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ORIGINAL RESEARCH

Disentangling the mesophotic zone: algal and invertebrate bioconstructions host distinct benthic assemblages in the Mediterranean Sea

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Abstract
A comprehensive overview of the benthic assemblages associated with bioconstructions in the mesophotic zone of the southern Adriatic Sea is provided through a comparison of algal- and invertebrate-based bioconstructions. To characterize these bioconstructions, sampling was conducted at six sites along the Apulian coast (Italy). Algal-based bioconstructions were found in shallower areas and corresponded to coralligenous sensu stricto, while two distinct invertebrate-based bioconstructions, built by scleractinians and bivalves, were observed at greater depths. A multi-taxa approach, which recorded 511 benthic taxa, revealed significant differences in the taxonomic composition of their associated benthic assemblages, although similar species richness values were observed across all types of bioconstructions. Given the marked difference in terms of primary constructor species between the coralligenous sensu stricto and invertebrate bioconstructions, we propose referring to the latter as Mesophotic Coral Bioconstructions (MCB) and Mesophotic Oyster Bioconstructions (MOB). β-diversity analysis identified a turnover in benthic fauna along the North–South gradient, with higher β-diversity values between distant sites and lower values between nearby sites, likely driven by North–South circulation dynamics in the region. Additionally, the distinctions observed along the depth gradient are consistent with the decrease in irradiance, which causes a shift from photoautotrophic to heterotrophic builder species. These findings underscore the role of mesophotic bioconstructions along the Apulian coast as biodiversity hotspots and confirm their importance in understanding mesophotic ecosystem dynamics in the Mediterranean Sea.

Keywords Calcareous bioconstructions · Coralligenous · Coral reefs · Habitat formers · Mesophotic · Oyster reefs

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Introduction

Marine bioconstructions are biogenic structures created through the aggregation and accumulation of the calcareous skeletons of benthic organisms that host a large diversity of associated species (Riding 2002). These carbonate structures occupy areas over a wide latitudinal gradient, from tropical to temperate waters, and are of critical ecological importance, largely contributing to the ecosystem services provided by the oceans (Laborel 1987; Ingrosso et al. 2018). They provide essential physical structures for numerous species and contribute significantly to ecosystem services such as nutrient cycling, coastal protection, carbon sequestration, tourism, recreation and related economic activities (Beaumont et al. 2007). Their role as biodiversity hotspots has led to their recognition as key habitats for conservation, being classified as habitats of community interest under international frameworks such as the EU Habitats Directive (Habitats Directive 92/43/CEE).

While in tropical waters the most widely recognized marine bioconstructions are coral reefs (Spalding and Grenfell 1997), in the temperate waters of the Mediterranean Sea the best-known biogenic structure is the coralligenous (Ballesteros 2006), mainly built by encrusting coralline algae, which act as primary builders developing primary or secondary hard substrates of biogenic origin. These algal-based bioconstructions occur under dim-light conditions and grow on vertical walls and horizontal platforms creating complex three-dimensional habitats that support a wealth of associated species (Laborel 1961; Pérès and Picard 1964). The composition and diversity of coralligenous assemblages are strongly influenced by biogeographic and environmental factors such as light availability, water temperature and depth gradients (Pinna et al. 2021; Piazzi et al. 2021). These structures have attracted the attention of the scientific community for decades (e.g. Hong 1982; Casellato and Stefanon 2008; Bracchi et al. 2015; Basso et al. 2022; Varzi et al. 2023) due to their ecological importance, serving as refuges, nurseries, and feeding grounds for a wide variety of marine organisms.

The exploration of mesophotic depths along the southeastern coast of Italy has, however, recently led to the discovery of remarkable bioconstructions built by invertebrates, mainly scleractinians and bivalves, rather than algae (Corriero et al. 2019; Cardone et al. 2020, 2022). The presence of such animal-based structures highlighted the great diversity of habitat-forming species in temperate mesophotic ecosystems, which are mostly found in the Mediterranean Sea, North Atlantic and Pacific Oceans (Pyle and Copus 2019; Cerrano et al. 2019; Bell et al. 2022). As these bioconstructions are not built by calcareous algae, they do not meet the definition of coralligenous sensu stricto (Ballesteros 2006). Previous studies (Montefalcone et al. 2021; Cerrano et al. 2015) have highlighted the importance of standardized terminology in the description of marine benthic habitats, to ensure a common framework and a shared technical terminology among scientists involved in this field. These authors distinguished between algae-dominated coralligenous bioconstructions and those dominated by invertebrates, based on the predominant taxonomic groups or facies present. In this paper, we emphasize the need for an additional nomenclature that considers the mesophotic bioconstructions in which algae play no role as bioconstructors and, therefore, cannot be classified as coralligenous sensu stricto (Ballesteros 2006).

Considering this, we provide an overview of the mesophotic bioconstructions recorded off the southern Adriatic Apulian coast (Italy), where the diversity of mesophotic habitat-forming species was first documented. We analysed two bioconstruction types: algal-based and invertebrate-based (scleractinians and/or oysters) at six sites along 400 km of the Adriatic coast of Apulia (Italy). Our main goal is to assess whether benthic assemblages

associated with algal-based bioconstructions (i.e. coralligenous, hereafter referred to as Mesophotic Algal Bioconstructions, MAB) and invertebrate-dominated bioconstructions are consistently different communities rather than the expression of a biocoenotic continuum. To achieve this, we adopted a multi-taxa approach that considered macroalgae, poriferans, cnidarians, molluscs, polychaetes, and bryozoans as the main taxa associated with the bioconstructions, to evaluate differences in terms of species composition and diversity. Moreover, we propose a new nomenclature for Mediterranean mesophotic invertebrate-based bioconstructions: Mesophotic Coral Bioconstructions (MCB), and Mesophotic Oyster Bioconstructions (MOB), to better describe an environment that is increasingly attracting scientific attention. This study represents an important step in expanding the conceptual framework for mesophotic bioconstructions in the Mediterranean, highlighting the need for new classifications that reflect the diversity of habitat-forming species and their ecological significance.

Materials and methods

Study area

This research was carried out at six sites along the Apulian coast, in southeastern Italy, where our previous studies revealed the presence of a complex spatial distribution of bioconstructions (Corriero et al. 2019; Cardone et al. 2020, 2022): the Tremiti Islands (TRM), Monopoli (MON), Capitolo (CAP), San Foca (SFC), Otranto (OTR) and Santa Maria di Leuca (SML) (Fig. 1; Table 1). Figure 2 provides a concise photographic overview documenting the main macroscale differences in the bioconstructions studied at the different sites.

At TRM (Fig. 2A, B), algal bioconstructions occur on vertical hard substrates at depths ranging from 25 to 30 m, depending on light exposure. Animal bioconstructions, mainly built by the bivalve *Neopycnodonte cochlear*, occur between 45 and 55 m in depth.

