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Subtidal benthic assemblages in a mediterranean bank along a depth gradient: Conservation perspectives of a vulnerable marine ecosystem

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ABSTRACT

Banks are ecologically relevant seafloor structures recognized as biodiversity hotspots, covering a wide range of depths in several geological contexts and encompassing heterogeneous habitat types and benthic assemblages. They support vulnerable species and habitats of conservation interest, including coralligenous outcrops that are well known as nursery areas for several species, including commercial fish species, and as carbon-flow regulating regions. The vulnerability of this habitat, characterized by species with slow growth rates, long recovery periods and exposed to multiple anthropogenic pressures, makes the implementation of appropriate conservation and management measures an urgent priority. The present work aimed to investigate: the diversity and patterns of distribution of this benthic habitat, with a focus on habitat-forming species, together with the abundance and composition of benthic litter of a protected Mediterranean bank at several depth ranges. Overall, ROV video analyses highlighted the presence of 73 taxa, including species of high biological interest protected by international conventions, and provided evidence of the presence of invasive species in the investigated bank, such as the native polychaete *Hermodice carunculata* and the non-indigenous seaweed *Caulerpa cylindracea*. Coralligenous outcrops are impacted by anthropogenic marine litter, confirming the exploitation of the bank as a fishing area. All marine litter was represented by artificial polymer materials, consisting of Abandoned, Lost or otherwise Discarded Fishing Gears (ALDFGs). The contextual high abundance of ALDFGs and the low abundance of erect habitat-forming species observed in the deep waters document a long history of mechanical disturbance caused by both operating and lost demersal fishing gears. This study represents an integrative baseline of information for the implemented Special Area of Conservation (SAC) "Secca di Amendolara" and the recently instituted homonymous regional marine park, showing the importance of fine scale data to support management measures aimed at increasing the effectiveness of ongoing conservation plans.

1. Introduction

Among biodiversity hotspots, seamounts are ecologically relevant geological structures that cover a wide range of depths in several geological contexts, with different origins and features. They are characterized by important oceanographic processes and host heterogeneous habitats and communities (Würtz and Rovere, 2015). Seamounts can significantly influence the productivity of marine and coastal ecosystems, as well as the patterns of distribution and abundance of marine species, with functional effects on biological assemblages in

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nearby shallow and deep-sea environments (McClain, 2007). In the Mediterranean, 242 seamounts and analogous formations have been identified (Würtz and Rovere, 2015). However, it is estimated that several small and deep Mediterranean seamounts remain unexplored (Morato et al., 2012). Global estimates suggest the existence of a wide number of submarine structures, ranging from a few thousand to approximately 25 million, including a great array of heterogeneous environments, such as seamounts, reefs, banks, ridges, knolls, rises, hill, spurs, seamount chains, seamount groups (Yesson et al., 2011). Seamounts can reroute currents, affecting seawater circulation, water flow, current speed, wave generation, formation of eddies, local upwelling, and water mass stratification (White and Mohn, 2004). With effects on pelagic and benthic ecosystems, both on the top, bottom, and around the structures, even at remarkable distances, seamounts attract nektonic species from several tens of kilometers away (Morato et al., 2008). However, while several studies have addressed the geological aspects of the seamounts, biological information is available for less than half of the known seamounts (Würtz and Rovere, 2015). Some studies have demonstrated that seamounts are distinct marine ecosystems (Clark et al., 2010; Staudigel et al., 2010; Würtz and Rovere, 2015), supporting vulnerable species and habitats of conservation interest, such as coralligenous outcrops, *Posidonia oceanica* meadows, and rhodolith beds (e.g. Chimienti et al., 2020; Piazzi et al., 2024). As Mediterranean seamounts can be defined as rocky, geographically isolated topographic features higher than 100 m on the seafloor (Staudigel et al., 2010; Würtz and Rovere, 2015), coralligenous outcrops are one of the most common habitats found on these structures, due to the growth of coralline algal bioconstructor species in low light conditions (Salomidi et al., 2012; Martin et al., 2014; Ballesteros, 2006). In the Mediterranean Sea, coralligenous formations represent an important habitat, providing nursery grounds for several species, including commercial fish species, and regulating carbon fluxes (Martin et al., 2013). Multiple threats, such as mechanical disturbance, sediment suspension, fishing activities, wastewater discharges, aquaculture (Ballesteros, 2006; Martin et al., 2014), abandoned fishing nets and longlines from professional, artisanal, and recreational fishing, as well as infrastructure construction activities and unregulated anchoring, exert negative effects on the ecosystem services provided by this habitat (Ballesteros, 2006; Salomidi et al., 2012; Bevilacqua et al., 2018; Rizzo et al., 2021a). Additionally, acidification, thermal anomalies, storms, and invasive species can heavily affect several key species of the coralligenous habitat (Cerrano et al., 2000; De Caralt and Cebrian, 2013; Teixidó et al., 2013). The vulnerability of coralligenous environments, characterized by species with slow growth rates and long recovery periods (Clark et al., 2010), coupled with multiple threats, makes the implementation of appropriate conservation and management measures an urgent priority (Watling and Auster, 2021; Klaoudatos et al., 2024), as recognized by the Convention on Biological Diversity (CBD), the Food and Agriculture Organization (FAO) for fisheries and the United Nations General Assembly for conservation (Schlacher et al., 2014; Würtz and Rovere, 2015). The Natura 2000 (N2000) network (Evans, 2012) is the largest coordinated multinational network of protected areas in the world. It serves as a crucial conservation tool and supports the preservation of the most valuable species and habitats (Kati et al., 2014; Orlikowska et al., 2016). The N2000 network consists of Special Protection Areas designated under the EU Birds Directive (BD, Council of the European Communities, 1979) and Special Areas of Conservation (SAC) under the Habitat Directive (HD, Council of the European Communities, 1992), which is the EU's instrument for implementing the Bern Convention on the Conservation of European Wildlife and Natural Habitats. The N2000 network aims to monitor the habitats and species listed in the directives and to manage them to reach or maintain a favorable conservation status (Epstein et al., 2015; Kriegl et al., 2021). The presence of seamounts in N2000 sites can strategically cover a range of habitats and species, ensuring ecological connectivity and resilience across different areas, while supporting the spatial and functional connectivity between areas under different levels of protection, biodiversity targets, and the long-term sustainability of marine resources (Maes et al., 2012). Although conservation and management plans should be based on scientific evidence, the implementation of conservation measures is often hampered by knowledge gaps, insufficient data, and, inadequate resources for research activities (Pullin et al., 2004; Maiorano et al., 2007; Kati et al., 2014).

The aim of this study is to investigate the coralligenous formations of the Amendolara Bank (AMBK) SAC in the central Mediterranean Sea, a submarine extension of one of the most prominent morphological features of the 45 km long, NW-SE Amendolara Ridge, characterized by three bathymetric highs: the AMBK, the Rossano Bank (RBK) and the Cariati Bank (CBK) (Santoro et al., 2012). It is already included in the Atlas of Mediterranean Seamounts due to its ecological relevance (Würtz and Rovere, 2015). This bank is well known among fishers and scuba divers for the abundance of fish and the species richness of its seabed. Previous studies have shown a rich algal community and mollusk fauna (Perrone, 1985; Cecere and Perrone, 1988), as well as the presence of Vulnerable Marine Ecosystems (VMEs) at depths between 80 and 166 m (Palummo et al., 2024). The final aims are to: i) fill gaps in the diversity of mega- and macro-organisms associated with the seascape; ii) analyze the abundances of marine habitat-forming species associated with coralligenous sea bottoms; iii) investigate the distribution patterns of marine sessile assemblages associated with the coralligenous habitat; and iv) determine the abundance and composition of benthic litter in the SAC "Secca di Amendolara" and in surrounding sea bottoms of the AMBK, at different depth ranges (i.e. 30-35 m, 40–45 m, 50–55 m). These data, along with further actions carried out by other research groups within the ongoing CRIMAC projects (Centro Ricerche ed Infrastrutture Marine Avanzate in Calabria, e.g. Palummo et al., 2024), will not only provide baseline information for the already implemented N2000 site "Secca di Amendolara" and the recently established "Secca di Amendolara" Regional Marine Park, but will also support future assessments of the effectiveness of ongoing conservation policies.

