



Biodiversity of Mediterranean mesophotic rhodolith beds: Macrofaunal community composition and structure (SW Italy)

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ABSTRACT

Rhodolith beds are structurally complex biogenic habitats that support high biodiversity of associated benthic organisms. In the Mediterranean Sea, they are recognized and protected under European Community legislation, yet their structural complexity and associated biodiversity remain poorly documented, particularly in deeper environments. This study investigates rhodolith beds and their associated macrofaunal assemblages at four mesophotic sublittoral sites (50–71 m) along the Tyrrhenian coast of the Campania Region (Capri Island, Secchiello Shoal, Ischia Island, and Cilento Coast). Significant differences among sites were observed in terms of rhodolith cover and morphotype diversity, quantified through a 3D Complexity Index as a proxy of habitat structural complexity, but no significant differences in terms of live/dead rhodolith ratio were found. Overall, the rhodolith-associated community was dominated by Polychaeta, Mollusca, Crustacea, and Echinodermata. Polychaetes accounted for the highest total abundance (1299 individuals across 65 species), while molluscs were the most species-rich group (109 species from 518 individuals). Crustaceans and echinoderms contributed less to overall diversity but were consistently present across sites. The Cilento site exhibited the highest rhodolith cover and complexity (3D Complexity Index = 1.83 ± 0.62) and correspondingly supported the most abundant and species-richest benthic assemblage (131.50 $\pm$ 41.83 individuals; 47 $\pm$ 4.15 species). A general positive correlation was found between rhodolith cover and macrofaunal abundance and richness, highlighting the importance of rhodoliths in enhancing benthic biodiversity. In terms of functional trophic structure, carnivores and deposit feeders emerged as the dominant feeding guilds (DI = 38% - DQ = 37%; DI = 33% - DQ = 23%, respectively), reflecting a complex food web supported by both prey availability and the capacity of the habitat to retain detrital material. Beyond their physical role as habitat-forming, rhodoliths also contribute functionally by facilitating the accumulation of particulate organic matter and supporting a detritus-based trophic web. In fact, trapped detritus and surface biofilms fuel their basal trophic levels, where deposit feeders act as key energy processors driving also a bottom-up control of the benthic food web. These results confirm that rhodolith beds act as ecosystem engineers and biodiversity enhancers in Mediterranean coastal ecosystems. Given their ecological significance and vulnerability, especially in underexplored mesophotic environments, targeted conservation efforts are urgently needed to protect these benthic biodiversity hotspots.

1. Introduction

Rhodolith or maerl Beds (RBs) are marine habitats formed by the accumulation of free-living, non-geniculate coralline algae (Corallinophycidae, Rhodophyta; Foster, 2001). They occur worldwide, typically on muddy, sandy, or pebbly substrates, from the low intertidal zone down to depths exceeding 150 m (Birkett et al., 1998; Steller et al., 2003; Aguilar et al., 2009; Foster et al., 2013). Indeed, their ability to thrive in mesophotic, low-light conditions is also related to the optical

properties of their carbonate skeleton (Balestrieri et al., 2025). These rhodolith-forming algae are recognized as ecosystem engineers (Hinojosa-Arango and Riosmena-Rodríguez, 2004; Rindi et al., 2019; Tuya et al., 2023) and primary foundation species (Bulleri et al., 2025), capable of building three-dimensional biogenic structures analogous to other complex marine habitats, such as coral reefs (Alvarez-Filip and Dulvy, 2009), vermetid reefs (Donnarumma et al., 2018a, 2018b), coralligenous assemblages (Ferrigno et al., 2024), seagrass beds (Heck and Wetstone, 1977), mangroves (Nagelkerken et al., 2008), and brown

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macroalgal forests (Graham, 2004; Rendina et al., 2023).

Due to their calcium carbonate skeleton, rhodoliths provide hard substrata for the settlement of epilithic macroalgae and invertebrates, while their branching morphology creates sheltered microhabitats that support rich infaunal communities (Steller et al., 2003; Harvey and Bird, 2008). These habitats provide several regulating, provision, cultural and supporting ecosystem services (Rendina et al., 2026), and offer multiple ecological functions: refuge from predation (Kamenos et al., 2004), food supply for suspension feeders and deposit feeders (Grall et al., 2006), and modification of local hydrodynamics that enhance larval retention and settlement (Johnson et al., 1991; Steller et al., 2003), providing a key nursery role (Kamenos et al., 2004; Coccozza di Montanara et al., 2025), also for species of commercial interest (Hall-Spencer et al., 2003, 2006; Grall and Hall-Spencer, 2025). Several studies report that rhodoliths host higher abundance and diversity of benthic fauna compared to surrounding and underlying sediment (Cabioch, 1970; Bosence, 1979; Rebecchi et al., 2022; Neves and Costa, 2022; Coccozza di Montanara et al., 2025). According to Steller et al. (2003), the structure of rhodolith-associated communities is shaped by various environmental and biological factors, including seasonal changes in light and temperature, substrate composition, live/dead rhodolith ratio, and thallus morphological complexity.

In the Mediterranean Sea, RBs are characterized by different combinations of coralline algal species and morphotypes (Chimienti et al., 2020; Rendina et al., 2020a; Bracchi et al., 2022; Caronni et al., 2023). Basso (1998) classified the main Mediterranean rhodolith morphotypes as "boxworks", "pralines", and "unattached branches". Boxworks are irregular rhodoliths with macroscopic voids that may trap sediments or host infauna. Pralines are compact, generally monospecific rhodolith nodules with a clear nucleus and no voids. If the algal portion comprises <50% of the nodule volume, they are referred to as "coated grains". Unattached branches, or "märl" *sensu stricto* (Jardim et al., 2025a), are branched rhodoliths lacking a central nucleus, typically composed of *Lithothamnion corallioides* or *Phymatolithon calcareum*.

These morphotypes contribute to the formation of spatially heterogeneous substrates, enhancing ecological niche availability for invertebrates that use rhodolith beds as refuge, feeding grounds, or nursery habitats (Soto, 1990; Mannino et al., 2002; Castriota et al., 2003; Pierri et al., 2024; Coccozza di Montanara et al., 2025). For this reason, Mediterranean rhodolith beds are increasingly recognized as biodiversity hotspots, alongside coralligenous reefs, *Posidonia oceanica* beds, and vermetid reefs (Ballesteros, 1989; Ramos-Esplá and Luque, 2004, 2008; Barberá et al., 2012; Basso et al., 2017).