At MON (Fig. 2C, D), a succession of biocoenoses occurs from photophilous to sciaphilous hard substrates starting at 25 m. Algal bioconstructions extend down to 55 m

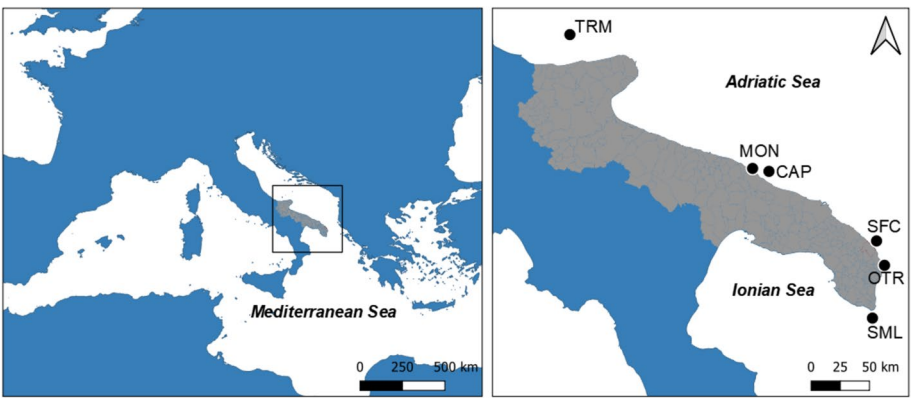


Fig. 1 Geographic location of the study area along the Apulian coast, (Italy), indicating sampling sites. *TRM* Tremiti, *MON* Monopoli, *CAP* Capitolo, *SFC* San Foca, *OTR* Otranto, *SML* Santa Maria di Leuca

Table 1 List of sampling sites with the indication of depth and geographic coordinates

Site	Bioconstructor	Depth	LAT	LONG
TRM	Calcareous algae	25–30 m	42.138	15.522
	Oysters	45–55 m	42.138	15.522
MON	Calcareous algae	25–35 m	40.982	17.286
	Scleractinians	50–55 m	40.982	17.286
CAP	Calcareous algae	25–35 m	40.947	17.449
	Oysters	53–64 m	40.947	17.449
SFC	Calcareous algae	25–35 m	40.324	18.466
	Scleractinians	45–53 m	40.324	18.466
OTR	Calcareous algae	25–35 m	40.128	18.520
	Oysters	45–64 m	40.128	18.520
SML	Calcareous algae	25–27 m	39.731	18.347
	Oysters	45–65 m	39.731	18.347

TRM Tremiti, *MON* Monopoli, *CAP* Capitolo, *SFC* San Foca, *OTR* Otranto; *SML* Santa Maria di Leuca

depth, where the mesophotic bioconstruction is primarily formed by two non-symbiotic scleractinian species, *Phyllangia americana mouchezii* and *Polycyathus muellerae*.

The same bioconstructors were detected at SFC (Fig. 2G, H), where a mosaic of scleractinian buildups, occurring between 45 and 53 m depth on a moderately steep slope, rises 0.5 to 4 m above the muddy bottom. Here, algal bioconstructions outcrops are found at depths ranging from 25 to 35 m on sandy bottoms.

At CAP (Fig. 2E, F), coralligenous outcrops form pinnacles 1–2 m high at depths of 25–35 m, while the mesophotic structure built by *N. cochlear* occurs between 53 and 64 m.

At OTR (Fig. 2I, J), coralligenous concretions develop in rims growing on a rocky cliff that rises from the sandy bottom at 25–35 m depth. *N. cochlear* bioconstructions were discontinuously detected along 600 m of coastline within the 45–64 m bathymetric range, reaching a total length of 200 m.

At SML (Fig. 2K, L), coralligenous bioconstructions form flat outcrops between 25 and 27 m depth. The carbonate formation built by *N. cochlear* extended along the northern and eastern sides of the cliff for a total length of about 450 m, within the 45–70 m bathymetric range. More detailed morphological and geological characteristics in each study area can be found in Corriero et al. (2019) and Cardone et al. (2020, 2022).

Sample collection and taxonomic analysis

To characterize the assemblages associated with the investigated bioconstructions, two samples (approximately 3 L each) of calcareous algal and animal bioconstructions were collected at each study site from horizontal surfaces by technical divers at both the shallowest (− 25–35 m) and deepest (− 45–65 m) areas (Table 1). Divers followed a random sampling pattern, keeping about 10 m between replicates. Collected samples were stored in plankton net bags with a 0.5 mm mesh size and transported to the laboratory, where they underwent initial macroscopic taxonomic classification.

Each sample was sorted into six target taxa (macroalgae, Porifera, Cnidaria, Mollusca, Polychaeta, and Bryozoa) and stored in a 70% ethanol solution. Collected specimens were identified to the lowest possible taxonomic level, following preparation and

identification procedures specific to each taxon. Coralline algae were identified based on thallus morphology, following Bressan and Babbiani (2003). Sponge identification involved skeleton and spicule preparations according to standard procedures (Rützler 1978), with taxonomic reference based on Systema Porifera (Hooper et al. 2002) and the World Porifera Database (WPD) (de Voogd et al. 2024). Cnidarians nomenclature followed Bouillon et al. (2004, 2006). Molluscs were identified based on their shell features, according to the systematic classification of Bouchet et al. (2017) for gastropods, and Bouchet et al. (2010) for bivalves, and referring the nomenclature to MolluscaBase (2024). Polychaetes identification included both vagile specimens and sessile worms in their tubes, with updated specialist literature such as the World Polychaeta Database. Bryozoan identification followed Zabala and Maluquer (1988), Rosso and Di Martino (2016), and Chimenz Gusso et al. (2014).

Data analysis

A single presence-absence data matrix was created using the benthic species associated with the detected bioconstructions in the study area. This involved merging our previously published data (Corriero et al. 2019; Cardone et al. 2020, 2022) with new data, to achieve a comprehensive dataset encompassing all species found in the area (Supplementary Material S1). To assess disparities among MAB, MOB, and MCB, the analysis focused on (i) measuring their α-diversity, (ii) quantifying the β-diversity between these groups, and (iii) comparing the multivariate composition of the assemblages.

α-diversity was computed as the number of species found at each study site and within each bioconstruction type. Differences in α-diversity between the bioconstructions were tested with the non-parametric Kruskal–Wallis test. β-diversity, i.e. the variation in species diversity among assemblages within the geographical area (Whittaker 1960), was calculated as a measure of species turnover between MAB, MOB, and MCB using the Whittaker Index $\beta_w = (S/\bar{\alpha}) - 1$, where S is the total number of species that results from merging the diversity of all sites and $\bar{\alpha}$ is the mean number of species per individual sample (Whittaker 1972; Koleff et al. 2003). Such measures were computed to evaluate the proportion by which the bioconstructions differed in species composition.

Finally, to explore differences and similarities in species composition of the benthic assemblages across sites, we employed nonmetric Multidimensional Scaling (nMDS) and cluster analysis. The nMDS ordination plot was based on the Ochiai (1957) similarity index, chosen for its sensitivity to species co-occurrence. To test for the stability of the groupings, we conducted additional ordinations using two alternative similarity indices, Sorensen (Legendre and De Caceres 2013) and Jaccard (1901). Trials with these indices yielded very similar results (see Supplementary Material S2). For the cluster analysis, we employed the Taxonomic Dissimilarity (Gamma+), a measure of dissimilarity between two samples that compared not only the present species but also their taxonomic distances (Clarke et al. 2006). This method allows a more comprehensive assessment of differences between samples by incorporating higher taxonomic levels.

Statistical significances were tested by a two-way PERMANOVA using the factors Site, with 6 levels, and Type of bioconstructions, with 3 levels and nested within Site. Analyses were run using PRIMER v6 + PERMANOVA (Anderson et al. 2019).

Fig. 2 Representative images of the algal bioconstructions (MAB: **a**, **c**, **e**, **g**, **i**, **k**), coral bioconstructions (MCB: **d**, **h**) and oyster (MOB: **b**, **f**, **j**, **l**) bioconstructions at each site:. TRM (**a**, **b**), MON (**c**, **d**), CAP (**e**, **f**), SFC (**g**, **h**), OTR (**I**, **j**) and SML (**k**, **l**)

Results

Benthic community diversity and structure

The taxonomic analysis of the samples collected across all study sites revealed a total of 511 taxa, with 467 (91%) identified at the species level (Supplementary Material S1). Porifera exhibited the highest species richness (194 species, 38%), followed by Annelida Polychaeta (136 species, 26.7%), Bryozoa (73 species, 14.3%), and Mollusca (57 species, 11.2%). This pattern in species distribution was consistent across all three types of bioconstructions (Fig. 3).