2. Materials and methods

2.1. Study area

The AMBK is a SAC within the N2000 network of protected areas, the European network that covers the most valuable and threatened species and habitats (https://natura2000.eea.europa.eu/Natura2000/SDF.aspx?site=IT9310053). This SAC is located in the Mediterranean Sea within the Gulf of Taranto in the northern Ionian Sea (Perrone, 1985; Cecere and Perrone, 1988; Palummo et al., 2024). The SAC, with an overall extent of 660 ha, corresponds to the top on the western side of a large morphologically irregular bank with peaks and valleys, ranging from 21 to 60 m in depth and reaching the bottom at 125–250 m in depth (Ferranti et al., 2012; Würtz and Rovere, 2015). The area is also characterized by coralligenous formations interspersed with coastal detritic habitat and muddy bottoms.

Recently the Calabria Region, through Regional Law No. 288 of December 16, 2022 (http://burc.regione.calabria.it) established the "Secca di Amendolara" Regional Marine Park with the following objectives: i) conserving animal and plant species, biological communities, and unique faunal elements; ii) protecting biodiversity and maintaining the overall balance of the area; iii) preserving and enhancing the landscape values of the territory; iv) advancing scientific understanding of flora and fauna for monitoring and census purposes, especially focusing on endemic and rare species; and v) promoting tourism, culture, education, and recreation in ways that are compatible with the conservation of nature and the landscape.

2.2. Data collection

Three bathymetric ranges (i.e. D1 = 30–35 m; D2 = 40–45 m; D3 = 50–55 m) were identified and within each bathymetric range, three linear transects of 200 m each, spaced approximately 50–100 m apart, were surveyed using a Remotely Operated Vehicle (ROV) in July 2022 (Fig. 1). The ROV, specifically a Deep Trekker DTG3, was equipped with a Full HD video camera for high-resolution video-photographic recording, as well as an internal compass for navigation, a coupled Ultra Short Baseline (USBL) geographic positioning system (Tritech MicronNav 100), a depth sensor, LED lights (1000 lumens), and two laser beams for area size estimation, with a separation of 10 cm (Chimienti et al., 2018, 2020), according to the European standards provided by the Marine Strategy Framework Directive (MSFD) (MATTM, 2019).

2.3. Benthic taxonomic richness of the Amendolara Bank

The acquisition of ROV videos were performed to characterize benthic biodiversity (both algal and faunal benthic taxa) of the AMBK and analyzed using VLC software, at the three depths surveyed. Updated taxonomy and nomenclature followed the World Register of Marine Species (WoRMS Editorial Board, 2024). Taxonomic richness indices were calculated for all transects for algae and invertebrates. Data are presented as mean ± standard error.

2.4. Habitat-forming species

Habitat formers were recorded, and their abundances calculated according to the extent of the coralligenous habitat within each transect. In addition, the percentage of epibiosis and necrosis on the species' tissue was assessed according to four categories (0–25%, 25–50%, 50–75%, 75–100%) and the habitat-forming species caught in the ALDFG were reported (MATTM, 2019). Data are reported as mean ± standard error.

2.5. Sessile benthic coverage of coralligenous formations

To evaluate the composition and structure of sessile benthic assemblages of coralligenous habitat, 20 frames were randomly extracted from each video transect. According to the minimal area proposed by Weinberg (1978) for the study of Mediterranean Sea benthic assemblages, each frame was selected to define an area of 2.5 ± 0.2 m^2, which was subsequentially applied for ROV imaging (Chimienti et al., 2018, 2020). ROV transects were planned based on previously acquired Multibeam Echosounder (MBES) information for the generation of the Digital Elevation Model (DTM) of the study area. After the MBES campaign, the second activity performed was the Side Scan Sonar (SSS) acquisition, and the data gathered led to the production of the habitat map on which the ROV transects were designed. The contribution of each taxon identified to the highest possible taxonomic resolution level to the percentage cover of the sessile benthic assemblage was calculated by analyzing each frame extracted from each video using photoQuad software (20 frames per transect, 60 frames per depth, 180 frames per area).

2.6. Litter

Benthic litter items were recorded and classified by material (e.g., cotton, glass, metal, nylon, paper, plastic, ceramics, concrete, rubber, synthetic fibers, and manufactured wood) and presumed land- or sea-based origin (Crocetta et al., 2020). Abandoned, lost, or otherwise discarded fishing gear (ALDFG) was recorded (Rizzo et al., 2021a, 2022, 2024). Abundance (items 100 m^{-2}) was calculated according to the transect area. Data are reported as mean ± standard error.

2.7. Statistical analyses

Multivariate and univariate analyses of variance (PERMANOVA, Anderson, 2001; McArdle and Anderson, 2001) were used to assess differences: i) in benthic taxonomic composition among depths; ii) in abundances of habitat-forming species; and iii) in litter abundances at different depths.

To explore patterns of spatial variability of the sessile benthic assemblage cover percentage, a PERMANOVA analysis was used to test for differences, using the following hierarchical sampling design: Depth (De, as a fixed factor with 3 levels), and Transect (Tr(De), as a random factor with 3 levels), with n = 20 frames from each ROV video transect. Univariate PERMANOVA analyses were based on Euclidean distances on untransformed data, and multivariate PERMANOVA analyses were based on Bray-Curtis dissimilarities for biological variables using 9.999 random permutations of the appropriate units (Anderson and Braak, 2003). When significant differences were encountered ($p < 0.05$), post-hoc pairwise tests for the fixed factor were used to determine the consistency of the differences. In cases of a restricted number of unique permutations, p-values were obtained from Monte Carlo sampling in the pairwise tests. Differences in benthic assemblages among investigated depths were illustrated through a Canonical Analysis of Principal coordinates (CAP) plot. To determine whether the environmental and biological conditions (i.e., depth, litter abundance, habitat-forming species abundance) influenced benthic composition associated with the coralligenous habitat, we carried out multivariate multiple regression analyses (Distance-based linear models, DistLM, McArdle and Anderson, 2001) and performed distance-based Redundancy Analysis (dbRDA) plots. Analyses were performed using the PRIMER v. 6 software including the PERMANOVA add-on package (Clarke and Gorley, 2001; Anderson, 2008).

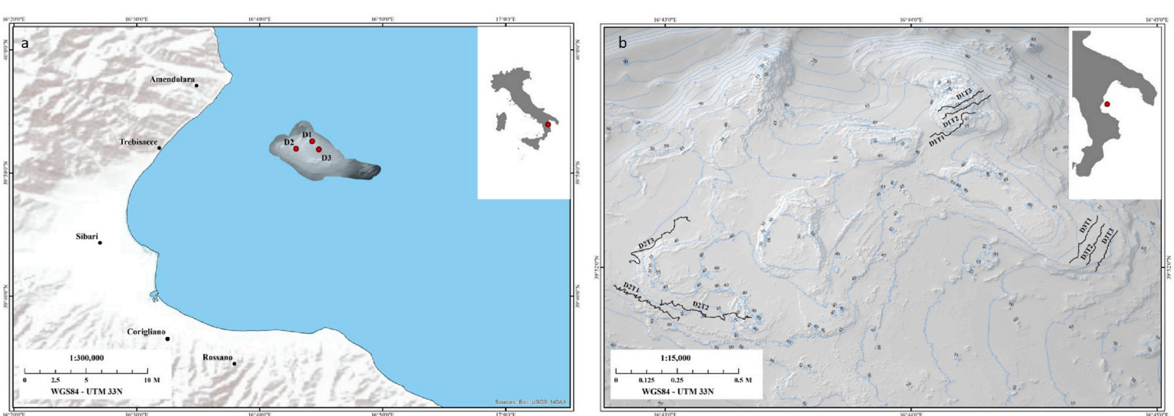

Fig. 1. a) The Gulf of Taranto and its position in the Mediterranean Sea (top right). Small coastal town are highlighted in black. Investigated areas (D1: ~30–35 m; D2: ~40–45 m; D3: ~50–55 m) are highlighted by a red point on DEM of the Amendolara Bank (AMBK); b) Position of the transects on hillshade model of the AMBK and bathymetry lines (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article).

