





## RESEARCH ARTICLE

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# Invertebrate diversity associated with a shallow rhodolith bed in the Mediterranean Sea (Mar Piccolo of Taranto, south-east Italy)

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## Abstract

1. Rhodoliths, formed by free-living coralline algae, are distributed worldwide, and the rhodolith beds (RBs) that they form are recognized as structurally complex habitats. In the Mediterranean, they are generally distributed in the mesophotic zone, at depths of 30–100 m; so far, only a few shallow RBs (<2 m) have been reported (e.g. Îles Kuriat, Tunisia, and Stagnone Marsala, Italy).
2. Here a shallow-water RB located in the Mar Piccolo of Taranto (south-eastern Italy, Mediterranean Sea) is described. The diversity of associated invertebrates, the rhodolith-forming algal species, the type of sediments, and the bed extent are characterized.
3. The RB investigated extends over 5 ha at depths of 0.5–1.5 m. The rhodoliths vary in shape and size, from pralines to large spherical structures, and are formed by a single species, *Neogoniolithon brassica-florida*, growing around nuclei of both natural and anthropogenic origin. The associated fauna consisted of 158 taxa, 79 (50%) of which were new basin records. The associated diversity was approximately twice that of the underlying and nearby sediments.
4. The structural complexity of the RBs promotes biodiversity and provides shelter, food, and a breeding ground for numerous species, including seahorses, which are a conservation priority in this basin.

## KEYWORDS

conservation, invertebrates, maerl, *Neogoniolithon brassica-florida*, non-indigenous species, seahorses

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## 1 | INTRODUCTION

Rhodoliths are unattached forms of red calcareous algae that, when occurring at high densities, form large heterogeneous beds (Bosence, 1976; Foster, 2001; Basso et al., 2016). Although some are composed entirely of coralline algae (mäerl), others may have a nucleus of different origin (e.g. shell fragments or rocks). They are distributed worldwide and can be found at tropical (Amado-Filho et al., 2012; Costa et al., 2020; Moura et al., 2021), temperate (Foster et al., 1997; Steller et al., 2003; Hinojosa-Arango & Riosmena-Rodríguez, 2004; García et al., 2014; Bracchi et al., 2019; Bracchi et al., 2022; Chimienti et al., 2020; Longo et al., 2020; Rendina et al., 2020; Romagnoli et al., 2021), and polar (Konar, Riosmena-Rodríguez & Iken, 2006; Teichert et al., 2014; Ward et al., 2021) latitudes.

Rhodolith beds (RBs) are recognized as structurally complex substrata that host higher associated diversity than the underlying sediments and surrounding habitats (Hall-Spencer, 1998; Steller et al., 2003; Foster et al., 2013; Gabara et al., 2018; Melbourne et al., 2018; Stelzer et al., 2021). Indeed, their three-dimensional structure provides a variety of ecological niches for many species, including epibenthic, epiphytic, cryptic, and infaunal species (De Grave, 1999; Steller et al., 2003; Kamenos, Moore & Hall-Spencer, 2004; Grall et al., 2006; Amado-Filho et al., 2007; Figueiredo et al., 2007; Foster et al., 2007; Peña & Bárbara, 2008a; Peña & Bárbara, 2008b; Riul et al., 2009), and they are therefore classified as 'ecological engineers' (Jones, Lawton & Shachak, 1994; Steller et al., 2003; Nelson et al., 2014; Teichert, 2014; Fredericq et al., 2019). The associated fauna consists mainly of small annelids, crustaceans, molluscs, nematodes, and other groups that use rhodoliths for hiding and feeding (Figueiredo et al., 2007; Costa et al., 2019; Otero-Ferrer et al., 2019; Sánchez-Latorre et al., 2020; Neto et al., 2021; Stelzer et al., 2021). RBs can also serve as nursery grounds for several commercial species, such as clams and scallops (Kamenos, Moore & Hall-Spencer, 2004; Foster et al., 2013; Pereira & da Gama Bahia, 2021; Tuya et al., 2023).

The RBs occur in waters down to 150 m of depth (Bosence, 1983; Foster, 2001; Konar, Riosmena-Rodríguez & Iken, 2006; Foster et al., 2013; Rendina et al., 2020), near channels, islands, submarine dunes, and various sedimentary structures where bottom currents occur (Basso et al., 2017; Bracchi et al., 2019). In the Mediterranean Sea, RBs are generally distributed in the mesophotic zone at depths between 30 and 100 m (Barbera et al., 2012; Basso et al., 2017) and are rarely found in shallow waters. Indeed, their occurrence has been recorded at depths of 9–10 m in Israel (Ramos-Esplá, Riosmena-Rodríguez & Galil, 2012) and at depths of 9–24 m in Punta de la Mona in southern Spain (Del Rio et al., 2022), whereas very shallow RBs (at depths of <2 m) have been described in Îles Kuriat in Tunisia (CAR/ASP-PNUE/PAM, 2011) and Stagnone di Marsala, Trapani, Italy (Calvo, Drago & Sortino, 1980; Mazzola & Vizzini, 2005).