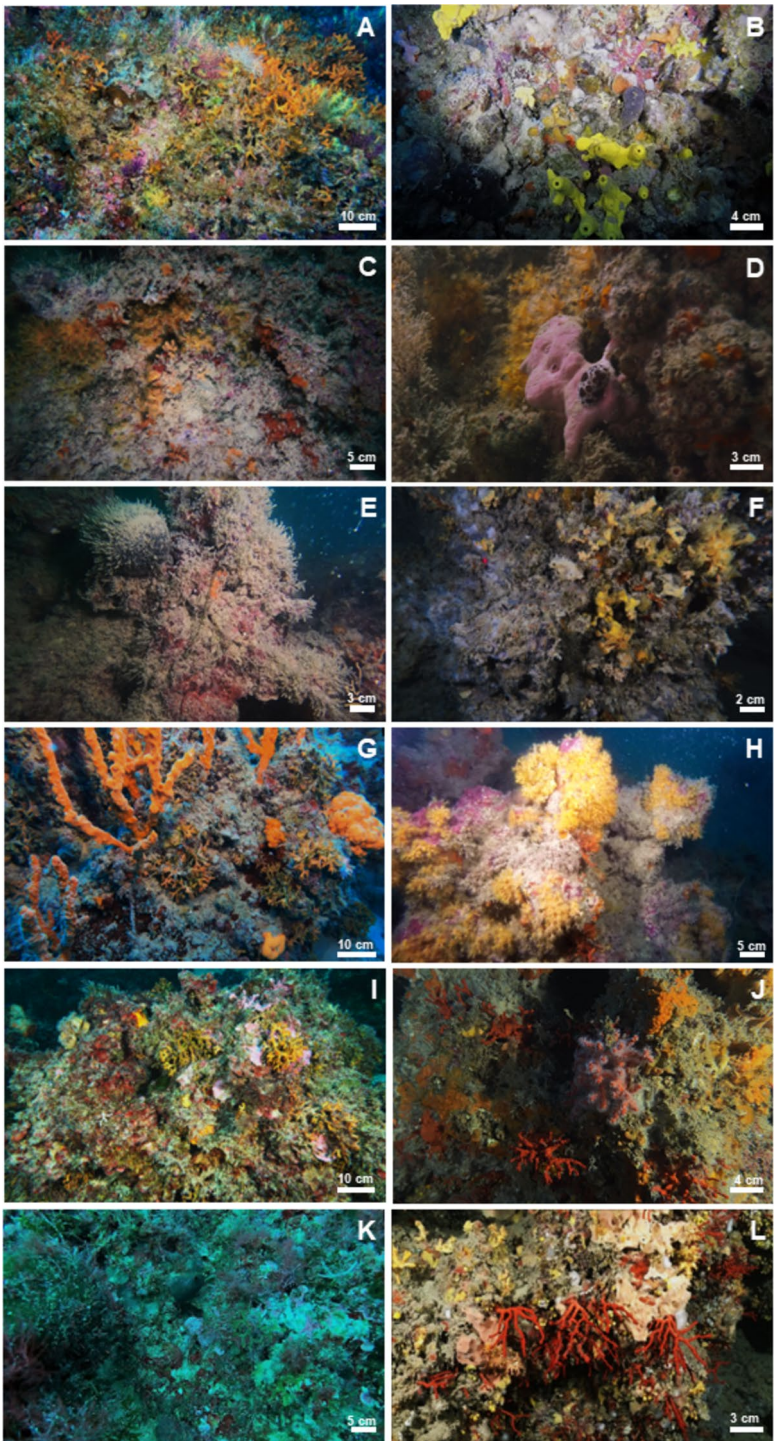
MAB showed the highest number of exclusive taxa among macroalgae, Porifera, Annelida, and Mollusca, while MOB had the highest number of exclusive taxa for Bryozoa and Cnidaria (Fig. 4). Cnidaria stood out with the highest number (41%) of taxa common to the three types of bioconstructions, followed by Annelida (26%) and Porifera (23%).

Species richness of the communities associated with the bioconstructions, used as a measure of α-diversity, did not show significant variation between bioconstruction types or sites. The mean species richness was 117 for MAB, 123 for MOB, and 135, for MCB ($H = 0.23$, $p = 0.88$). The highest number of taxa was found at MON, for algal- (140) and oyster- (166) based bioconstructions. Oyster-based bioconstructions also exhibited high α-diversity at OTR and SML, with 134 and 147 taxa, respectively. In contrast, the lowest species richness (103) was observed at CAP, for both algal- and oyster-based bioconstructions (Fig. 5).

The non-metric multidimensional scaling (nMDS) plot based on Ochiai dissimilarities (Fig. 6) arranged the site points in two different clouds corresponding to MAB and MCB / MOB types of bioconstructions. These groups remained significantly distinct, as confirmed by the PERMANOVA analysis (Table 2).

The results of the cluster and nMDS analyses, which evaluated the level of similarity based on taxonomic distinctness between bioconstructions across different sites are shown in Fig. 7. Two main clusters differentiate algal-based bioconstructions from invertebrate-based bioconstructions. Within the invertebrate-based bioconstructions, a minor distinction was observed between coral- and oyster-based bioconstructions, mainly driven by the exclusive presence of certain species within each bioconstruction type. In particular, MOB was characterized by a higher number of exclusive bryozoans, mainly from the family Calloporidae (e.g. *Callopora dumerilii* and *Copidozoum planum*), as well as polychaete species, predominantly from the family Serpulidae (*Nidificaria clavus*, *Semivermilia agglutinate* and *Spirobranchus lima*, among others). In contrast, MCB exhibited a more heterogeneous composition, with exclusive species distributed across multiple polychaete families. Additionally, differences in molluscan assemblages further contributed to this distinction, with MOB hosting a higher proportion of exclusive gastropods (e.g. *Carinorbis clathrata*, *Thylacodes arenarius*, *Fossarus ambiguous*), while MCB supported a more diverse bivalve community (e.g. *Rocellaria dubia*, *Barbatia barbata*) (see "Composition of benthic assemblages" section for composition details).

The β-diversity analysis highlighted species turnover along the geographical gradient, with mean values of 0.60 for the algal-based (Table 3) and invertebrate-based (Table 4)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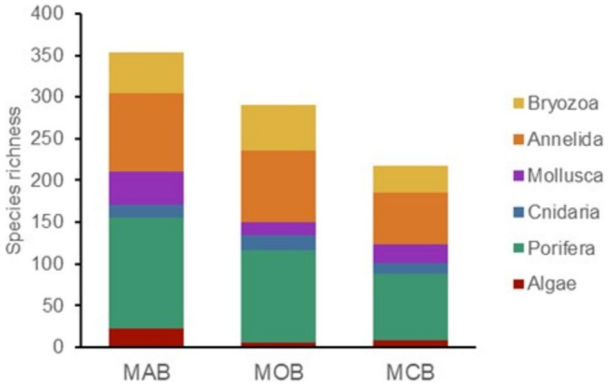

Fig. 3 Species richness of mesophotic algal (MAB), oyster (MOB) and coral (MCB) bioconstructions