3. Results

3.1. Benthic taxonomic richness of the Amendolara Bank

Overall, the analysis of the ROV videos revealed the presence of 73 taxa in the AMBK. Among the recorded taxa, the non-indigenous species (NIS) *Caulerpa cylindracea* Sonder, and the native invasive polychaete *Hermodice carunculata* (Pallas, 1766), were reported. The AMBK seabed hosts some megabenthic species of high biological interest protected by international conventions, such as the sponges *Aplysina aerophoba* (Nardo, 1833), *Axinella cannabina* (Esper, 1794), *Geodia cydonium* (Linnaeus, 1767), and *Sarcotragus foetidus* Schmidt, 1862, listed in Annex II of the Barcelona Convention; the echinoderm *Centrostephanus longispinus* (Gmelin, 1791) and the pen shell *Pinna nobilis* Linnaeus, 1758, in Annex IV of the Habitat Directive and Annex II of the Barcelona Convention; the tonnid gastropod *Tonna galea* (Linnaeus, 1758) and the sponge *Axinella polypoides* Schmidt, 1862, both in Annex II of the Barcelona Convention and Annex II of the Bern Convention, and the European spiny lobster *Palinurus elephas* (Fabricius, 1787), listed in Annex III of the Barcelona Convention and Annex III of the Bern Convention.

Significant differences in taxonomic richness were observed at D3 (13.16 ± 1.82 taxa 100 m^{-2}) when compared with benthic assemblages found at D1 (17.80 ± 1.47 taxa 100 m^{-2}) and D2 (8.24 ± 0.64 taxa 100 m^{-2}) (Tables 1 and 2, Fig. 2). Multivariate PERMANOVA on the taxon presence/absence matrix showed significant differences in the composition of the benthic assemblages found at D1 and D3 (Tables 1 and 2), which were mainly characterized by sponges at D3 and algal species at D1 (Fig. 3). More specifically, the benthic community at D1 was dominated by algal species (8.19 ± 0.47 taxa 100 m^{-2}), as *C. cylindracea*, *Codium bursa* (Linnaeus) C. Agardh, *Cystoseira* species, *Dictyota* species, and *Palmophyllum crassum* (Naccari) Rabenhorst. Algal diversity was significantly reduced at D2 (3.78 ± 0.24 taxa 100 m^{-2}) and D3 (4.07 ± 0.37 taxa 100 m^{-2}), (Fig. 2, Tables 1 and 2). Significant low values of faunal richness were found at D2 (4.47 ± 0.41 taxa 100 m^{-2}) when compared to the diversity found at D1 (9.61 ± 1.05 taxa 100 m^{-2}), and D3 (9.09 ± 1.46 taxa 100 m^{-2}) (Table 1, Fig. 2).

3.2. Habitat-forming species

The AMBK was characterized by five main potential habitat-forming

Table 1
Results of the univariate permutational analyses (PERMANOVA) on taxonomic richness related to benthic organisms, algae and benthic fauna and multivariate permutational analysis (PERMANOVA) on taxon presence/absence among depths (D1: ~30–35 m; D2: ~40–45 m; D3: ~50–55 m). De - depth; Res - residual; Tot - total; df - degrees of freedom; MS - mean squares; Pseudo-F - F critic; P(perm) - permutational level of probability. * - $p < 0.05$; ns - not significant.

Source	df	MS	Pseudo-F	P(perm)
Benthic diversity				
De	2	68.53	11.62	*
Res	6	5.90		
Tot	8			
Algal diversity				
De	2	18.29	44.64	*
Res	6	0.41		
Tot	8			
Faunal diversity				
De	2	24.05	7.05	*
Res	6	3.41		
Tot	8			
Taxon presence/absence matrix				
De	2	1378.90	2.48	*
Res	6	5156.64		
Tot	8			

Table 2
Results of the pairwise tests on taxonomic richness related to algal assemblages at the investigated depths (D1: ~30–35 m; D2: ~40–45 m; D3: ~50–55 m). *vs* - *versus*; t - pairwise tests; P(MC) - probability level after Monte Carlo simulations; * - $p < 0.05$; ns - not significant.

Groups	t	P(MC)
Benthic diversity		
D1 *vs* D2	5.96	**
D1 *vs* D3	1.98	ns
D2 *vs* D3	2.55	ns
Algal diversity		
D1 *vs* D2	8.40	**
D1 *vs* D3	6.93	**
D2 *vs* D3	0.67	ns
Faunal diversity		
D1 *vs* D2	4.54	*
D1 *vs* D3	0.29	ns
D2 *vs* D3	3.05	*
Taxon presence/absence matrix		
D1 *vs* D2	1.12	ns
D1 *vs* D3	2.12	*
D2 *vs* D3	1.41	ns

species, the Mediterranean gorgonian *Eunicella singularis* Verrill, 1869, the erect bryozoans *Myriapora truncata* (Pallas, 1766), and *Pentapora fascialis* (Pallas, 1766) and the sponges *Axinella polypoides*, *Axinella cannabina* and *Sarcotragus foetidus*. At D2, three colonies of *Pentapora fascialis* were trapped in ALDFG. The abundance of each habitat-forming species varied among the three investigated depths, with D1 and D2 mostly characterized by the bryozoans *Pentapora fascialis* (6.81 ± 2.81 and 11.98 ± 4.36 col. 100 m^{-2}) and *Myriapora truncata* (1.47 ± 0.85 and 1.53 ± 1.15 col. 100 m^{-2}) and D3 by the sponges *Axinella polypoides* (2.52 ± 1.23 ind. 100 m^{-2}), and *Sarcotragus foetidus* (8.81 ± 3.73 ind. 100 m^{-2}). However, no differences in their abundance were observed among depths, the gorgonian *Eunicella singularis* was only present at D2, with an average of 4.34 ± 0.80 col. 100 m^{-2} (Table 3, Fig. 4). The percentage of necrosis/epibiosis on each specimen/colony recorded fell into the lower category (0–25%).

3.3. Sessile benthic assemblages

Multivariate permutational analysis of variance on bio-coverage revealed strong significant differences among transects within the investigated depths, as indicated by the significant Tr(De) term (Table 4). Multivariate pseudo variance components showed that residual variability among assemblages, from one replicate to the next, was larger than the component of variation measured among transects, indicating that small-scale variability was relevant (Table 4). Pairwise comparisons showed significant differences between D3 and D1, while no differences were found between D1 and D2 and D2 and D3 (Table 5). The CAP plot showed the dominance of algal components (*Dictyota* species, *Dudresnaya verticillata* (Withering) Le Jolis, *Cystoseira* species, *Codium bursa*, *Caulerpa cylindracea*) at the shallow depths D1 and D2, while the benthic assemblages at D3 were mainly characterized by massive sponges (*Sarcotragus foetidus*, *Chondrosia reniformis* Nardo, 1847; *Ircinia* species) (Fig. 5).