During routine monitoring, a shallow RB (at depths of 0.5–2.0 m) was discovered at Mar Piccolo (south-eastern Italy) (Pierr

et al., 2020), a semi-enclosed basin connected to the Mar Grande of Taranto, which in turn is connected to the Gulf of Taranto in the Northern Ionian Sea. The total area of the basin is approximately 21 km<sup>2</sup> and it consists of two distinct inlets. Owing to its peculiar hydrological characteristics, low hydrodynamic conditions, high freshwater inputs, geographical confinement, eutrophication, and the prevalence of soft-bottom substrate, it can be compared with a brackish lake, although the salinity of around 36‰ is consistent with average seawater values (Caroppo & Cardelicchio, 1995; Annichiarico et al., 2009). Hard natural substrata are scarce, whereas those resulting from human activities are abundant and diverse, including iron poles and concrete blocks, used to anchor mussel farms, stones and debris, ropes, and materials abandoned by mussel farmers and anglers. Mussel farms occupy most of the seabed, increasing the availability of hard substrata and providing mechanical obstacles to fishing with towed gears (Bracchi et al., 2016). Many long-standing human activities occur in the basin, including naval military bases, shipyards, and one of the major Italian industrial centres, which have affected the quality of the environment over time (Rizzo et al., 2022a, 2022b; Lisco et al., 2023).

The basin has been the object of numerous taxonomic, ecological, chemical, and geological studies, and research surveys on species and habitats of conservation interest, leading to the description of more than 750 species (e.g. Parenzan, 1969; Tursi, Pastore & Panetta, 1974; Gherardi & Lepore, 1981; Panetta, 1981; Tursi et al., 1984; Tursi et al., 1985; Gherardi, Lepore & Sciscioli, 1993; Longo et al., 2004; Mastrototaro, D'Onghia & Tursi, 2008; Lisco et al., 2016; Valenzano et al., 2018). This basin is also considered a hotspot for non-indigenous species, principally as a result of the importation of mussels and the presence of large international civilian and military ports that constitute major introduction vectors (Gravili et al., 2010; Servello et al., 2019). Despite the numerous anthropic pressures, Mar Piccolo of Taranto hosts important biological resources (Prato et al., 2020; Mercurio et al., 2021) and, since 2020, it has been included in the homonymous Regional Natural Reserve.

Here, the structure, extent, and associated fauna of the RBs of Mar Piccolo have been described, underlining the conservation importance of RBs. In particular, the epi- and cryptofauna of RBs and the fauna of the sediments under the beds and in the surroundings, where no rhodoliths occur, have been studied using an all-taxa approach that included Annelida, Arthropoda, Bryozoa, Echinodermata, Foraminifera, Mollusca, Porifera, and Sipuncula.

Specifically, the present study aimed to: (i) investigate the contribution of rhodoliths to the species diversity of the area; (ii) verify any differences in sediment-associated macrobenthic communities, in terms of species richness, assemblage structure, and species abundance of the most dominant taxa; and (iii) provide a first preliminary description of the role that this peculiar biological association can play in the Mar Piccolo of Taranto. The ultimate aim of this research was to gain new insights into the biology and associated species diversity of this shallow-water habitat.