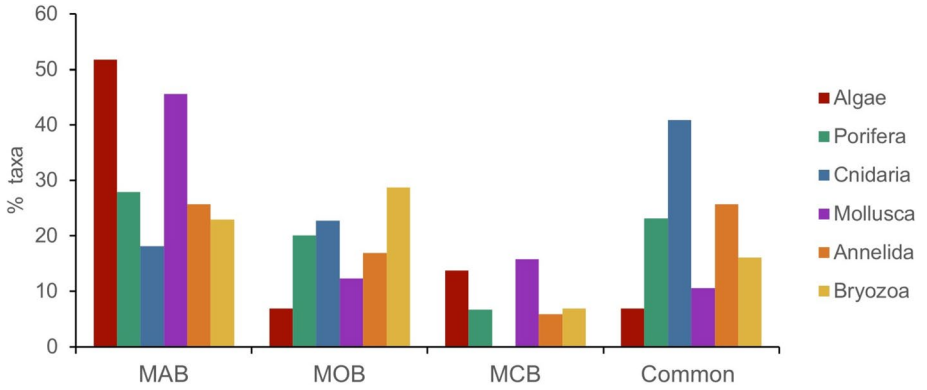

Fig. 4 Percentage of exclusive taxa identified within each bioconstruction type (histograms on the left). The last histogram (on the right) shows the percentage of taxa shared by the three types of bioconstructions (common taxa). *MAB* mesophotic algal bioconstructions, *MOB* mesophotic oyster bioconstructions, *MCB* mesophotic coral bioconstructions

bioconstructions. The highest β-diversity values were consistently observed for distant sites, such as CAP-SML and TRM-SML. In contrast, the lowest values of Whittaker's index were recorded between nearby sites, i.e. OTR- SML, for both algal and invertebrate bioconstructions, and SFC-OTR for invertebrate bioconstructions. Some exceptions were observed, with higher-than-average β-diversity values recorded between some nearby sites, such as MON-CAP for both bioconstruction types and CAP-OTR for invertebrate bioconstructions. The remaining β-diversity values aligned with the average.

Composition of benthic assemblages

A total of 29 non-structuring macroalgal taxa were censused, comprising 17 red algae (mainly from the Class Florideophyceae), five green algae (mainly Class Ulvophyceae), and seven brown algae (Class Phaeophyceae) (Table 5). All green and brown algal species were exclusively observed in the algal bioconstructions, while red algae were predominantly found in association with invertebrate bioconstructions.

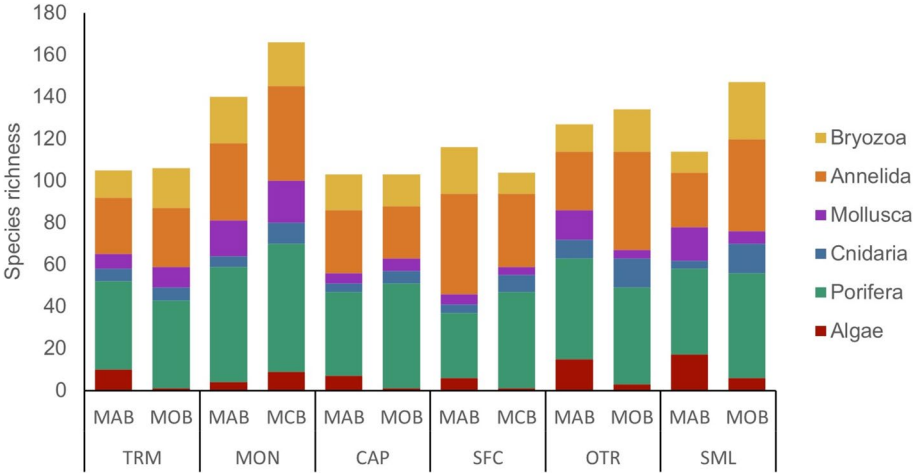

Fig. 5 Species richness of the benthic assemblages associated with algal, oyster and coral mesophotic bioconstructions at the six study sites. *MAB* mesophotic algal biocostructions, *MOB* mesophotic oyster biocostructions, *MCB* mesophotic coral biocostructions

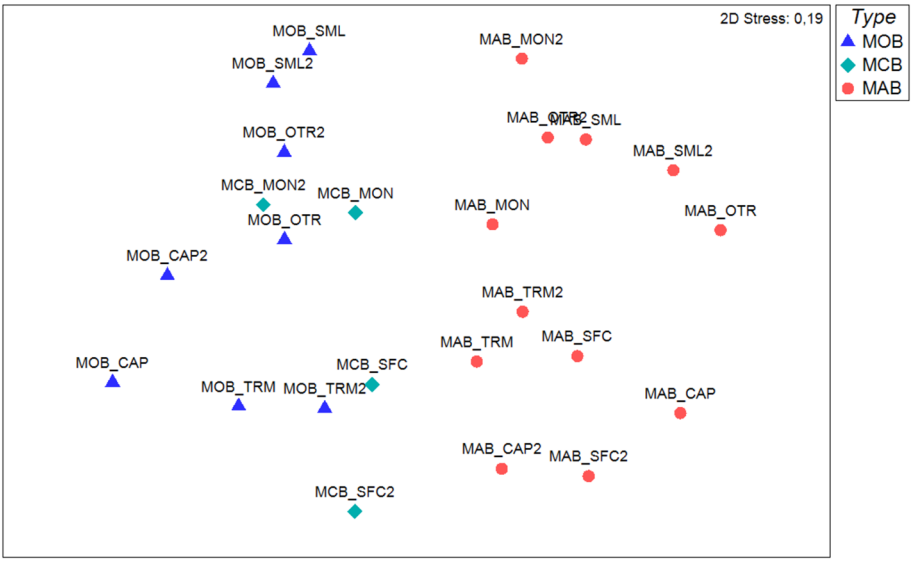

Fig. 6 nMDS plot based on distance among centroids obtained from Ochiai dissimilarities on the benthic communities associated with algal (MAB), coral (MCB) and oyster (MOB) bioconstructions. *MAB* mesophotic algal biocostructions, *MOB* mesophotic oyster biocostructions, *MCB* mesophotic coral biocostructions. Stress = 0.19

Table 2 Results of PERMANOVA analysis performed for site and type of bioconstructions *p < 0.05