3.4. Benthic litter

The AMBK SAC was affected by 24 items. The source of pollution was exclusively marine (i.e., ALDFG), and the only material category reported was artificial polymer. The highest litter abundance was found at D3 (2.55 ± 1.07 items 100 m^{-2}), followed by the abundance recorded at D1 (0.96 ± 0.05 items 100 m^{-2}) and D2 (0.52 ± 1.16 items 100 m^{-2}). However, the PERMANOVA analysis on the total litter abundance (expressed in the number of items 10 m^{-2}) revealed no differences due to the high variability of the data (Table 6). The benthic litter included

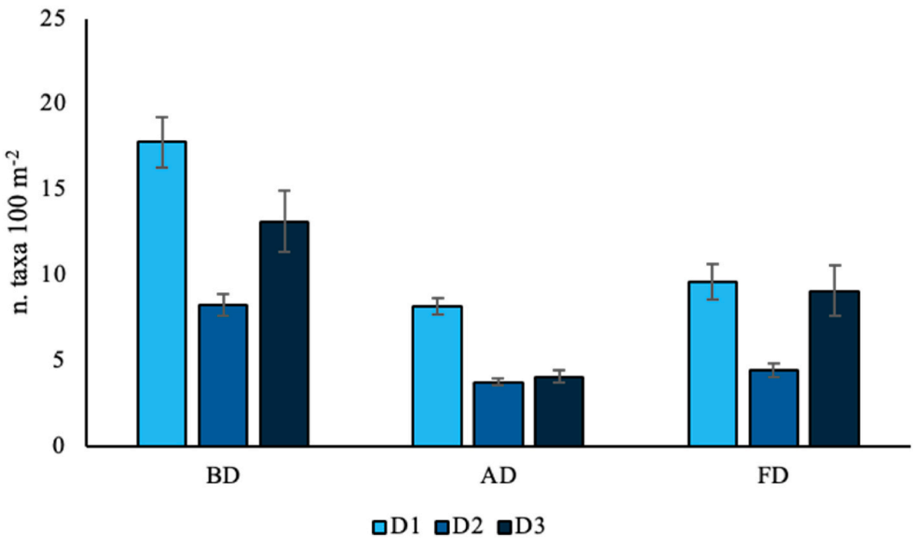

Fig. 2. Taxonomic richness index for benthic (bd), algal (ad) and faunal (fd) diversity, at the three investigated depths (D1: ~30–35 m; D2: ~40–45 m; D3: ~50–55 m).

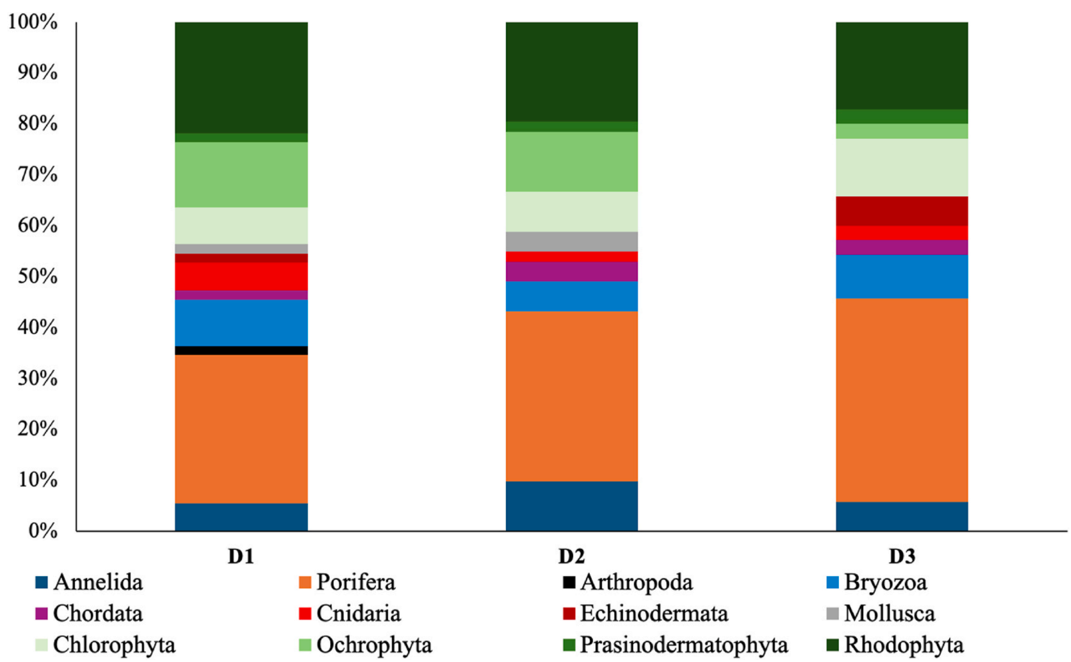

Fig. 3. Stacked bar-plot of the benthic taxonomic richness at phylum level at the investigated depths (D1: ~30–35 m; D2: ~40–45 m; D3: ~50–55 m).

fishing lines and ropes at D1 and D2, while in deeper water (i.e., D3), fishing lines and nets were found (Table 6). PERMANOVA analyses performed on each litter type highlighted the presence of discarded ropes only at D1 and D2 (D1 vs D3, $t = 4.82$, $p < 0.01$; D2 vs D3, $t = 3.32$, $p < 0.05$), since this litter type was absent at D3 (Fig. 6).

The results of the DistLM analyses revealed that depth significantly explained variations in benthic composition (36%), followed by litter abundance (13%) and abundance of habitat forming species (7%). Together, these investigated variables altogether explained cumulatively 56% of the variation in benthic taxonomic composition (Table 7). The results of the dbRDA analysis indicated that depth and litter abundance cumulatively explained about 49% of the variation in benthic composition for the first two axes (Fig. 7).

4. Discussion

4.1. The mesophotic benthic assemblages of the Amendolara Bank

Bathymetric gradients play a crucial role in the structure of benthic assemblages strongly influencing the distribution of organisms along changes in light, temperature, salinity, and pressure with depth (Irving and Connell, 2002; Martí et al., 2005; Terlizzi et al., 2007; Manokaran et al., 2022). Mapping activities of the AMBK revealed that this area is extremely rich in biodiversity with values and taxa composition comparable to other Mediterranean areas explored using ROVs (Bo et al., 2012a; Rizzo et al., 2021a), including banks and shoals (De la Torriente et al., 2018; Enrichetti et al., 2019, 2023). In addition, as observed in other shoals (Enrichetti et al., 2019, 2023), the AMBK bottoms host some benthic species of high biological interest, protected by international conventions, which require appropriate conservation measures.

Table 3
Results of the univariate permutational analyses (PERMANOVA) on abundances of habitat forming species (i.e. *Axinella cannabina, A. polypoides, Eunicella singularis, Myriapora truncata, Pentapora fascialis, Sarcotragus foetidus*) among depths (D1: ~30–35 m; D2: ~40–45 m; D3: ~50–55 m). De - depth; Res - residual; Tot - total; df - degrees of freedom; MS - mean squares; Pseudo-F - F critic; P(perm) - permutational level of probability. * - $p < 0.05$; ** - $p < 0.01$; ns - not significant.

Source	df	MS	Pseudo-F	P(perm)
Axinella cannabina (colonies 100 m^{-2})				
De	2	0.12	0.68	ns
Res	6	0.17		
Tot	8			
Axinella polypoides (colonies 100 m^{-2})				
De	2	4.56	2.55	ns
Res	6	1.79		
Tot	8			
Eunicella singularis (ind 100m^{-2})				
De	2	18.81	29.39	*
Res	6	0.64		
Tot	8			
Myriapora truncata (colonies 100 m^{-2})				
De	2	1.25	0.60	ns
Res	6	2.08		
Tot	8			
Pentapora fascialis (colonies 100 m^{-2})				
De	2	102.26	3.79	ns
Res	6	27.02		
Tot	8			
Sarcotragus foetidus (colonies 100 m^{-2})				
De	2	36.57	1.69	ns
Res	6	21.69		
Tot	8			

Our results further support the idea that accurate marine mapping is critical to support a wide variety of marine policies (Fraschetti et al., 2024). Large areas remain unmapped and current knowledge still predominantly focus on physical aspects of marine habitats and lack sufficient biological resolution. Fine scale knowledge is needed to better represent the linkages between the seabed and water column in three dimensions: most of these species are suspension feeders, a diversified group that performs fundamental functions in benthic-pelagic coupling, by transferring energy and organic matter (Rizzo et al., 2021b; Rossi and Rizzo, 2021; Rossi et al., 2019, 2022). Previous studies at similar depths (Irving and Connell, 2002; Terlizzi et al., 2007) have shown that benthic assemblages are mostly characterized by algal components at shallow depths, while algal diversity decreased significantly in the deeper transects. Sessile benthic assemblages associated with the coralligenous habitat followed a similar bathymetric trend, exhibiting significant differences between the rocky communities found at 30–45 m and those recorded at 50–55 m. The development of different coralligenous communities depends on a variety of ecological factors changing with depth

Table 4
Results of the multivariate permutational analysis (PERMANOVA) and multivariate variance components (VC) on percentage cover values of sessile organisms among depths (D1: ~30–35 m; D2: ~40–45 m; D3: ~50–55 m). De - depth; Res - residual; Tot - total; df - degrees of freedom; MS - mean squares; Pseudo-F - F critic; P(perm) - permutational level of probability. * - $p < 0.05$; *** - $p < 0.001$.