Nonetheless, despite their ecological significance and EU-level protection, knowledge about Mediterranean RBs remains insufficient (Rendina et al., 2022), particularly concerning their distribution, structural complexity, and associated community structure (Schermer et al., 2010; Gondim et al., 2014; Basso et al., 2017; Otero-Ferrer et al., 2019). This gap is partly due to the logistical challenges of studying these mesophotic habitats compared to extra-Mediterranean shallower beds.

For this reason, the aims of the present study are (i) to analyse the rhodolith abundance and structural complexity (rhodolith morphotypes) in four sites of the Mediterranean Sea (Italy), (ii) to evaluate the associated benthic community composition and structure, and (iii) to compare RB and associated community structures to understand the role of rhodolith complexity as biodiversity enhancer.

2. Materials and methods

2.1. Sampling design

The study areas were chosen based on records of four rhodolith deposits along the Campania Coast, in the eastern Tyrrhenian Sea (Italy). These RBs have previously been mapped and characterized in terms of their spatial extent, geomorphological features, and coralline algal

composition (Rendina et al., 2020a), as well as marine litter and fishing gear occurrence (Rendina et al., 2020b). Additionally, two of these beds were investigated for meiofaunal community composition (Coccozza di Montanara et al., 2025). However, no data were previously available on their macrofaunal community composition and structure. This study was carried out during the summer season, between 2016 and 2017, in four sites (Fig. 1): Capri Island (June 2016; 40°32'11.638"N 14°13'21.213"E), sampled between 55 and 62 m depth; Secchitiello Shoal (June 2016; 40°34'45.024"N 14°17'14.880"E), sampled between 68 and 71 m depth; Ischia Island (June 2017; 40°44'25.354"N 13°50'26.506"E), sampled between 58 and 62 m depth; Cilento Coast (July 2017; 40°7'8.642"N 15°3'42.021"E), sampled between 55 and 65 m depth. At each site, six random samples were collected using a 25 l Van-Veen grab, within zones characterized by high rhodolith cover identified during previous remotely operated vehicle surveys.

A sieve of 1 mm mesh was used to separate macrofauna. Samples were fixed in a 4% formalin-seawater solution and then transported to the laboratory. After 48 h, samples were transferred into a 70% ethanol solution. For each sample, all rhodoliths and sediment were carefully analysed under a stereomicroscope. In detail, unattached branches and praline morphotypes were thoroughly inspected, and all macro-invertebrates associated with algal branches and protuberances were removed. Boxwork rhodoliths, when present, were additionally examined and gently fractured, when necessary, to inspect internal cavities and retrieve associated fauna. When possible, all macrobenthos was identified at species level, under a Leitz stereomicroscope. Invertebrate nomenclature follows the World Register of Marine Species database (WoRMS Editorial Board, 2025).

2.2. Data analysis

In order to establish the RB features, all rhodoliths from each sample were disposed on a 35 × 35 cm² square (corresponding to the grab sampling area) and then photographed to obtain high resolution images. For each square/image, the surface percentage cover by rhodoliths, live/dead rhodolith ratio, and rhodolith morphotypes (pralines, boxworks, and unattached branches, *sensu* Basso et al., 2016) were estimated using the image analysis software VidAna© 1.0 (Hedley, 2003). The adopted morphotype classification follows the standardized protocol proposed for Mediterranean RBs by Basso et al. (2016), currently applied within the framework of the EU Marine Strategy Framework Directive (European Parliament, 2008). This approach is specifically designed to assess bed-scale structural heterogeneity and provides a regionally consistent framework for ecological monitoring and comparison among Mediterranean RBs. Moreover, to estimate and quantify the three-dimensional (3D) structure of each bed a 3D Complexity Index (3DCI) was implemented, based on the different combination of rhodolith morphotypes:

$$3DCI = e^{(\alpha^* \ln \alpha) + (\beta^* \ln \beta) + (\gamma^* \ln \gamma)}$$

Where α , β , and γ represent the relative percentage cover of pralines, boxworks and unattached branches, respectively. The index ranges between 1 and 3, where 1 indicates the exclusive presence of one morphotype (lower structural complexity) and 3 equal abundances of the three morphotypes (higher structural complexity).

Total cover of rhodoliths, relative cover of live-to-dead rhodoliths and the 3DCI among the four sites were analysed by univariate PERMANOVAs, based on similarity matrixes of Euclidean distances, and pairwise tests were run to estimate differences between pairs of sites (Anderson, 2001).

Faunal assemblages were analysed using sinecological indices, *i.e.* species richness (SR), number of individuals (N), Shannon-Weaver diversity (H'), and Pielou's Evenness (J). The quantitative and qualitative dominances (%DI and %DQ, respectively) of the main taxa Mollusca, Polychaeta, Crustacea and Echinodermata were also calculated.