Source	Pseudo-F	P(perm)
Si	2,0793	0,001*
Ty (Si)	2,1266	0,001*

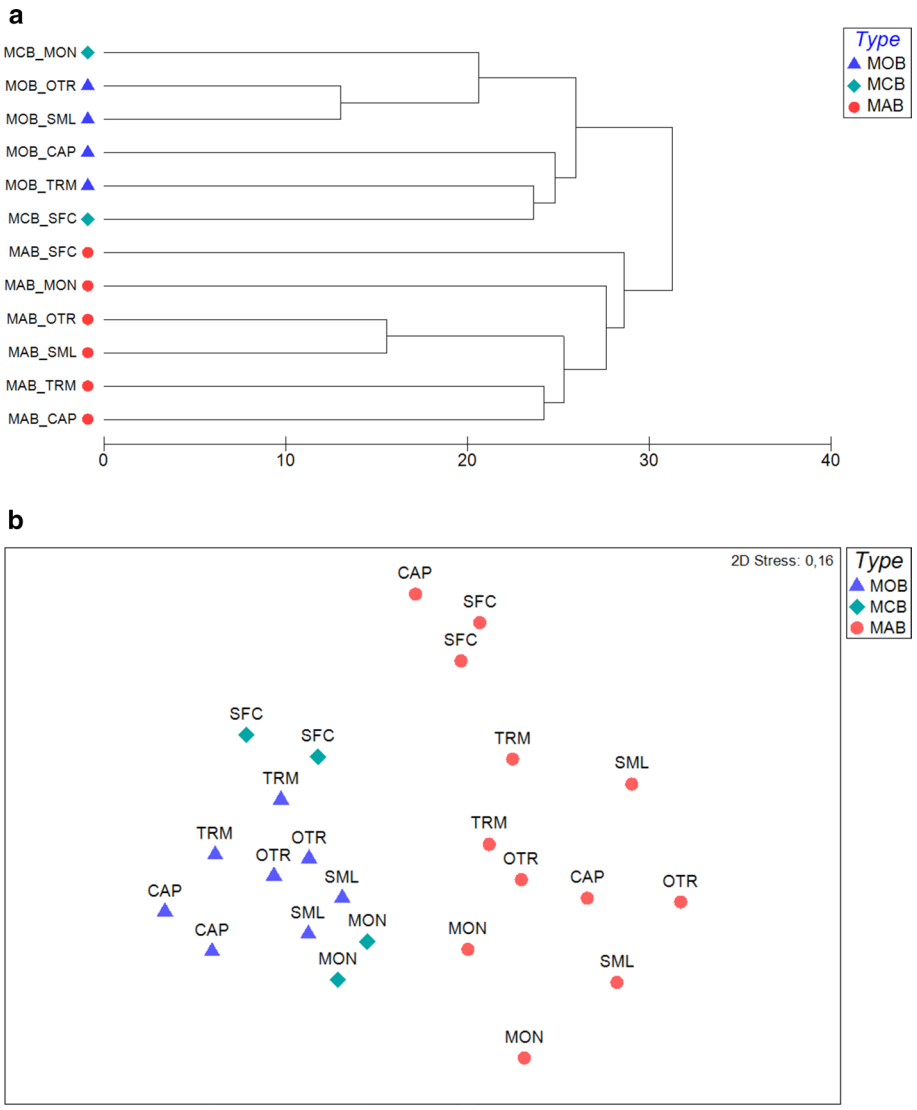

Fig. 7 Dendrogram **a** and nMDS **b** plots based on data of the benthic communities associated with algal (MAB), coral (MCB) and oyster (MOB) bioconstructions using taxonomic distinctness (Gamma+)

Table 3 Paired values of β-diversity computed using Whittaker's βw measure at the mesophotic algal bioconstructions investigated

	TRM	MON	CAP	SFC	OTR	SML
TRM	0.000					
MON	0.622	0.000				
CAP	0.559	0.658	0.000			
SFC	0.632	0.656	0.618	0.000		
OTR	0.601	0.384	0.613	0.605	0.000	
SML	0.653	0.612	0.694	0.646	0.384	0.000

Table 4 Paired values of β-diversity computed using Whittaker's βw measure at the mesophotic invertebrate (Coral and Oyster) bioconstructions investigated

	TRM	MON	CAP	SFC	OTR	SML
TRM	0.000					
MON	0.679	0.000				
CAP	0.613	0.647	0.000			
SFC	0.523	0.584	0.556	0.000		
OTR	0.613	0.480	0.650	0.556	0.000	
SML	0.667	0.566	0.719	0.628	0.349	0.000

Table 5 Summarized values of the main phylum and classes found in each type of bioconstruction

	MAB	MOB	MCB
Rhodophyta	11	9	6
Florideophyceae	11	8	6
Stylonematophyceae	–	1	–
Chlorophyta	5	–	–
Ulvophyceae	5	–	–
Ochrophyta	6	–	–
Phaeophyceae	6	–	–
Prasinodermatophyta	1	–	–
Palmophyllophyceae	1	–	–
Porifera	133	81	111
Calcarea	4	–	–
Demospongiae	126	79	107
Homoscleromorpha	3	2	4
Cnidaria	15	12	17
Hexacorallia	9	9	10
Hydrozoa	3	2	2
Octocorallia	3	1	5
Mollusca	40	22	16
Bivalvia	23	13	9
Gastropoda	16	9	7
Polyplacophora	1	–	–
Annelida	93	62	86
Polychaeta	87	60	84
Sipuncula	6	2	2
Bryozoa	41	28	46
Gymnolaemata	39	26	44
Stenolaemata	2	2	2

Sponges represented the group with the highest species richness, with a total of 194 taxa. Of these,133 were recorded in algal bioconstructions, 111 in oyster bioconstructions, and 81 in scleractinian bioconstructions. The site with the highest sponge species richness was MON, hosting 56 taxa in algal bioconstructions and 60 in scleractinian bioconstructions. The class of Demospongiae was the most abundant, with 191 taxa spanning 17 orders, 43 families, and 90 genera and showing only slight differences between algal and invertebrate bioconstructions.

However, at the species level, a notable 28% of the sponge taxa were exclusive to algal bioconstructions (e.g. *Cacospongia mollior*, *Petrosia clavata*, *Didiscus stylifer*).

Cnidarians displayed an overall diversity of 22 species, with the highest species richness recorded in oyster bioconstructions (17 species). Nine of which (*Alcyonium coralloides*, *Caryophyllia (Caryophyllia) inornata*, *Caryophyllia (Caryophyllia) smithii*, *Corallium rubrum*, *Corallium rubrum*, *Hoplangia durotrix*, *Monomyces pygmaea* and *Stenocyathus vermiformis*) were exclusive to invertebrate bioconstructions. In contrast, 15 cnidarian species were identified in algal bioconstructions, with only two species exclusive of this type of bioconstructions (*Cladocora caespitosa* and *Madracis pharensis*).

Regarding molluscs, a total of 57 taxa were censused, with a higher number of species occurring in algal bioconstructions (40 species *vs.* 22 on MCB and 16 on MOB). Bivalves and gastropods exhibited similar species richness: 23 bivalves species identified in MAB, 13 in MCB, and 9 in MOB; while 16 gastropods were recorded in MAB, 9 in MCB, and 7 in MOB. The percentages of exclusivity were 15.8% for MCB (e.g. *Odostomella doliolum*, *Clanculus cruciatus*, *Turritellinella tricarinata*), 12.3% for MOB (e.g. *Carinorbis clathrata*, *Anomia ephippium*, *Sandalia triticea*) and 45.6% for MAB (e.g. *Mathilda gemmulata*, *Tectura virginea*, *Talochlamys multistriata*).

Among the 136 polychaete annelids detected, 119 (88%) were identified at the species level. Notably, 93 taxa were found in MAB, 62 in MCB, and 86 in MOB. Families Serpulidae, Syllidae, and Eunicidae were the most represented as species richness, with 39, 26, and 13 species, respectively across all bioconstruction types. The composition of exclusive species greatly varied among the different bioconstructions: at MAB, exclusive species were given by polychaetes from seven families represented mostly by one species each (except Phyllodocidae, which contained four species). In contrast, MOB was dominated by Serpulidae, which accounted for the highest percentage of exclusive species (56%).

Finally, of the 73 taxa of Bryozoa identified, 41 were found in MAB, 28 in MOB, and 46 in MCB. Almost all taxa belonged to the class Gymnolaemata and only one to Stenolaemata. The highest number of bryozoans taxa (27) was observed at SML, in association with oyster bioconstructions, while the lowest richness (10 species) was observed both in the algal bioconstructions of SML and the coral bioconstructions of SFC. Encrusting bryozoans exhibited nearly twice the species richness of erect forms in invertebrate bioconstructions, while upright forms dominated in mesophotic algal bioconstructions. Here, *P. fascialis*, *S. serratimargo*, *S. cervicornis*, *Scrupocellaria scrupea,* and *M. truncata* were the most frequent rigid erect species. Among the few flexible erect species observed, *Caberea boryi* and members of the family Bugulidae were the most common.