Source	df	MS	Pseudo-F	P(perm)
De	2	4333.40	2.33	*
Tr(De)	6	1855.80	3.36	***
Res	171	551.90		
Tot	179			
Estimates of components of variation				
Source	Estimate	Square root		
S(De)	41.29	6.43		
V(Tr(De))	65.20	8.07		
V(Res)	551.90	23.49		

Table 5
Results of the pairwise tests on percentage cover values of sessile organisms among depths (D1: ~30–35 m; D2: ~40–45 m; D3: ~50–55 m). *vs* - *versus*; t - pairwise tests; P(MC) - probability level after Monte Carlo simulations; * - $p < 0.05$; ** - $p < 0.01$; *** - $p < 0.001$; ns - not significant.

Groups	t	P(MC)
D2 *vs* D1	1.43	ns
D2 *vs* D3	1.45	ns
D1 *vs* D3	1.69	*

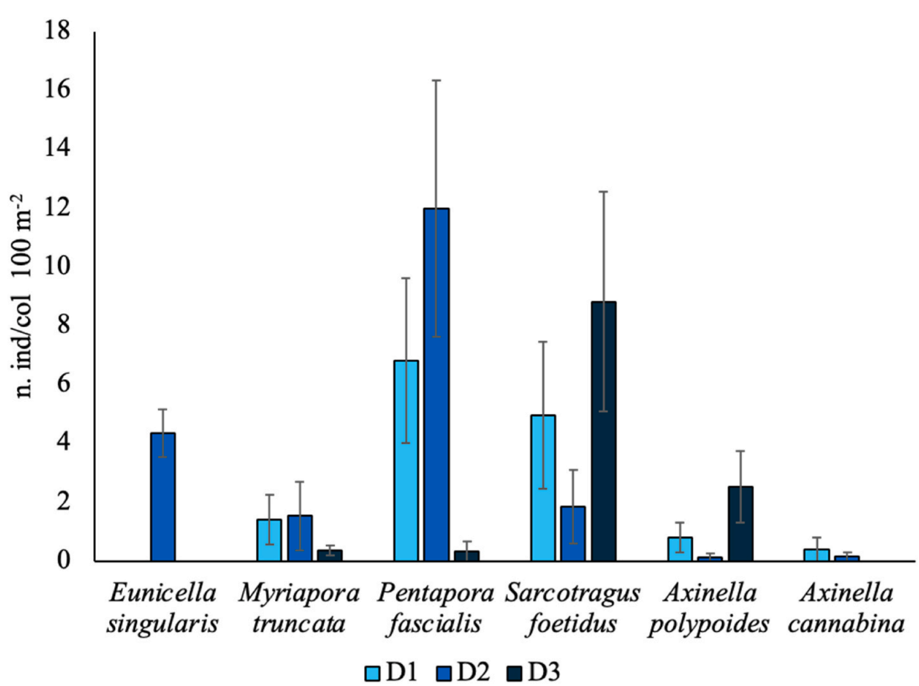

Fig. 4. Abundances of habitat forming species found at the three investigated depths (D1: ~30–35 m; D2: ~40–45 m; D3: ~50–55 m).

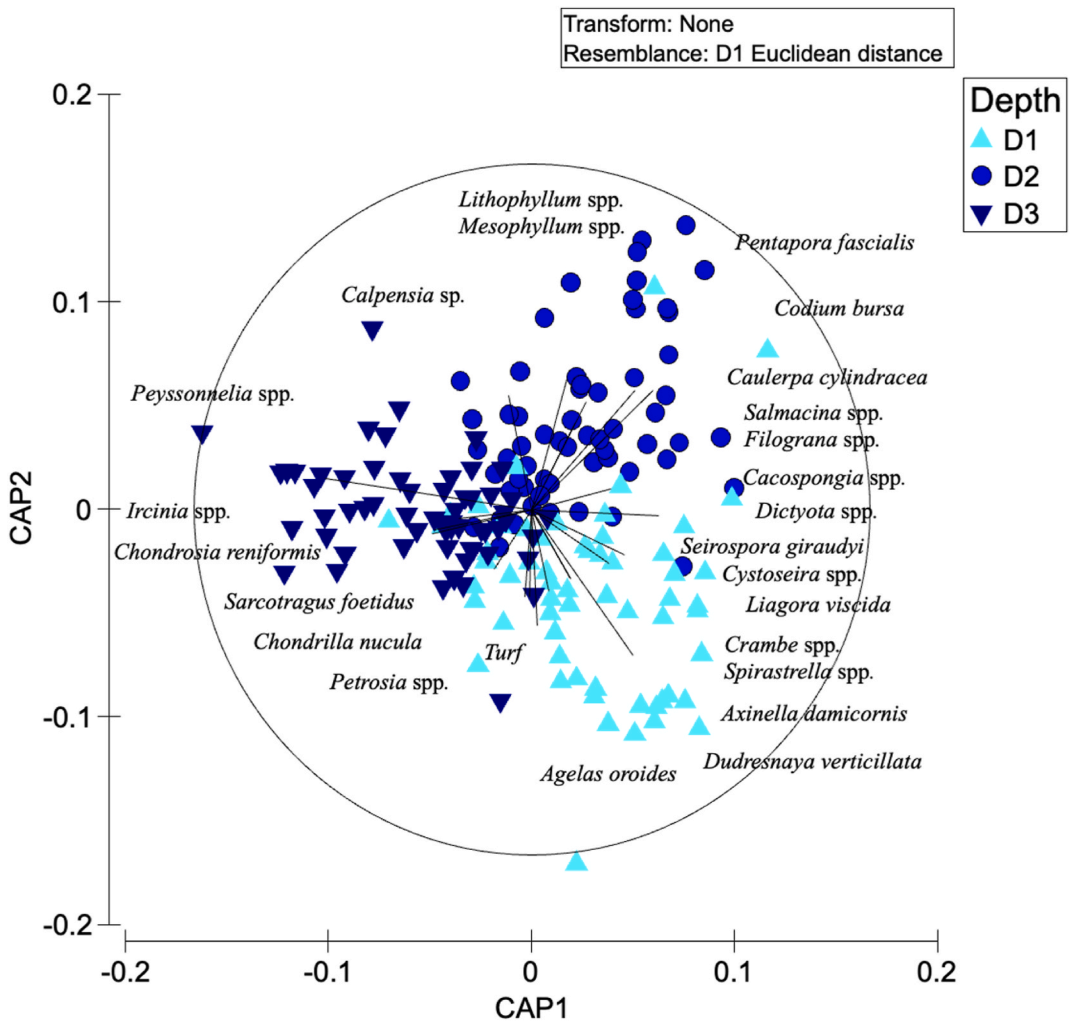

Fig. 5. Canonical analysis of principal coordinates (CAP) plot showing the discrimination based on percentage cover values of sessile organisms among depths ((D1: ~30–35 m; D2: ~40–45 m; D3: ~50–55 m). Vectors are proportional to the Pearson correlation (r > 0.2).