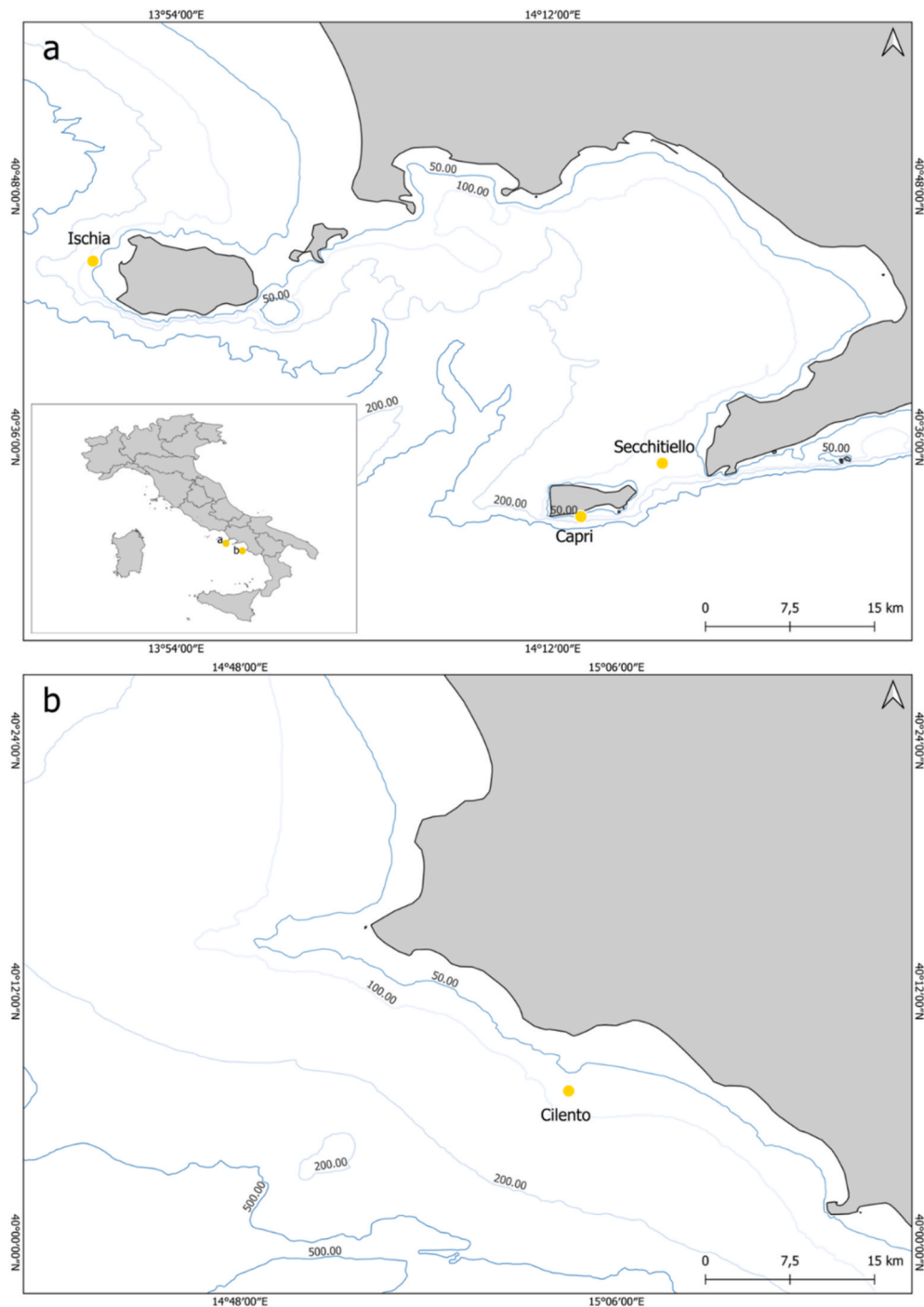


Fig. 1. Map of the study areas along the Campania Coast (Tyrrhenian Sea, Italy). (a) Capri, Punta Campanella, Secchitiello, and Ischia sites. (b) Cilento site.

PERMANOVA analyses based on Euclidean distance were performed to assess differences among sites of each sinecological index. A one-way model with “site” as fixed factor was used. With the same design, PERMANOVA analysis based on Bray-Curtis similarity was performed to assess differences among the four sites in the structure of faunal assemblages and the pairwise test was applied to evaluate differences between pairs of sites. Raw data were $\log(x+1)$ transformed to reduce the effect of the dominant *taxa* in the samples (Clarke and Warwick, 2010), and 4999 permutations of the transformed data were computed to obtain *p*-values. The differences in composition of the faunal assemblages among the four sites were visualised using a nonmetric multidimensional scaling ordination (nMDS), based on the Bray-Curtis

similarity (Bray and Curtis, 1957), and a SIMPER analysis was carried out to identify the species that mostly contribute to the similarity among the four sites (Bray and Curtis, 1957).

To estimate the trophic diversity, a feeding guild was assigned to each species according to literature data. A total of 5 feeding guilds were identified: suspension feeders, which feed on seston; deposit feeders, which mainly feed on the bottom detritus; herbivores, which graze on micro- and macro-algae; carnivores, both predators and scavengers; omnivores, which may behave as carnivores, herbivores, and/or detritus-feeders.

Finally, to estimate a possible relationship of faunal abundance and species richness with both rhodolith cover and 3D structural complexity

of beds (3DCI), linear regressions were calculated for all sites, and separately for each site.

3. Results

3.1. Rhodolith cover, vitality, and morphotypes

Rhodolith cover was significantly different among sites (PERMANOVA analysis, $F = 22.86$, $p = 0.0001$). Cilento and Ischia were characterised by the highest rhodolith cover ($98 \pm 2\%$ and $80 \pm 24\%$, respectively), followed by Capri ($65 \pm 27\%$), while the lowest values were detected at Secchitiello ($11 \pm 6\%$) (Fig. 2a). Live/dead rhodolith ratio was not significantly different among sites (PERMANOVA analysis, $F = 1.93$, $p = 0.153$). However, highest covers of dead thalli were found in Cilento ($53 \pm 34\%$), followed by Ischia ($45 \pm 19\%$), Secchitiello ($37 \pm 25\%$), and Capri ($23 \pm 6\%$) (Fig. 2b).

The sites were structured by different combination of rhodolith morphotypes, although pralines were the most abundant morphotype in all samples ($>60\%$; Fig. 3). Capri showed a low diversity of morphotypes, being composed mostly by pralines (99%) and few unattached branches (1%). Secchitiello was composed by pralines (84%), boxworks (13%), and unattached branches (3%). Ischia was composed by pralines (75%), unattached branches (16%), and boxworks (9%). Cilento was composed by pralines (64%) and unattached branches (36%).

The sites showed a significantly different 3D structure (PERMANOVA analysis, $F = 5.72$; $p = 0.006$; Fig. 4), with higher 3DCI values at Ischia (1.83 ± 0.62) and Cilento (1.61 ± 0.33), and lower values at Capri (1.03 ± 0.07) and Secchitiello (1.21 ± 0.27).