Several species of high conservation importance were identified within the analyzed mesophotic bioconstructions. Among cnidarians, the Mediterranean endemic *Cladocora caespitosa* (Annex II) and the red coral *Corallium rubrum* (Annex III) are protected under the Barcelona Convention. The bivalve *Lithophaga lithophaga*, also under strict protection, was found within perforated calcareous substrates. Similarly, *Spongia officinalis* is included in Annex III of the Barcelona Convention among poriferans.

Discussion

The considerable number of sites investigated in this study provides a comprehensive overview of the biodiversity patterns of the bioconstructions present in the mesophotic zone along the entire Apulian Adriatic coast. Our findings reveal significant variations in the

bioconstructions present within the twilight zone of the circalittoral plane. Major differences in taxonomic composition emerged in terms of both the builder species, responsible for constructing these structures, and the benthic communities they host. In particular, our study highlights a remarkable distinction in the taxonomic composition of the communities associated with algal and invertebrate-based bioconstructions. Although each community had a unique identity, they shared high levels of α-diversity.

Two major categories of bioconstructors were identified: encrusting calcareous coralline algae and, among invertebrates, scleractinians and bivalves. The distribution patterns of these bioconstructors are likely influenced by the gradual attenuation of solar radiation in the water column with increasing depth. Where both bioconstruction types coexist, invertebrate bioconstructions were arranged at greater depths than those built by algae. At our sampled sites, coralline algae, particularly *Peyssonnelia* and *Lithophyllum* species, dominated within the depth range of 25–35 m. In this zone, they built calcareous concretions composed of multiple smooth and thin carbonate layers a few centimetres thick, resulting in a relatively compact texture and making the bioconstructions ascribable to Coralligenous sensu Ballesteros (2006). These structures were locally rendered looser by cavities and holes produced by the action of bioeroders, such as boring sponges, as well as by discontinuities in the superposition of calcareous algal layers and animal skeletal clusters, in line with previous findings (Bracchi et al. 2022; de Luca et al. 2022, 2023). Although the species richness of these algae decreased with depth, their role as bioengineers can extend to depths of up to 120 m, depending on water transparency (Ballesteros 2006).

Along the Apulian Adriatic coast, at greater depths (45–65 m), bioconstructions were built by invertebrates with calcareous skeletons, specifically the nonsymbiotic scleractinian species *Phyllangia americana mouchezii* and *Polycyathus muellerae*, along with the bivalve *Neopycnodonte cochlear*. These invertebrate-dominated bioconstructions, unique for their large-scale extension and thickness, have recently been recorded in the Mediterranean Sea (Corriero et al. 2019). Scleractinian reefs represent a unique case of coral bioconstructions in coastal Mediterranean environments, differing from those built by other deep-water species, such as *Desmophyllum pertusum* and *Madrepora oculata*, which dominate in the Mediterranean bathyal environment (Tursi et al. 2004; Mastrototaro et al. 2010).

In the case of molluscs, comparable invertebrate-based bioconstructions have also been recorded in the Mediterranean Sea, where the congeneric deep-sea oysters *Neopycnodonte cochlear* and *N. zibrowii* are known to build up bioconstructions. While *N. zibrowii* has been identified as a bioengineer species, playing a key role in deep cold-water coral ecosystems (Taviani et al. 2011), *N. cochlear* was found to form biogenic structures in the mesophotic zone along both the northern (Angeletti and Taviani 2020) and southern Apulian coasts (Cardone et al. 2020, 2022). Similar to algal-based bioconstructions, these invertebrates structured complex bioconstructions, resulting in highly heterogeneous habitats that can reach several decimetres in thickness. These structures, characterized by numerous holes, cavities, and crevices, provide essential settlement opportunities for a diverse range of associated fauna.

The benthic communities associated with both algal- and invertebrate-based bioconstructions, showed similar levels of α-diversity but displayed remarkable differences in taxonomic composition across sites and bioconstruction types. While a partial overlap of benthic assemblages was observed, relatively few taxa were shared between the different bioconstructions. Differences in the composition of exclusive species, instead, likely contributed to the minor distinctions observed between MOB and MCB. In particular, molluscs and polychaetes mostly contributed to this separation, with MOB showing a higher proportion of exclusive gastropods and polychaetes species belonging

to the family Serpulidae, whereas MCB exhibited a more heterogeneous composition and a more diverse bivalve community. The presence of unique taxa in each bioconstruction type suggests distinct ecological niches (Gravina et al. 2021), highlighting the structural and functional importance of MOB and MCB as diverse components of mesophotic benthic ecosystems.

Some sponges, such as the massive demosponges *Agelas oroides*, *Axinella cannabina*, and *Petrosia ficiformis*, were shared across all types of bioconstructions. These sponges act as shapers of three-dimensional habitats, positively impacting local biodiversity (Longo et al. 2018). A similar role was played by bryozoans, with erect (e.g., *Myriapora truncata*, *Pentapora fascialis, Schizoretepora serratimargo*) and encrusting multilaminar (*Schizoporella mamillata* and *Schizomavella* spp.) colonies. Bryozoans occurred throughout the entire bathymetric range, with higher species richness in shallower layers, with extensive *P. fascialis* facies. Furthermore, in invertebrate bioconstructions, bryozoans mainly acted as binders, rather than as primary builders, forming small-sized encrusting colonies, such as *Microporella truncata, Cribrilaria setiformis* and *Puellina radiata* (Giampaoletti et al. 2020).

Polychaetes performed similar functions in both algal and invertebrate bioconstructions, where small vagile species thrived in cryptic microhabitats within the concretions, as observed in most Mediterranean coralligenous communities (Zibrowius 1968; Ballesteros 2006; Casoli et al. 2016). In contrast, numerous Serpulidae species acted as secondary builders, significantly contributing to the bioconstructions by shaping the structure, consolidating parts, increasing surface heterogeneity, and creating new microhabitats.

Finally, a key shared feature of both bioconstruction types was the presence of boring organisms. This functional group, comprising sponges (*Cliona celata, C. viridis*), molluscs (*Rocellaria dubia*, *Lithophaga litophaga*), polychaetes from the families Eunicidae and Cirratulidae, and sipunculids from the family Aspidosiphonidae, played a crucial role in maintaining the established balance between construction and bioerosion of the calcareous substrate (Glynn and Manzello 2015). The absence of bioeroders typically found in bioconstructions at an early stage, such as polychaetes from the family Spionidae (Casoli et al. 2015, 2019; Gravina et al. 2019), confirmed the mature stage of these bioconstructions.

Our results highlighted the crucial role of bioengineer diversity in driving habitat complexity and creating new substrates that increase the structural heterogeneity of the seabed in the mesophotic zone. The complexity of these structures provides new opportunities and niches with differentiated hydrodynamic, sedimentary, and microtopographic features, which are available for benthic communities. Indeed, the primary substrate, determined by the type of builder, has a strong influence on the diversity and species richness of the associated fauna, as also supported by studies on temperate and tropical bioconstructions, such as those in the eastern Atlantic and the Red Sea, where structurally complex habitats are created by similar bioengineering species (Beck 1998; Cerrano et al. 2019; Stefanoudis et al. 2019; Bell et al. 2022).

Our analysis of β-diversity revealed species turnover, mainly along the North–South geographical gradient, with the highest β-diversity values observed between the northernmost and southernmost sites. This pattern is consistent with oceanographic dynamics, particularly surface currents (Zavatarelli and Pinardi 2003), which flow from northwest to southeast along the Italian Adriatic coast, and play a key role in species connectivity and distribution. The transport of larvae and propagules along this gradient has been identified as a major factor influencing the differentiation and similarity of benthic assemblages in the mesophotic zone, as confirmed by studies on individual taxonomic groups, e.g. bryozoans (Giampaoletti et al. 2020) and polychaetes (Gravina et al. 2021).

