf appeared highly diversified with a dominance of erect habitat-forming anthozoans. This pattern confirms data reported for some deep shoals and rocky outcrops reported for other Sardinian areas (Bo et al., 2015; Cau et al., 2015). The presence of extensive and well diversified mesophotic animal forests stresses the importance to improve the conservation of the western Sardinian continental shelf (Rossi et al., 2017), since this habitat plays key structural and functional ecological roles (Gori et al., 2017). In a climate change scenario where many shallower assemblages are threatened by climatic anomalies (Gómez-Gras et al., 2021), these mesophotic communities may act as refugia and source for the recolonization of impacted shallow areas (Holstein et al., 2016; Soares et al., 2019), at least for depth-generalist coralligenous species. Moreover, almost all mesophotic species are long-lived organisms with slow population dynamics (Teixidó et al., 2011). These characteristics make them particularly vulnerable to each small physical factor variation, justifying the need to maintain the semi-pristine environmental conditions to achieve the conservation of the mesophotic habitats. In the Mediterranean Sea, pristine or semi-pristine animal forests are considered rare and confined in some remote sites (*e.g.* Bo et al., 2011; Garrabou et al., 2017) or in areas where fishing activities have been limited due to legal restrictions or complex geomorphologies (Bo et al., 2014b; 2015; Mastrototaro et al., 2017). Thus, the extensive presence of diversified animal forests in the western continental shelf of Sardinia suggests the importance of enhancing both conservation measures (Cau et al., 2017a) and monitoring programs to assess the temporal dynamics of forest structure and their ecological status.

The present study evaluated for the first time the variability of mesophotic coralligenous megafauna at multiple spatial scales. Results highlighted that spatial variability of mesophotic animal forests change depending on the scale considered. Spatial patterns can influence the functioning of the mesophotic habitats, as the regulation of competitive and facilitative processes is intimately related to the presence of megafaunal organisms and to patterns of their distribution (Cerrano et al., 2019). Thus, considering the spatial variability of mesophotic systems becomes crucial. In this context, the findings of the present study suggest the importance of using multiscale approaches and a high