3.2. Benthic community composition

A total of 2312 individuals were identified across the four sites, belonging to 7 taxonomic groups, (Supplementary Table S1). Polychaetes, molluscs and crustaceans were the dominant taxa, with a cumulative abundance of 2063 individuals (DI 89.23% of the total). Polychaetes were the dominant group in abundance (1299 ind., DI 56.19%; 65 sp., DQ 27.78%), but molluscs were dominant in species richness (519 ind., DI 22.45%; 105 sp., DQ 44.87%), while crustaceans were the third group both in abundance and species richness (245 ind., DI 10.6%; 52 sp., DQ 22.22%). The dominance of these three ecologically relevant taxonomic groups was consistent across sites (Fig. 5). Polychaetes were the most abundant group at all sites (Capri: 181 ind., 54.19% - Secchitiello: 353 ind., 63.95% - Ischia: 308 ind., 64.44% - Cilento: 457 ind., 65.38%), while molluscs were the most species diverse group at all sites (Capri: 36 sp., 42.35% - Secchitiello: 45 sp., 39.82% - Ischia: 52 sp., 45.61% - Cilento: 49 sp., 40.16%). Crustacea showed the highest abundance and species richness in Capri (75 ind., 22.46%; 20 sp., 23.53%), while lower, and similar values, were observed at the other three sites (Secchitiello: 54 ind., 9.78%; 24 sp., 21.24% - Ischia: 48 ind., 10.04%; 19 sp., 16.67% - Cilento: 68 ind., 9.73%; 27 sp., 22.13%).

Overall, 32/234 species were widely distributed across all sites, while 67/234 were found exclusively at one site; in addition, 25% of the whole community was represented by just 10 species belonging to

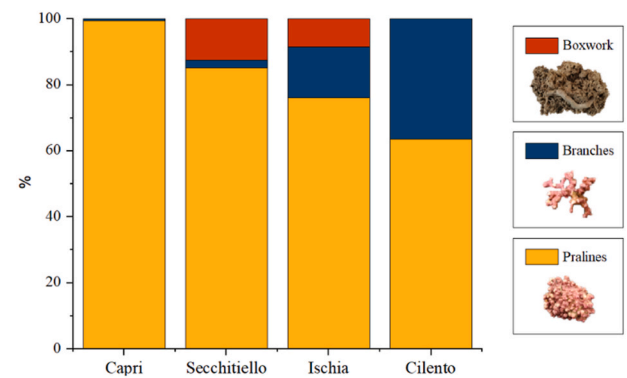


Fig. 3. Cover % of rhodolith morphotypes (pralines, unattached branches, and boxworks) at each site (Capri, Secchitiello, Ischia, and Cilento).

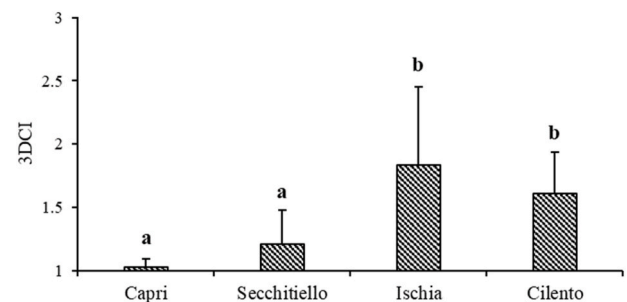


Fig. 4. 3D Complexity Index (3DCI) ($\pm$ SD) at each site (Capri, Secchitiello, Ischia, and Cilento). Letters (a, b) indicate significant similarities/differences among sites.

polychaetes, molluscs, and crustaceans. The polychaetes *Galathowenia oculata* (Zachs, 1923), *Onuphis eremita* Audouin and Milne Edwards, 1833 and *Owenia fusiformis* Delle Chiaje, 1844 were the main representative species, with a total of 390 individuals, contributing 17% to the total macrozoobenthic community. Among molluscs, the gastropod *Bittium latreillii* (Payraudeau, 1826) and the bivalves *Coripia corbis* (R. A. Philippi, 1836), *Gonilia calliglypta* (Dall, 1903) and *Goodallia triangularis* (Montagu, 1803) were dominant, with a total of 120 individuals and a DI of 5%. For crustaceans, the isopods *Natatolana borealis* (Liljeborg, 1851) and *Cymodoce truncata* Leach, 1814 and the amphipod *Lysianassa costae* H. Milne Edwards, 1830 were the main representatives, with a total of 59 ind. and a DI of 3%.

The least represented taxa were sipunculid worms of the genus *Aspidosiphon* (135 ind., 5.84%), followed by echinoderms (95 ind. across 9 species), with *Echinocyamus pusillus* (O.F. Müller, 1776) accounting for 59 individuals. Pycnogonids were represented by 17 individuals (DI 0.74%). Finally, two *Branchiostoma lanceolatum* (Pallas, 1774), the “amphioxus” belonging to the phylum Chordata, were also recorded.

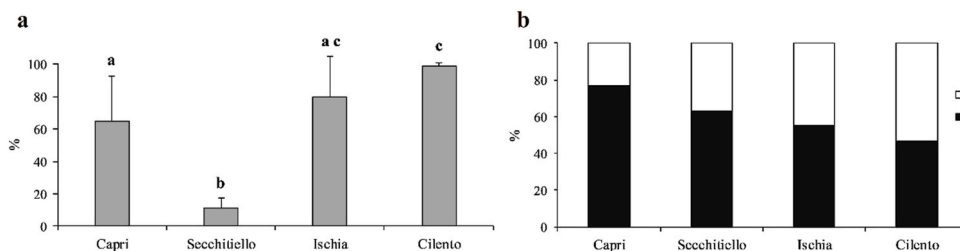


Fig. 2. (a) Rhodolith cover % ($\pm$ SD) at each site (Capri, Secchitiello, Ischia, and Cilento). Letters (a, b, and c) indicate significant differences among sites. (b) Live/dead rhodolith ratio at each site.