Furthermore, β-diversity analysis revealed distinct individuality traits within algal bioconstructions, where high levels of species turnover have been recorded even between close sites. These findings align with the complex characterization of Apulian mesophotic habitats, where coralligenous formations are described as highly diversified and widely distributed biocenosis, covering over 400 km^2 (BIOMAP 2014). This bioconstruction gives rise to a heterogeneous mosaic of outcrops, dominated mainly by encrusting macroalgae and invertebrates, which allow several different assemblages to coexist in a small space (Parenzan 1983; Terlizzi et al. 2007; Ingrosso et al. 2018; Longo et al. 2018; Gimenez et al. 2022). Similarly, invertebrate bioconstructions exhibited a comparable degree of species turnover among nearby sites. Therefore, for the first time along the Italian coastline, our findings confirm the high spatial patchiness and structural complexity of invertebrate-based bioconstructions and their associated benthic communities, which were found to be similar to those recorded for algae-dominated bioconstructions.

Conclusion

Our study revealed that, despite sharing certain traits, the bioconstructions investigated in the mesophotic zone of the Apulian Adriatic coast exhibited additional distinctions in terms of primary builders and associated benthic assemblages, influenced by differences in geographic location. These variations are likely shaped by hydrological patterns that affect the dispersion of larvae and propagules, as well as by the decrease in irradiance with depth, which drives a shift in taxonomic composition from photoautotrophic species (algae) to heterotrophic species (scleractinians and oysters).

Both algal- and invertebrate-dominated bioconstructions generate highly heterogeneous habitats supporting unique faunal assemblages. In particular, invertebrate bioconstructions are structured by a combination of primary habitat formers and secondary builders, that promote the establishment of highly diverse associated communities. As a result, mesophotic bioconstructions emerge as remarkable biodiversity hotspots, hosting a wide range of species, many of which are of conservation concern. Within this framework, the Apulian coast represents a particularly valuable area, characterized by pronounced patchiness and high levels of both α- and β-diversity, as observed in this study. Given the increasing anthropogenic pressures on these ecosystems, these ecological features should be considered when implementing effective conservation measures.

Despite growing research on mesophotic bioconstructions, our understanding of their community dynamics and underlying ecological processes is still limited. A deeper understanding of their functional roles and connectivity with coralligenous assemblages in the Mediterranean Sea will inevitably improve our overall comprehension of mesophotic ecosystems and their potential contribution to the resilience of benthic communities.

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Declarations

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References

Anderson M, Gorley RN, Clarke KP (2019) for Primer: Guide to Software and Statistical Methods; PRIMER-e: Plymouth, UK, 2008

Angeletti L, Taviani M (2020) Offshore *Neopycnodonte* oyster reefs in the Mediterranean Sea. Diversity. https://doi.org/10.3390/d12030092

Ballesteros E (2006) Mediterranean coralligenous assemblages: a synthesis of present knowledge. Oceanogr Mar Biol Annu Rev 44:123–195

Basso D, Bracchi VA, Bazzicalupo P et al (2022) Living coralligenous as geo-historical structure built by coralline algae. Front Earth Sci 10:961632

Beaumont NJ, Austen MC, Atkins JP et al (2007) Identification, definition and quantification of goods and services provided by marine biodiversity: implications for the ecosystem approach. Mar Pollut Bull 54:253–265

Beck MW (1998) Comparison of the measurement and effects of habitat structure on gastropods in rocky intertidal and mangrove habitats. Mar Ecol Prog Ser 169:165–178

Bell JJ, Micaroni V, Harris B et al (2022) Global status, impacts, and management of rocky temperate mesophotic ecosystems. Conserv Biol. https://doi.org/10.1111/cobi.13945

BIOMAP (2014) A.A.V.V. Biocostruzioni Marine in Puglia (BIOMAP). P.O. FESR 2007/2013 - ASSE IV. Linea 4.4 - Interventi per la rete ecologica. Final technical report 250 pp.

Bouchet P, Rocroi J-P, Bieler R et al (2010) Nomenclator of bivalve families with a classification of bivalve families. Malacologia 52:1–184

Bouchet P, Rocroi J-P, Hausdorf B et al (2017) Revised classification, nomenclator and typification of gastropod and monoplacophoran families. Malacologia 61:1–526

Bouillon J, Medel MD, Pagès F et al (2004) Fauna of the Mediterranean hydrozoa. Sci Mar 68:5–438

Bouillon J, Gravili C, Pagès F, et al (2006) An introduction to Hydrozoa. Muséum national d'Histoire naturelle, Paris, 591 p. Mémoires du Muséum national d'Histoire naturelle 194

Bracchi V, Savini A, Marchese F et al (2015) Coralligenous habitat in the Mediterranean Sea: a geomorphological description from remote data. Italian J Geosci 134:32–40

Bracchi VA, Bazzicalupo P, Fallati L et al (2022) The main builders of Mediterranean coralligenous: 2D and 3D quantitative approaches for its identification. Front Earth Sci. https://doi.org/10.3389/feart.2022.910522

Bressan G, Babbiani L (2003) Corallinales del Mar Mediterraneo: Guida alla determinazione. Erredi Grafiche Editoriali S.n.c., Genova