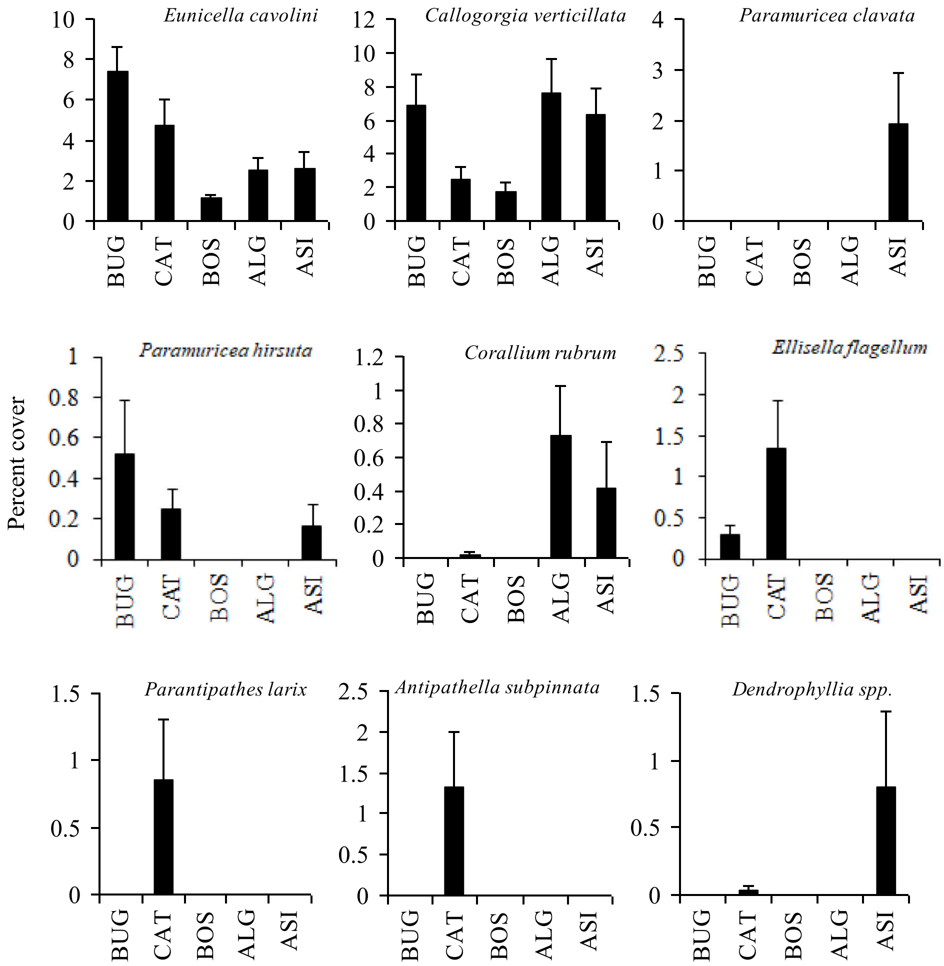


**Fig. 3.** Percent cover (mean + SE) of the main anthozoans (n = 60). Bugerru (BUG), Catalano (CAT), Bosa (BOS), Alghero (ALG), Asinara (ASI).

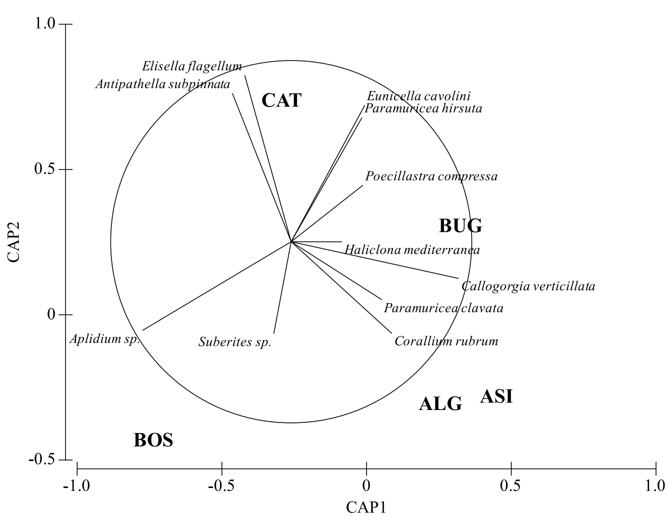


**Fig. 4.** CAP analysis of coralligenous bank assemblages. Bugerru (BUG), Catalano (CAT), Bosa (BOS), Alghero (ALG), Asinara (ASI).

**Table 2**
Results of PERMANOVA and pair-wise test. Bugerru (BUG), Catalano (CAT), Bosa (BOS), Alghero (ALG), Asinara (ASI). Significant effects are in bold.

| Source | df | MS | Pseudo-F | P (perm) |
|---|---|---|---|---|
| Sector = Se | 4 | 21137 | 1.93 | **0.017** |
| Site(Se) = S | 10 | 11034 | 1.43 | 0.083 |
| Transect (S(Se)) | 15 | 7672 | 2.92 | **0.001** |
| Residual | 240 | 2623 | | |
| | | | | |
| Pair-wise test (Se) | P (perm) | | | |
| BUG, CAT | **0.001** | | | |
| BUG, BOS | **0.001** | | | |
| BUG, ALG | **0.001** | | | |
| BUG, ASI | **0.001** | | | |
| CAT, BOS | **0.001** | | | |
| CAT, ALG | **0.015** | | | |
| CAT, ASI | **0.001** | | | |
| BOS, ALG | **0.001** | | | |
| BOS, ASI | **0.001** | | | |
| ALG, ASI | **0.001** | | | |

replication at the smallest spatial scales in the monitoring programs and impact evaluation studies of mesophotic coralligenous megafauna.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence

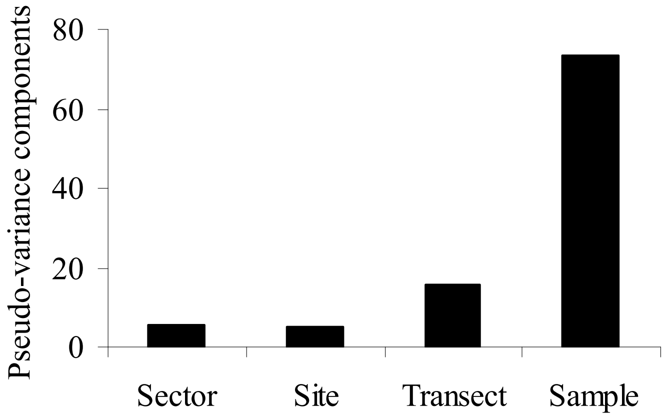


**Fig. 5.** Pseudo-variance components of Sardinian coralligenous bank assemblages.

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.csr.2022.104790.

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