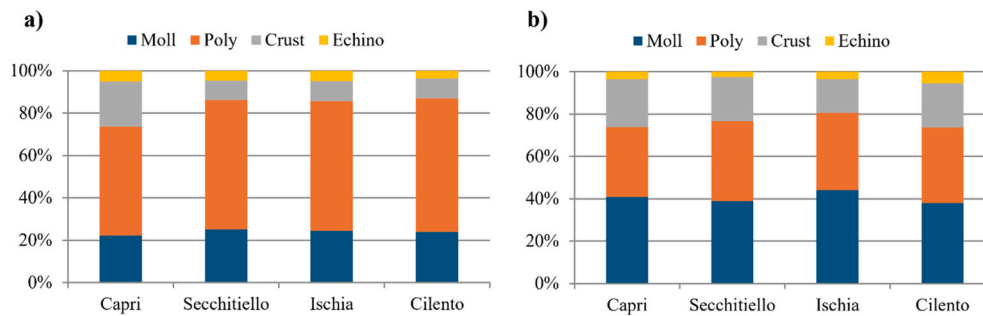


Fig. 5. (a) Percentages of abundance (%DI) and (b) species richness (%DQ) of Polychaeta, Mollusca, Crustacea, and Echinodermata at each site (Capri, Secchitiello, Ischia, and Cilento).

3.3. Benthic community structure

The RBs showed significant differences of some sinecological indices. Cilento had highest values of abundance (N) and species richness (SR), Secchitiello and Ischia had intermediate and quite similar values, while Capri showed the lowest ones (Table 1). No significant differences among sites were detected for the Shannon-Weaver diversity (H') and equitability (J).

However, significant differences in macrofaunal composition were found among the four sites (PERMANOVA: $F = 2.6583$, $p = 0.0002$). Pairwise comparisons revealed differences between all sites, except for Ischia and Cilento (Table 2). The nMDS plot well showed differences among the six replicates of the four sites (Fig. 6). Ischia and Cilento replicates were grouped, accounting for the highest similarity (30.96%), while those of Capri and Secchitiello were clearly separated (lowest similarity of 20.39%). The SIMPER analysis highlighted species that better contributed to similarity among sites (Table 3 – Average similarity %). Overall, similarity across all sites was of 27.76% due to 21 dominant taxa, and only 10 taxa contributed to more than 50% of the cumulative contribution of similarity (Table 3).

3.4. Rhodolith beds and benthic macrofauna relationship

Pooling all data together, the linear regression models showed no correlation between rhodolith cover and macrofaunal abundance ($R^2 = 0.10$) and species richness ($R^2 = 0.27$) (Fig. 7), although with significant differences [$p = 5 \times 10^{-5}$ and 1×10^{-9} , respectively]. However, when sites were analysed separately, some significant correlations were found. For faunal abundance (Fig. 8a–d), positive correlations were observed only at Ischia ($R^2 = 0.81$) [$p = 0.01$; difference among replicates 60%] and Secchitiello ($R^2 = 0.77$) [$p = 0.40$; difference among replicates 15%]. For species richness (Fig. 8e–h), positive and significant correlations occurred at Capri ($R^2 = 0.76$) [$p = 0.0005$; difference among replicates 80%] and Ischia ($R^2 = 0.76$) [$p = 0.007$; difference among replicates 60%]. At Cilento, the low variability in rhodolith cover (98 ±

Table 1

Sinecological indices ($\pm$ SD): N (number of individuals), SR (species richness), H' (Shannon-Weaver diversity) and J (evenness) at each site (Capri, Secchitiello, Ischia, and Cilento) and results of PERMANOVA test (F: F-value; p (perm)).

Sites	N	SR	H'	J
Capri	61.83 ± 15.14	30.5 ± 4.89	4.49 ± 0.28	0.89 ± 0.03
Secchitiello	105.17 ± 50.74	38.5 ± 13.19	4.43 ± 0.80	0.82 ± 0.07
Ischia	86.83 ± 16.85	40.33 ± 6.68	4.84 ± 0.42	0.91 ± 0.03
Cilento	131.50 ± 41.83	47 ± 4.15	4.92 ± 0.21	0.89 ± 0.04
PERMANOVA test	F 4.2921 p 0.0116	4.2593 0.0172	2.3051 0.0994	1.7496 0.1712

Table 2

Results of PERMANOVA pairwise comparisons among sites and percentage of average similarity (SIMPER) between sites.

Pairwise test	t	p (MC) (Unique perms < 463)	Average similarity (%)
Capri vs Secchitiello	1.8475	0.0064	20.39
Capri vs. Ischia	1.5585	0.0276	26.11
Capri vs. Cilento	1.669	0.018	24.50
Secchitiello vs. Ischia	1.5953	0.0216	26.80
Secchitiello vs. Cilento	1.6699	0.0216	26.26
Ischia vs. Cilento	1.3868	0.071	30.96

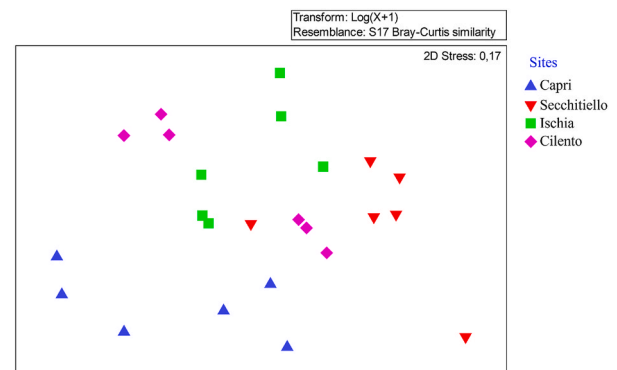


Fig. 6. Nonmetric multidimensional scaling (nMDS) ordination based on the Bray-Curtis similarity matrix for all replicates of each site (Capri, Secchitiello, Ischia, and Cilento).

2%) likely limited the robustness of the regression analysis. Regarding the RB structural complexity (3DCI), no correlation was observed with macrofaunal abundance ($R^2 = 0.197$) [$p = 0.49$] and species richness ($R^2 = 0.541$) [$p = 0.26$].

3.5. Trophic diversity

Overall, the benthic communities were dominated by carnivores (792 ind., DI 38.02%; 85 sp., DQ 36.79%) and deposit feeders (694 ind., DI 33.31%; 54 sp., DQ 23.37%), followed by suspension feeders (376 ind., DI 18.05%; 55 sp., DQ 23.80%), herbivores (168 ind., DI 8.06%; 30 sp., DQ 12.98%), and omnivores (53 ind., DI 2.54%; 7 sp., DQ 3.03%) (Fig. 9).