Cardone F, Corriero G, Longo C et al (2020) Massive bioconstructions built by Neopycnodonte cochlear (Mollusca, Bivalvia) in a mesophotic environment in the central Mediterranean Sea. Sci Rep. https://doi.org/10.1038/s41598-020-63241-y
Cardone F, Corriero G, Longo C et al (2022) A system of marine animal bioconstructions in the mesophotic zone along the Southeastern Italian coast. Front Marine Sci. https://doi.org/10.3389/fmars.2022.948836
Casellato S, Stefanon A (2008) Coralligenous habitat in the northern Adriatic Sea: an overview. Mar Ecol 29:321–341. https://doi.org/10.1111/j.1439-0485.2008.00236.x
Casoli E, Ricci S, Belluscio A et al (2015) Settlement and colonization of epi-endobenthic communities on calcareous substrata in an underwater archaeological site. Mar Ecol 36:1060–1074
Casoli E, Bonifazi A, Ardizzone G, Gravina MF (2016) How algae influence sessile marine organisms: the tube worms case of study. Estuar Coast Shelf Sci 178:12–20
Casoli E, Ricci S, Antonelli F et al (2019) Colonization dynamic on experimental limestone substrata: the role of encrusting epilithics favouring boring polychaetes. Hydrobiologia 842:101–112
Cerrano C, Bastari A, Calcinai B et al (2019) Temperate mesophotic ecosystems: gaps and perspectives of an emerging conservation challenge for the Mediterranean Sea. Eur Zool J 86:370–388. https://doi.org/10.1080/24750263.2019.1677790
Cerrano C, Bakran-Petricioli T, Bastari A, et al (2015) Adriatic Sea: description of the ecology and identification of the areas that may deserve to be protected
Chimenz Gusso C, Nicoletti L, Bondanese C (2014) Briozoi, Biologia Marina Mediterranea
Clarke KR, Somerfield PJ, Chapman MG (2006) On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray-Curtis coefficient for denuded assemblages. J Exp Mar Biol Ecol 330:55–80. https://doi.org/10.1016/j.jembe.2005.12.017
Corriero G, Pierri C, Mercurio M et al (2019) A Mediterranean mesophotic coral reef built by non-symbiotic scleractinians. Sci Rep. https://doi.org/10.1038/s41598-019-40284-4
de Luca A, Lisco S, Acquafredda P et al (2023) The coralligenous in the present-day system from the Salento coast (southern Adriatic Sea). Rendiconti Online della Società Geologica Italiana 59:1–7. https://doi.org/10.3301/ROL.2023.16
de Luca A, Lisco S, Acquafredda P, et al (2022) An image analysis procedure to study the growth patterns of present-day coralligenous assemblages. In: 2022 IEEE International Workshop on Metrology for the Sea; Learning to Measure Sea Health Parameters (MetroSea). IEEE, pp 339–343
de Voogd NJ, Alvarez B, Boury-Esnault N, et al (2024). World Porifera Database. Accessed at https://www.marinespecies.org/porifera on 2024-03-11. https://doi.org/10.14284/359
Giampaoletti J, Cardone F, Corriero G et al (2020) Sharing and distinction in biodiversity and ecological role of bryozoans in Mediterranean mesophotic bioconstructions. Front Marine Sci. https://doi.org/10.3389/fmars.2020.581292
Gimenez G, Corriero G, Beqiraj S et al (2022) Characterization of the coralligenous formations from the marine protected area of Karaburun-Sazan, Albania. J Marine Sci Eng 10:1458. https://doi.org/10.3390/jmse10101458
Glynn PW, Manzello DP (2015) Bioerosion and coral reef growth: a dynamic balance. In: Birkeland C (ed) Coral reefs in the anthropocene. Springer, Netherlands, pp 67–97
Gravina MF, Antonelli F, Sacco Perasso C et al (2019) The role of polychaetes in bioerosion of submerged mosaic floors in the underwater archaeological park of Baiae (Naples, Italy). Facies 65:1–13
Gravina MF, Pierri C, Mercurio M et al (2021) Polychaete diversity related to different mesophotic bioconstructions along the southeastern Italian coast. Diversity. https://doi.org/10.3390/d13060239
Hong J-S (1982) Contribution à l'étude des peuplements d'un fond de concrétionnement Coralligène dans la région marseillaise en Méditerranée nord-occidentale. Ocean Polar Res 4:27–51
Hooper JNA, van Soest RWM, Philippe W (2002) Systema Porifera : a guide to the classification of sponges. Kluwer Academic/Plenum Publishers
Ingrosso G, Abbiati M, Badalamenti F et al (2018) Mediterranean bioconstructions along the Italian coast. Advances in marine biology. Academic Press, pp 61–136
Jaccard P (1901) Distribution de la flore alpine dans le bassin des Dranses et dans quelques régions voisines. Bull Soc Vaudoise Sci Nat 37:241–272
Koleff P, Gaston KJ, Lennon JJ (2003) Measuring beta diversity for presence–absence data. J Anim Ecol 72:367–382. https://doi.org/10.1046/j.1365-2656.2003.00710.x
Laborel J (1961) Le concrétionnement algal "coralligène" et son importance géomorphologique en Méditerranée. Rec Trav Stat Mar Endoume 23:37–60
Laborel J (1987) Marine biogenic constructions in the Mediterranean, a review. Sci Rep Port-Cros Natl Park 13:97–126

Legendre P, De Cáceres M (2013) Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. Ecol Lett 16:951–963. https://doi.org/10.1111/ele.12141
Longo C, Cardone F, Pierri C et al (2018) Sponges associated with coralligenous formations along the Apulian coasts. Mar Biodivers 48:2151–2163. https://doi.org/10.1007/s12526-017-0744-x
Mastrototaro F, D'Onghia G, Corriero G et al (2010) Biodiversity of the white coral bank off Cape Santa Maria di Leuca (Mediterranean Sea): an update. Deep-Sea Res Part II: Top Stud Oceanogr 57:412–430. https://doi.org/10.1016/j.dsr2.2009.08.021
MolluscaBase eds. (2024). MolluscaBase. Accessed at https://www.molluscabase.org on 2024-03-20. https://doi.org/10.14284/448
Montefalcone M, Tunesi L, Ouerghi A (2021) A review of the classification systems for marine benthic habitats and the new updated Barcelona convention classification for the Mediterranean. Mar Environ Res 169:105387
Ochiai A (1957) Zoogeographic studies on the Soleoid fishes found in Japan and its neighbouring regions. Bull Jap Soc Sci Fisher 22:526–530
Parenzan P (1983). Puglia Marittima 2. Congedo Editore, Galatina.
Pérès J-M, Picard J (1964) Nouveau manuel de bionomie benthique de la mer Méditerranée. Station Marine d'Endoume
Piazzi L, Cinti MF, Guala I et al (2021) Variations in coralligenous assemblages from local to biogeographic spatial scale. Marine Environ Res. https://doi.org/10.1016/j.marenvres.2021.105375
Pinna F, Piazzi L, Cinti MF et al (2021) Vertical variation of coralligenous cliff assemblages in marine biogeographic areas. Estuar Coast Shelf Sci 261:107554
Pyle RL, Copus JM (2019) Mesophotic coral ecosystems: introduction and overview. In: Loya Y, Puglise KA, Bridge TCL (eds) Mesophotic coral ecosystems. Springer, Cham, pp 3–27
Riding R (2002) Structure and composition of organic reefs and carbonate mud mounds: concepts and categories. Earth Sci Rev 58:163–231. https://doi.org/10.1016/S0012-8252(01)00089-7
Rosso A, Di Martino E (2016) Bryozoan diversity in the Mediterranean Sea: an update. Mediterranean Marine Sci 17:567. https://doi.org/10.12681/mms.1706
Rützler K (1978) Sponges in coral reefs. Coral reefs: research methods: monographs on oceanographic methodology
Spalding MD, Grenfell AM (1997) New estimates of global and regional coral reef areas. Coral Reefs 16:225–230. https://doi.org/10.1007/s003380050078
Stefanoudis PV, Rivers M, Smith SR et al (2019) Low connectivity between shallow, mesophotic and rariphotic zone benthos. R Soc Open Sci 6:190958. https://doi.org/10.1098/rsos.190958
Taviani M, Angeletti L, Antolini B et al (2011) Geo-biology of Mediterranean deep-water coral ecosystems. Marine Res CNR 6:705–719
Terlizzi A, Anderson MJ, Fraschetti S, Benedetti-Cecchi L (2007) Scales of spatial variation in Mediterranean subtidal sessile assemblages at different depths
Tursi A, Mastrototaro F, Matarrese A et al (2004) Biodiversity of the white coral reefs in the Ionian Sea (Central Mediterranean). Chem Ecol 20:107–116. https://doi.org/10.1080/02757540310001629170
Varzi AG, Fallati L, Savini A et al (2023) Geomorphology of coralligenous reefs offshore southeastern Sicily (Ionian Sea). J Maps 19:2161963. https://doi.org/10.1080/17445647.2022.2161963
Whittaker RH (1960) Vegetation of the Siskiyou mountains, Oregon and California. Ecol Monogr 30:279–338
Whittaker RH (1972) Evolution and measurement of species diversity. Taxon 21:213–251. https://doi.org/10.2307/1218190
Zabala M, Maluquer P (1988) Illustrated keys for the classification of Mediterranean Bryozoa. Museu de Zoologia, Ajuntament de Barcelona
Zavatarelli M, Pinardi N (2003) The Adriatic Sea modelling system: a nested approach. In: Annales Geophysicae. Copernicus GmbH, pp 345–364
Zibrowius H (1968) Etude morphologique, systematique et ecologique, des Serpulidae (Annelida, Polychaeta) de la region de Marseille. Rec Trav St Mar Endoume Bull 43:81–252

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