Table 6
Results of the univariate permutational analyses (PERMANOVA) on abundances of benthic litter and litter types among depths (D1: ~30–35 m; D2: ~40–45 m; D3: ~50–55 m). De - depth; Res - residual; Tot - total; df - degrees of freedom; MS - mean squares; Pseudo-F - F critic; P(perm) - permutational level of probability. ** - $p < 0.01$; ns - not significant.

Source	df	MS	Pseudo-F	P(perm)
Litter abundance (n items 100 m^{-2})				
De	2	3.42	2.93	ns
Res	6	1.17		
Tot	8			
Fishing line abundance (n items 100 m^{-2})				
De	2	3.51	2.53	ns
Res	6	1.39		
Tot	8			
Rope abundance (n items 100 m^{-2})				
De	2	0.48	12.54	**
Res	6	0.04		
Tot	8			
Net abundance (n items 100 m^{-2})				
De	2	0.26	2.74	ns
Res	6	0.09		
Tot	8			

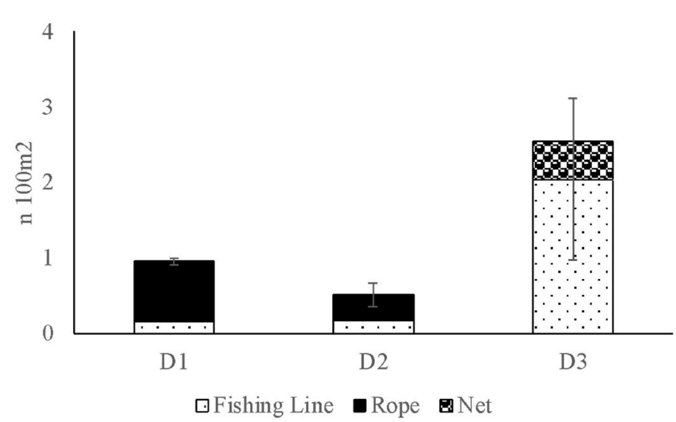

Fig. 6. Abundances of benthic litter found at the three investigated depths (D1: ~30–35 m; D2: ~40–45 m; D3: ~50–55 m).

(Ingrosso et al., 2018) and holds true regionally for coralligenous assemblages along the Apulian coasts (Longo et al., 2018; Piazzi et al., 2019). A high small-scale variability also emerged, in line with the high structural and spatial variability of coralligenous assemblages reported in the literature for the Mediterranean basin and the Apulian continental shelf (Terlizzi et al., 2007; Piazzi et al., 2019; Casoli et al., 2024).

Table 7
DistLM analyses estimating the proportion of taxonomic composition variation explained singularly (marginal tests) and cumulatively (sequential tests) by biological and environmental conditions. *** - $p < 0.001$; * - $p < 0.05$; ns - not significant. Prop. - proportion of explained variance. Cumul. - cumulative results.

MARGINAL TESTS			
Variable	p	Prop.	
Depth	***	0.36	
Litter abundance	*	0.28	
Habitat forming species abundance	ns	0.07	
SEQUENTIAL TESTS			
Variable	p	Prop.	Cumul.
Depth	***	0.36	0.36
Litter abundance	ns	0.13	0.49
Habitat forming species abundance	ns	0.07	0.56

Despite its relative proximity to the Calabrian coast (located about 6 M away), no strong links with the nearest littoral assemblages have been highlighted and the AMBK can be considered a typical temperate mesophotic rocky reef (Cerrano et al., 2019; Bell et al., 2022). Indeed, the nearby northern Calabrian and Lucanian Ionian coasts are characterized by an alternation of pebble and sandy beaches, extending to the north-western hard coast of Puglia (Taranto, 40 M NE) and the southern Calabrian coast (Punta Alice, 34 M SE; Promontory of Capo Rizzuto, 60 M SE) (Angiolillo et al., 2009; Canese et al., 2009; Cardinali et al., 2009; Bo et al., 2012a; Giakoumi et al., 2013; Bracchi et al., 2016; Longo et al., 2018). The multiple slopes, depth and exposure gradients due to the complex topographic features of this bank favor the co-occurrence of several benthic organisms, making the area an hotspot of biodiversity (Perrone, 1985; Cecere and Perrone, 1988; Palummo et al., 2024). Other two mesophotic morphological features are known in the area, the RBK and the CBK, still remaining unexplored (Würtz and Rovere, 2015). Baseline studies and mapping efforts including also these features would increase local biodiversity knowledge with the potential of defining present status and potential connections among the three banks within the northern Ionian basin.

4.2. Habitat-forming fauna of the coralligenous habitat in the Amendolara Bank

The habitat-forming fauna includes several benthic suspension feeders from coastal to deep waters, with ecological relevance as biodiversity hotspots, nursery grounds, and ecosystem service providers (Rossi et al., 2019, 2022). A recent survey of the AMBK in the 80–166 m depth range highlighted several VME species indicators, including the black coral *Antipathella subpinnata* (Ellis & Solander, 1786), the red coral *Corallium rubrum* (Linnaeus, 1758), the yellow coral *Dendrophyllia cornigera* (Lamarck, 1816), and the orange fan sponge *Poecillastra compressa* (Bowerbank, 1866) (Palummo et al., 2024). The shallow depth range (30–55 m) investigated here emphasized different habitat-forming species. The observed stratified structure of the coralligenous assemblages reflects general features of the Mediterranean Sea coralligenous habitat (Casoli et al., 2024), where encrusting algae form the basal layer, bryozoans create the intermediate layer, and anthozoans dominate the upper layer. At all depths investigated, the coralligenous habitat was structured by erect bryozoans including *Myriapora truncata* and