Carnivores were quali-quantitatively dominant in 3/4 sites: Capri (135 ind., DI 38.79%, 29 sp., DQ 32.58%), Ischia (216 ind., DI 44.72%; 44 sp., DQ 37.60%) and Cilento (257 ind., DI 36.45%; 44 sp., DQ 34.92%). The most abundant carnivore species were the polychaetes *L. torquata* in Capri (22 ind.), and *O. eremita* in Ischia (56 ind.) and

Table 3

Taxa responsible for more than 50% of similarity across all sites (SIMPER analysis).

Taxa	Av. Abund	Av. Sim	Sim/ SD	Contrib %	Cum. %
<i>Onuphis eremita</i> (Audouin and Milne Edwards. 1833)	1.51	2.13	1.08	7.69	7.69
<i>Sipuncula</i>	1.46	2.02	1.11	7.28	14.96
<i>Galathowenia oculata</i> (Zachs. 1923)	1.33	1.70	0.71	6.12	21.08
<i>Arabella iricolor</i> (Montagu. 1804)	1.03	1.56	1.31	5.61	26.69
<i>Glycera fallax</i> (Quatrefages. 1850)	1.00	1.46	1.25	5.27	31.96
<i>Echinocyamus pusillus</i> (van Phelsum. 1774)	0.98	1.41	1.00	5.07	37.03
<i>Nereis</i> sp.	0.94	1.15	0.83	4.15	41.18
<i>Owenia fusiformis</i> (Delle Chiaje. 1844)	0.99	1.10	0.74	3.97	45.15
Syllidae	0.81	0.83	0.72	3.00	48.15
<i>Leodice torquata</i> (Quatrefages. 1866)	0.81	0.80	0.51	2.87	51.02

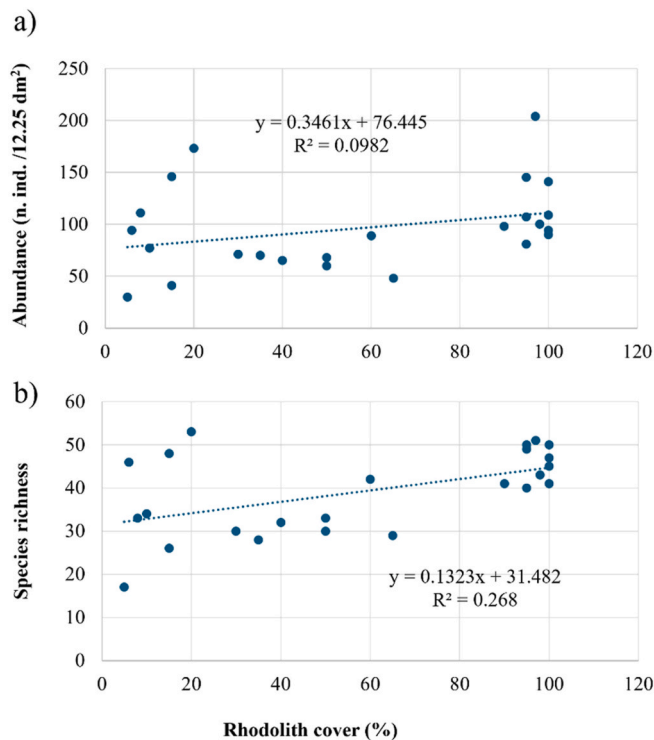


Fig. 7. Linear regression analysis between rhodolith cover and macrofaunal (a) abundance and (b) species richness, for the replicates of all the sites (Capri, Secchitiello, Ischia, and Cilento) pooled together.

Cilento (46 ind.). Instead, at Secchitiello, deposit feeders were quantitatively dominant (216 ind., DI 38.57%), while carnivores were qualitatively dominant (38 sp., DQ 33.63%). These two latter guilds were mainly represented by the polychaetes *G. oculata* (76 ind.) and *O. eremita* (38 ind.), respectively.

4. Discussion

Habitats characterized by a high structural complexity and heterogeneity often promote higher faunal abundance and richness (Way et al., 1995; Beck, 2000; Boyero, 2003; Hinojosa-Arango and Riosmena-Rodríguez, 2004; Christie et al., 2007; Hansen et al., 2011; Molokwu et al., 2014; Cacabelos et al., 2016; Donnarumma et al., 2018a; Otero-Ferrer

et al., 2019). RBs are considered structurally complex benthic ecosystems since their heterogeneity enhances habitat availability and ecological niches by increasing interstitial space, which provides refuge from predation, promotes food retention, and facilitates larval settlement (Bosence, 1983; Johnson et al., 1991; Steller et al., 2003; Kamenos et al., 2004; Grall et al., 2006; Steneck, 1986; Foster, 2001; Foster et al., 2013; Basso et al., 2016; Stelzer et al., 2021; Tuya et al., 2023; Jardim et al., 2022, 2025b; Solano-Barquero et al., 2022; Macedo et al., 2025; Tãmega et al., 2024a, 2024b). Beyond the structural complexity of the beds, site-specific environmental conditions likely contribute to shaping both rhodolith cover and morphology and associated macrofaunal assemblages. RB communities are known to be mostly influenced by light availability, temperature, substrate type, sedimentation rates, and hydrodynamic regime (Bosence, 1985). Moderate bottom currents are essential to prevent burial and to maintain rhodolith mobility (Foster et al., 1997; Marrack, 1999), while excessive sediment input may reduce live cover and alter faunal composition (Steller et al., 2003).

In our study, although these environmental parameters were not directly measured, the observed spatial variability among sites may partially reflect differences in local hydrodynamic and sedimentary conditions (Bracchi et al., 2019; Rendina et al., 2020a). In this context, the assessment of rhodolith cover, live/dead thalli ratio, and morphotype composition provided a useful proxy for quantifying RB structural complexity and vitality, and allowed the evaluation of their relationship with macrofaunal assemblages. The proportion of dead rhodoliths ranged from 23% to 53%, although no significant differences in the live/dead ratio were found among sites. This is consistent with literature indicating that live RBs generally include at least 10% of dead thalli or fragments (Basso et al., 2016), suggesting that a partial rhodolith mortality may not be necessarily linked to poor conservation conditions. Hence, it is not easy to determine whether a bed is in a good conservation status or not. In any case, even dead rhodoliths play a 3D functional role by providing microhabitats for various organisms, although they are more prone to dissolution processes driven by ocean acidification (Martin and Hall-Spencer, 2017).

The broader ecological role of morpho-structural complexity in shaping benthic communities is well documented in both Mediterranean and extra-Mediterranean RBs, including the North Atlantic (Cabioch, 1970; Bosence, 1979), the Eastern Atlantic (Otero-Ferrer et al., 2019), and the Eastern Pacific (Steller et al., 2003; Hinojosa-Arango and Riosmena-Rodríguez, 2004; Gabara et al., 2018). In this study, some trends emerged when comparing rhodolith cover and 3D Complexity Index (3DCI) among the four investigated sites. The Cilento site exhibited the highest rhodolith cover and 3DCI values and also showed the highest macrofaunal abundance (N) and species richness (SR) (Table 2). Conversely, Capri and Secchitiello displayed lower faunal metrics together with lower rhodolith cover and morphotype composition (mainly warty or lumpy/fruticose pralines, *sensu* Woelkerling et al., 1993). However, since no significant correlations were detected between 3DCI and either macrofaunal abundance or species richness, a direct causal role of 3D habitat structural complexity in shaping macrofaunal communities cannot be inferred from the present study.

However, the positive correlation between rhodolith cover and species richness, particularly when rhodolith cover exceeded 60%, suggests that habitat availability may represent a more consistent factor influencing macrofaunal diversity. These results are also consistent with previous comparisons between rhodolith beds and adjacent unvegetated soft sediments, where rhodolith beds consistently host richer and more abundant macrofaunal assemblages (Cabioch, 1970; Bosence, 1979; Steller et al., 2003; Gabara et al., 2018). In contrast, the positive correlation between rhodolith cover and species richness suggests that habitat availability may play a more consistent role in shaping macrofaunal diversity, particularly when rhodolith cover exceeded 60%, supporting the hypothesis that rhodoliths act as biodiversity enhancers by offering structurally diverse microhabitats (Cocozza di Montanara et al., 2025). These findings are consistent with previous studies

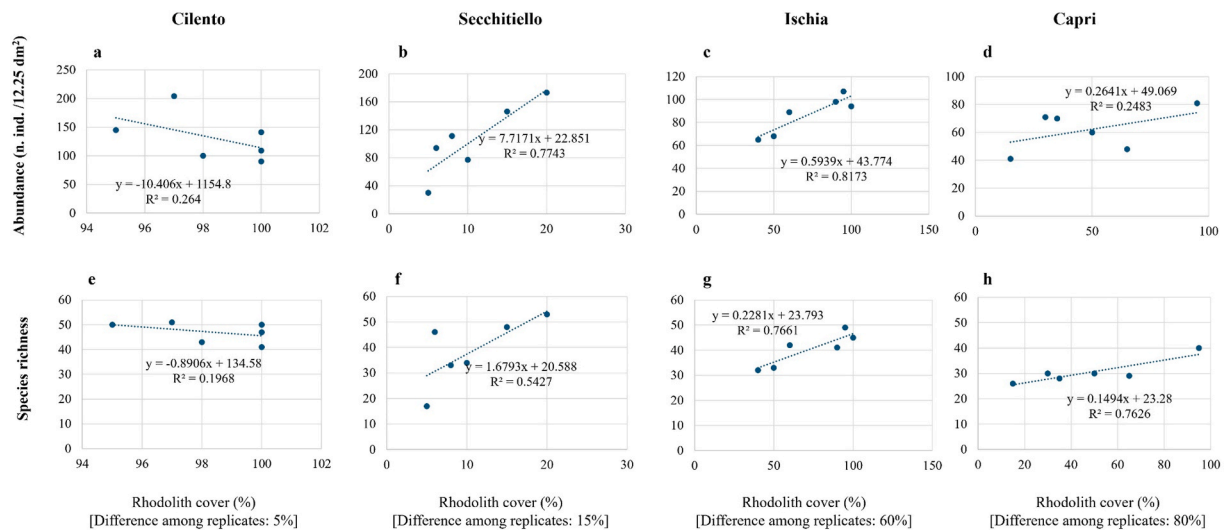


Fig. 8. Linear regression analysis between rhodolith cover and macrofaunal (a–d) abundance and (e–h) species richness, for the six random replicates at each site (Capri, Secchitiello, Ischia, and Cilentò).

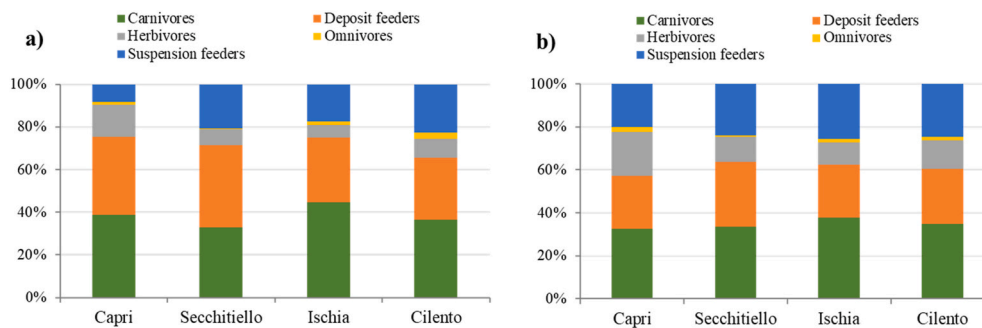


Fig. 9. Trophic contribution of each feeding guild (carnivores, deposit feeders, herbivores, omnivores, suspension feeders) to (a) quantitative (%DI) and (b) qualitative (%DQ) dominances at each site (Capri, Secchitiello, Ischia, Cilentò).

showing that RBs generally support richer and more abundant macrofaunal assemblages compared with adjacent unvegetated soft sediments (Cabioch, 1970; Bosence, 1979; Steller et al., 2003; Gabara et al., 2018).