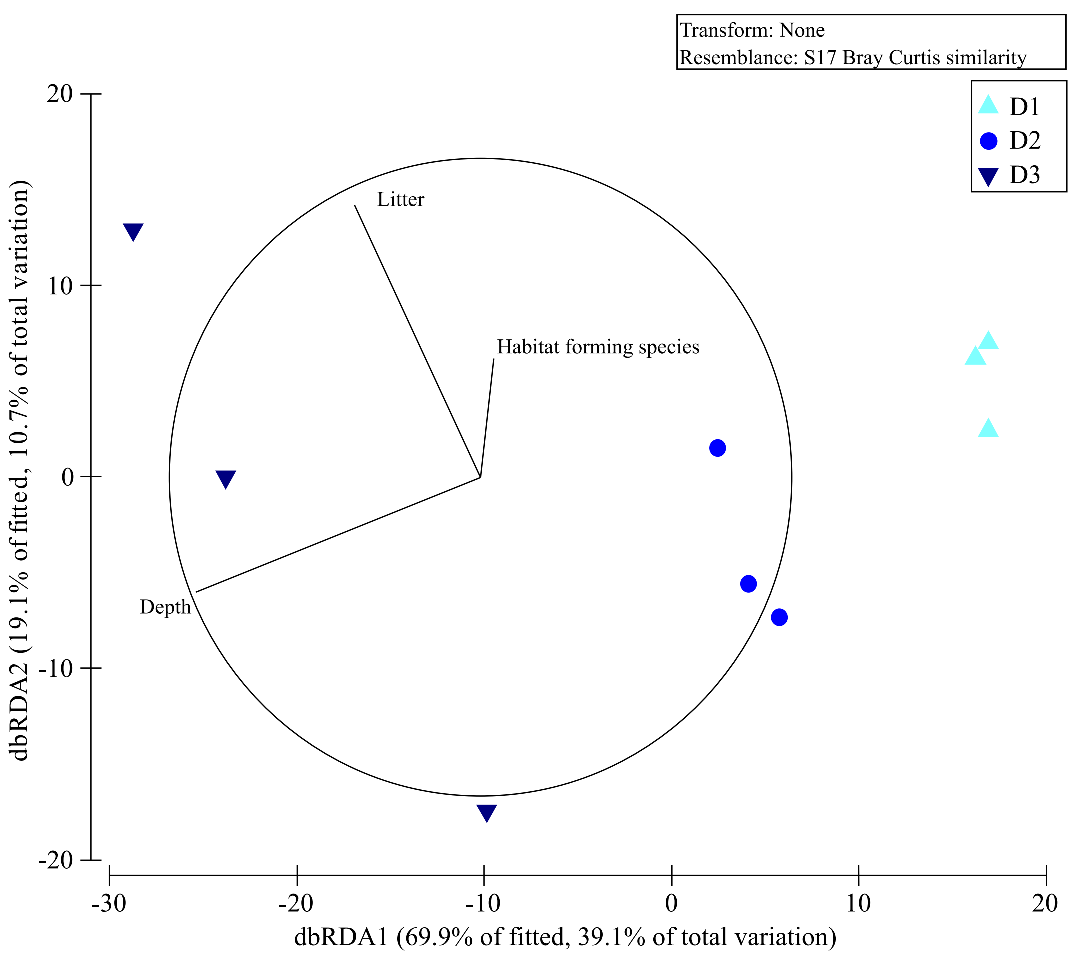

Fig. 7. DbRDA ordination after DistLM analysis, showing the relationships among the biologica and environmental conditions and taxonomic benthic composition. D1: ~30–35 m; D2: ~40–45 m; D3: ~50–55 m.

Pentapora fascialis. The branched bryozoan *Myriapora truncata* occurs in the Mediterranean Sea and along the Atlantic coasts of southern Spain on sheltered hard substrates from the shallow subtidal to 60 m depth (Ballesteros, 2006), while the bryozoan *Pentapora fascialis* develops into wide erect foliose structures reaching 20–30 cm in diameter and occurs along the coasts of Britain and the Mediterranean Sea basin, providing habitat for other species and representing an important benthic carbonate producer (Cocito and Ferdeghini, 2001). In the Gulf of Taranto, these species have also been reported at a distance of 65 M from the Promontory of Capo Rizzuto, in the coralligenous habitat of Gallipoli (on the Apulian side), and in previous surveys in the AMBK at similar depths (SICDM-MSFD, 2024). Molecular studies of these habitat-forming bryozoans are needed to understand the potential genetic connectivity of these populations.

The transects conducted at 40–45 m depth were characterized by the presence of the zooxanthellate *Eunicella singularis*, one of the most representative gorgonians of the Mediterranean Sea sublittoral communities. This species can acquire additional carbon and nitrogen from its symbionts, as evidenced by the carbon used to construct the spicules, which is mainly derived from the external medium via the activity of its symbiotic zooxanthellae (Cocito et al., 2013). The records of this species reported here represent the first record for the Ionian-Calabrian coasts, although the species is also reported for the Calabrian-Tyrrhenian coast and in the Apulian-Ionian Sea (e.g., Nicotera, Gallipoli; SICDM-MSFD, 2024).

The deeper transects performed in this study at 50–55 m depth are characterized by a few erect habitat-forming species, consisting of the forementioned erect bryozoans and the sponge *Axinella polypoides*. The habitat-forming sponge *Sarcotragus foetidus* was found associated with other massive sponges (e.g., *Ircinia* species). Keratose-sponge grounds are common in the Mediterranean Sea, although historically they have been reported as more abundant along coastal cliffs and shoals (Enrichetti et al., 2023). In general, sponges represent an important component of coralligenous communities in terms of taxonomic richness, actively contributing to the creation and destruction of biogenic substrates since the Porifera phylum can act as both habitat builders and eroders. Therefore, further investigations of their distribution throughout the bank could help to assess the ecosystem functions performed in the regional system of the northern Ionian Sea.

Overall, there are still some gaps in the knowledge of the bioconstructions of the Calabrian Ionian coasts. Despite the relatively large distances between coralligenous coastal areas in the northern Ionian Sea, they could be connected to each other and to the several banks (e.g., AMBK, CBK, RBK). The few explorations of this long coast have shown very rich communities (e.g. Bo et al., 2011, 2012a, 2012b; MoBioMarCal Project; SICDM-MSFD, 2024). The scarcity of published data prevents a comprehensive overview of the biodiversity associated with the coralligenous habitat in the AMBK with the adjacent rocky subtidal coastal areas (e.g., Taranto, Capo Rizzuto, Cetraro, Capo Colonna). However, the framework of the MSFD should provide an excellent opportunity to provide new information on both “Biodiversity” and “Sea-floor Integrity” descriptors of the “Good Environmental Status” (GES) which should be regularly monitored to ensure that the structure and the functioning of these ecosystems are safeguarded and benthic ecosystems are not adversely affected,. Therefore, systematic studies on the patterns of distribution of biodiversity in nearby areas could represent an important opportunity to explore the benthic rocky biodiversity of the RBK and CBK and to evaluate the potential ecological connections with the investigated AMBK. Furthermore, the conservation of VMEs is a legal obligation for Regional Fishery Management Organizations, the Food and Agriculture Organization of the United Nations (FAO) General Fishery Commission for the Mediterranean (GFCM), however, once again, the scarce information on the distribution of VMEs species represents a severe constraint in implementing local protection (Auster et al., 2011; Marín et al., 2019). Therefore, further investigations will be crucial to ascertain whether the bank supports distinct characteristics in species abundance and composition compared to the others and the coast.

4.3. Pressures on the Amendolara Bank: environmental status and conservation perspectives

The historical exploitation of the Amendolara Bank is well-known (Würtz and Rovere, 2015), with evidence of the extensive impact of fishing activities on its megabenthic communities reported by Palummo et al. (2024) and in the present study. Banks and shoals are commonly exploited worldwide and in the Mediterranean Sea, as substantial aggregations of mid- and deep-water fishes can be the target of highly developed commercial fisheries (Morato et al., 2007; Würtz and Rovere, 2015; Palummo et al., 2024). In the present research, all marine litter was represented by artificial polymer materials, in particular, all items were ALDFGs, confirming the exploitation of the bank as a fishing area. Fishing gear accounted for almost the total litter in other Mediterranean areas (Angiolillo et al., 2015; Consoli et al., 2019; Rizzo et al., 2024) and is known to cause marine habitat degradation, sediment suspension, and a reduction in species abundance and diversity (Crocetta et al., 2020; Consoli et al., 2019; Soares et al., 2020, 2023). As revealed in the present research, several mesophotic Mediterranean sites are also known to be affected by fishing activities (Bo et al., 2014; Angiolillo et al., 2015; Angiolillo and Fortibuoni, 2020; Enrichetti et al., 2019, 2023), which can lead to declines in both target and non-target species, causing indirect effects on marine communities, and altering the structure and function of aquatic ecosystems (Lleonart and Maynou, 2003; Worm et al., 2006). The composition of the benthic litter suggests that artisanal and recreational fishing are the main sources of anthropogenic litter in the AMBK. Unfortunately, it was not possible to distinguish the source of litter between recreational and artisanal fishing. The risk of seabed entanglement with nets, longlines, and ropes may be frequent and increasing in the deepest bathymetry surveyed. The recorded litter suggests that fishers tend to deploy their gear directly over coralligenous outcrops, increasing the potential number of entanglements, as also shown in other shoals (Richardson et al., 2021; Enrichetti et al., 2019, 2023). However, European trends indicate a decrease in artisanal fishing effort due to low average income from catches, fuel costs, and the risk of losing fishing gear, occasionally coupled with an increase in recreational fishing in coastal waters (Lloret et al., 2018; Enrichetti et al., 2019, 2023).