The composition of the main taxonomical groups of macrofauna was consistent across sites, being dominated by polychaetes, molluscs, and crustaceans, also globally reported as dominant in RB habitats, both shallow and mesophotic (Bordecire et al., 2003; Foster et al., 2007; Hinojosa-Arango and Riosmena-Rodríguez, 2004; Steller et al., 2003; Berlandi et al., 2012; Grall and Hall-Spencer, 2025). Molluscs were dominant in terms of species-richness at all sites. In particular, the class Bivalvia was the most represented one, and *G. triangularis* was the most abundant species. This result is in line with Bosence (1979), who reported Mollusca, and especially bivalves, as the qualitatively dominant taxon in the Mannin Bay shallow maërl bed of Galway (Ireland). Similar patterns have been reported from Southwestern Atlantic RBs, where molluscs represent a remarkably diverse component of the associated fauna, accounting for more than 10% of the total gastropod diversity recorded in the region based on both shallow and mesophotic sites in Brazil (de Mello Cesar et al., 2024). These findings highlight the role of RBs as key reservoirs of molluscan biodiversity across continental margins worldwide. Polychaetes are reported as the most quantitative dominant taxon in several studies on RBs. Specifically, a study on the shallow RB of Western Port (southern Australia) showed that polychaetes comprise the 89% of the community (Harvey and Bird, 2008). Polychaetes were also the most abundant group in the shallow maërl bed community from the Bay of Brest (France), followed by crustaceans and molluscs (Grall et al., 2006), and in two mesophotic maërl beds from

Spain, comprising 65 ÷ 76% of the community (Bordecire et al., 2003). Also in the present study, polychaetes were dominant in terms of abundance, accounting for 56% of all the sampled benthic communities, followed by molluscs (22%). The polychaetes *O. eremita* and *G. oculata* were the most abundant in all sites. These worldwide distributed species, in Mediterranean usually also occur in the well sorted fine sand biocoenosis, *sensu* Pérès and Picard (1964).

Crustaceans, particularly amphipods, were the most abundant taxon after molluscs. Sciberras et al. (2009) reported amphipods as the most abundant and species-rich group at Maltese mesophotic maërl beds. Echinoderms did not constitute a dominant group, although the irregular echinoid *E. pusillus* was quite abundant at all sites.

There are only few studies addressing the trophic ecology of RBs, but similar trends were observed in both Atlantic and Pacific beds. For instance, Grall et al. (2006) reported a similar trophic structure dominated by carnivores, filter feeders, and deposit feeders in an Atlantic maërl bed off the Bay of Brest (France), while Gabara (2014, 2020) observed comparable patterns in a Pacific RB off Santa Catalina Island (California). Hacker Teper et al. (2022, 2024) demonstrated that RB food webs are primarily driven by bottom-up processes, with planktivores and detritivores acting as key energy processors limiting the population sizes and biomass of organisms at higher trophic levels. Indeed, our findings showed that the trophic structure of the macrofaunal community was dominated by carnivores (38%), followed by deposit feeders (33%), and suspension feeders (18%). This pattern highlights a dual functional capacity of the habitat: (i) to trap suspended organic matter and retain detritus, providing trophic resources for both

deposit and suspension feeders; (ii) to provide high prey availability due to habitat complexity, enhancing the predominance of carnivores, also suggesting a mature and structured food web. The complex architecture of rhodoliths likely enhances the retention of particulate organic matter, sustaining a benthic community that relies on both suspended particles from the water column and bottom organic matter, mainly composed of benthic diatoms and microbial biofilms (Grall et al., 2006; Kelly and Scheibling, 2012). Indeed, the rhodolith thallus itself, being heavily calcified, is rarely grazed directly (McCoy and Kamenos, 2015). As a result, the herbivorous taxa recorded in this study, mainly represented by macrograzers, likely rely primarily on epiphytic diatoms and microbial biofilms growing on the surface of rhodoliths rather than on the heavily calcified algal tissue itself. Detritivores and planktivores thus occupy the basal levels of the trophic web, transferring energy to higher-level consumers and reinforcing the role of RBs as productive and structurally complex benthic habitats.

It is worth noting that the RBs investigated here host a high diversity of coralline algae, with approximately 12 taxa reported per site and the genus *Lithothamnion* representing the dominant component, c.a. 50% of the total cover (Rendina et al., 2020a). The elevated macrofaunal biodiversity observed in the present study therefore occurs within a structurally and taxonomically diverse algal community, suggesting that the overall biological heterogeneity of these beds may contribute to their role as Mediterranean biodiversity hotspots. These results support the idea that the ecological function of RBs extends beyond structural habitat provision. These habitats shape trophic networks, stabilize benthic-pelagic coupling, and enable the differentiation of ecological niches, confirming their role as essential ecosystem engineers of the Mediterranean Sea.

5. Conclusions

This study highlights the ecological importance of Mediterranean rhodolith beds as complex and functionally rich habitats supporting high macrofaunal biodiversity. In the four studied sites along the Campania coast, variability in rhodolith cover and morphotype diversity strongly influenced faunal abundance and species richness. Polychaetes, molluscs, and crustaceans were consistently dominant across all sites, with carnivores and deposit feeders emerging as the main trophic guilds. A positive correlation was observed between rhodolith cover and abundance and richness of the associated fauna, underlining the role of rhodoliths in shaping benthic communities.

These findings provide further evidence that rhodolith beds function as biodiversity enhancers and ecological engineers in Mediterranean coastal ecosystems. In addition to their role as physical habitat providers, rhodoliths trophically contribute by facilitating the accumulation and biological processing of particulate organic matter. Their surface biofilms and retained detritus support detritus-based food web, where deposit feeders drive bottom-up trophic dynamics, while the abundant carnivores exert a top-down control. Given their vulnerability and ecological significance, more targeted efforts are needed to map, monitor, and conserve these habitats and their associated biodiversity, particularly in deeper environments that remain still underexplored.

CRedit authorship contribution statement

Francesco Rendina: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Luigia Donnarumma:** Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Federica Ferrigno:** Methodology, Investigation. **Giovanni Fulvio Russo:** Writing – review & editing, Supervision, Resources, Project administration.

Specimen availability statement

All specimens are stored at the marine laboratory facilities of the Department of Science and Technology, University of Naples Parthenope, Naples, Italy. Macrofaunal specimens were preserved in 70% ethanol. Rhodolith specimens were preserved in silica gel. Representative voucher specimens will be deposited in a recognized biological collection following the completion of ongoing investigations. Samples are available from the corresponding author upon reasonable request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.csr.2026.105682>.

Data availability

Data will be made available on request.

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