The reported litter density values are slightly lower than those found in the deeper seafloor of the AMBK by Palummo et al. (2024), where the authors identified a site heavily impacted by ALDFG from fishing (e.g., longlines), which can cause various types of impacts to benthic communities, especially on erect structuring benthic species leading to abrasion and entanglement (Angiolillo and Fortibuoni, 2020). This aligns with what was observed here, where three colonies of *Pentapora fascialis* were trapped by ALDFGs. It is noteworthy that in the deep transects investigated here a low abundance of erect habitat-forming species was observed alongside a high abundance of ALDFGs, suggesting a long history of mechanical stress caused by both operating and lost demersal fishing gears. Recently, a restrictive regulation on fishing activities adopted by the management body of the Regional Marine Park "Secca di Amendolara", which includes the investigated SAC, has contributed to preventing further damage to benthic assemblages and strengthening the effective management of the investigated Natura 2000 site, under investigation. As observed in other locations, fishing can cause changes in the size structure of anthozoan populations, provoking tissue necrosis and a consequent decline in marine populations (Enrichetti et al., 2023). However, the low signs of epibiosis observed here can typically characterize natural populations (Bo et al., 2014; Angiolillo et al., 2015), along with a few cases of trapped colonies. Overall, our results suggest a good to moderate environmental status, in line with the ecosystem health status of other shoals (Enrichetti et al., 2023). The investigated area was proposed as a Site of Community

Importance (SCI) in 1995 and designated as a SAC in 2017, representing a fundamental step toward achieving good management. Appropriate management measures for recreational and professional fishing activities must be implemented in the investigated area under Article 6 of HD, which requires the management organization (i.e., the Calabrian Region) to take measures within its Natura 2000 sites to maintain and restore habitats and species in a favorable conservation status, avoiding activities that could significantly disturb these species, result in the deterioration of their habitats or damage habitat types. The Advanced Marine Research and Infrastructure Center in Calabria (CRIMAC) is promoting regional sustainable development strategies in Calabria through constructive dialogue among researchers, policymakers and stakeholders. The activities of the CRIMAC projects are enhancing our understanding of the Calabrian marine coastal environments and in particular, the outcomes of the CRIMAC projects on AMBK have supported the establishment of the Regional Marine Park, thereby strengthening management measures. Indeed, without an effective implementation of management measures, Natura 2000 sites could risk being a "paper park", while unregulated resource exploitation, fishery malpractices, litter accumulation and illegal fishing activities could lead to a progressive degradation of benthic habitats (Matz-Lück and Fuchs, 2014).

Besides direct impacts on benthic assemblages, global environmental changes can lead to profound alterations in marine ecosystems. Rising temperatures can foster the ecological success of non-indigenous species and support the expansion of thermophilic native species (Carey et al., 2012). All the analyzed ROV videos showed the presence of the invasive alga *Caulerpa cylindracea*. This invasive seaweed is known to have negative effects on benthic habitats, both by modifying the composition of organic matter and microbial communities (Rizzo et al., 2016a, 2016b, 2020; Stabili et al., 2016, 2017). Additionally, we report here the presence of the Mediterranean Sea fireworm *Hermodice carunculata*, a thermophilic polychaete inhabiting rocky coastal habitats (Righi et al., 2020), which has recently been reported to have expanded its abundance and distribution northward in the Mediterranean Sea (Krželj et al., 2020; Righi et al., 2020; Toso et al., 2022), with potential negative impacts on the benthic food web, composition, and functioning of rocky habitats in the Mediterranean Sea (Krželj et al., 2020). Further studies are needed to assess the distribution and abundance of *H. carunculata* as well as specific studies aimed at monitoring NIS and implementing early detection of potentially invasive species and adopting appropriate management measures to reduce potential impacts on the benthic communities of the AMBK.

5. Conclusions

In mesophotic rocky environments of the AMBK, artisanal and recreational demersal gears are employed and sometimes lost on the seafloor causing the degradation of the environmental status of benthic assemblages by potentially reducing its distribution, abundance, and height of habitat-forming species. Further scientific knowledge regarding environmental and anthropogenic pressures will be essential to provide information for the implementation of effective management measures for the appropriate protection of benthic habitats, allowing the long-term sustainability of marine biological resources. Overall, considering the significant distance of the investigated area from the nearest coasts, the reduced exploitation by artisanal fishery, and the characteristics of the habitat investigated, the study area is characterized by generally good environmental conditions. However, our results suggest that the Management Body should pay attention to the effects of fishing activities, which are the main cause of the observed litter and related consequences for the benthic communities (ie., trapped colonies, damages or epibiosis phenomena of erect species). This calls for more restrictive management solutions. Although the pressure of artisanal fishery seems to be decreased in the last years, both professional and recreational fishing activities could require stricter management measures for the protection of coralligenous assemblages. Discarded gear has been observed affecting coralligenous substrates, protected under the Annex I of EU's Habitats Directive (1170 Reefs), the Bern Convention, and the European Red List of Marine Habitats. The recent establishment of the "Secca di Amendolara" Regional Marine Park represents an important step in this context and reinforces the current objectives aimed at biodiversity conservation, advancement of scientific knowledge of flora and fauna, as well as the promotion of sustainable tourism, culture, and education. As a complement to the existing measures, and based on the findings of the present study, the following management actions are suggested: i) restricted permissions for professional and recreational fishermen and the implementation of logbooks; ii) measures discouraging the use of vertical lines, trolling activities, and longlines, including limitations on the maximum length of nets and longlines; iii) an obligation to immediately discard non-target species within the fishing area; iv) adaptive management measures, including awareness campaigns and training courses for fishers, divers, and other stakeholders, aimed at promoting a sustainable and aware use of biological resources. Finally, since habitat-forming populations could be connected by larval dispersal, the management of all anthropogenic pressures should be harmonized within the network of Natura (2000) marine sites and Marine Protected Areas in the northern Ionian Sea to sustain population connectivity at regional level. The MSFD could provide significant tools to explore the benthic biodiversity of the RBK and CBK, evaluate their potential ecological connections with the investigated AMBK, and assess anthropogenic pressures on their seafloors, in line with Target 1 of the EU Biodiversity Strategy which calls for important improvements in the conservation status of species and habitats protected under the EU HD. Extending the boundaries of the protected area to include the whole AMBK and the nearby RBK and CBK would result in more effective protection for the northern Ionian area, including the protection of several types of coralligenous habitats. Furthermore, the extension of the boundaries is in line with the most recently updated international policy, which aims to protect at least 30% of the world's oceans by 2030, including several habitats. Finally, complementary approaches should include the implementation of environmental marine litter cleanup campaigns and the definition of education and sensibilization programs for artisanal and tourist/recreational fishers, to achieve the full sustainability of marine coastal activities.

CRediT authorship contribution statement

Lucia Rizzo: Writing – review & editing, Writing – original draft, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Andrea Picciolo:** Writing – review & editing, Methodology, Formal analysis, Data curation. **Giulio Tarantino:** Writing – review & editing, Methodology, Formal analysis, Data curation. **Luciana Muscogiuri:** Writing – review & editing. **Simonetta Fraschetti:** Writing – review & editing, Funding acquisition. **Antonio Terlizzi:** Writing – review & editing, Funding acquisition. **Paolo D'Ambrosio:** Writing – review & editing, Funding acquisition.

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Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: The present study was supported by the "Core-Calabria" project of the Centro Ricerche ed Infrastrutture Marine Avanzate in Calabria (CRIMAC, CUP C64I20000320001), Ministero dell'Università e della Ricerca (MUR, Roma) from FSC 2014–2020 resources, by the project "The role of marine animal forests in protecting marine resources from the invasive species" (MANIFEST, CUP B53D23023660001) funded by the European Union - Next Generation EU and the Italian Ministry for Universities and Research within the PRIN-PNRR 2022, and by the National Recovery and Resilience Plan (NRRP), Project code CN_00000033, Concession Decree No. 1034 of June 17, 2022 adopted by the Italian Ministry of University and Research, Project title "National Biodiversity Future Centre - NBFC". The contribute of the EU project HORIZON-CL6-2021-BIODIV-01-12 "MarinePlan—Improved trans-disciplinary science for effective ecosystem-based maritime spatial planning and conservation in European Seas", No 101059407 is also acknowledged.

Data availability

Data will be made available on request.

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