## 2 | METHODS

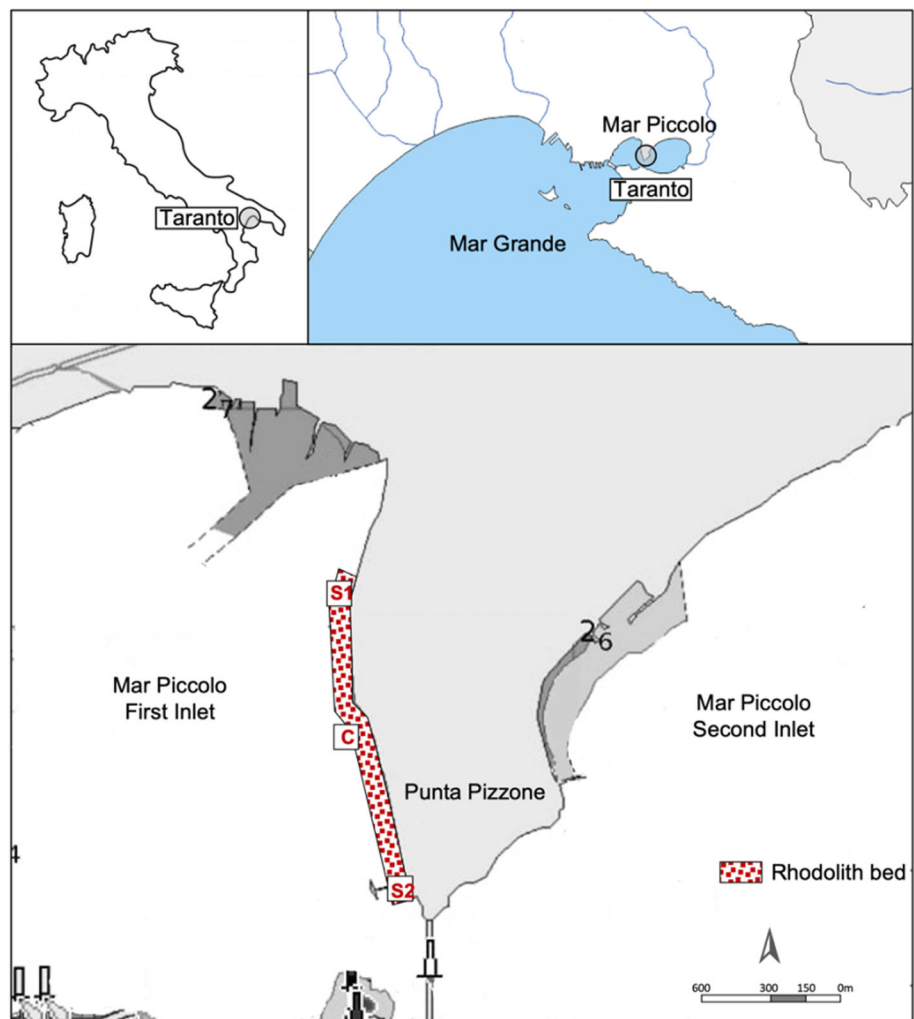
### 2.1 | Study area and sampling

The study area is in the north-eastern portion of the first inlet of Mar Piccolo of Taranto, in south-eastern Italy (Figure 1). The bottom was characterized by shallow sandy banks with sparse flat stones covered by *Cystoseira sensu lato*, and patches of *Caulerpa prolifera* and *Cymodocea nodosa*, down to a depth of approximately 3 m. Thereafter, the bottom was muddy and sloped rapidly to a depth of 6 m, where a dense bed of benthopleustophytic form of *Cladophora prolifera* was present. The studied RB extended over the portions of a sandy substratum without any significant cover of algae or phanerogams (for a more detailed description of the habitats in the area, see Pierri et al., 2020).

In February 2021, a remotely operated vehicle (ROV) was used to estimate the extent of the RB and its depth range. In March of the same year, samples of the epi- and cryptofauna (i.e. organisms living on and within rhodoliths, respectively) and infauna (i.e. organisms living in the sediments below the rhodoliths) were collected at two

randomly chosen sampling stations (S1 and S2) and at a nearby control station (C), where only the sediments were sampled as no rhodoliths were observed. All stations were located at a depth of 1 m. At each station three replicate samples were collected, at 10 m apart from one another. At the sampling stations and for each replicate, all rhodoliths in an area of 20 × 20 cm were also collected; samples were stored in 70% alcohol for subsequent sorting and taxonomic identification of the associated fauna. At each station, the first 10 cm of sediments were collected in three replicate samples using corers of 10 cm in diameter; at S1 and S2, sediments were collected underneath previously collected rhodoliths. All samples were sieved *in situ* using a 500- $\mu$ m mesh and stored following the same procedure. A total of six replicates (three replicates from two stations) of rhodoliths (S1 and S2) and nine replicates (three replicates from three stations) of sediments (S1, S2, and C) were collected and analysed.

In addition, at the same sampling stations, all rhodoliths from a 20 × 20 cm square were collected and used for morpho-structural analysis. For granulometric analysis, 300 g of sediment was collected at the water-sediment interface at each station, in accordance with standard procedures (Poppe et al., 2000).



**FIGURE 1** Rhodolith areas investigated (red dots) at the Mar Piccolo of Taranto, south-eastern Italy, and details of the three sampling stations (S1, S2, and C).

## 2.2 | Rhodolith analysis

The rhodoliths were examined with scanning electron microscopy (SEM). Fragments of algae were mounted on aluminium stubs using acrylic glue, sonicated with a Vitec sonicator (Carlsbad, CA, USA) to remove sediments and diatoms, and then coated with a thin layer of chromium using a Quorum Q150T ES (Quorum Technologies, Lewes, UK) coater and analysed with a Zeiss GeminiSEM 300 (Zeiss, Oberkochen, Germany) at a working distance (WD) of 8–11 mm. Identification was made following the relevant literature (Woelkerling, Penrose & Chamberlain, 1993; Penrose, 1996; Bressan & Babbini, 2003; Cormaci, Furnari & Alongi, 2017; Auer & Piller, 2020) and AlgaeBase.

For the morpho-structural analysis, rhodoliths, including algal growth, were oven-dried. Dry rhodoliths were then impregnated with low-viscosity epoxy resins to preserve the original structure and were cut perpendicular to the structure development with a circular saw. Sample images were taken with a high-resolution scanner.

The long (L), intermediate (I), and short (S) axes of the rhodoliths ( $n = 100$ ) were measured to obtain shape classes according to Sneed & Folk (1958) and Bosence (1976, 1983). The data were plotted on Microsoft Excel (Microsoft, Redmond, WA, USA) triangular diagram spreadsheet (TRI-PLOT; Graham & Midgley, 2000) to represent the shape classes.

## 2.3 | Faunal analysis

In the laboratory, the sampled material was sorted into taxonomic macro-categories, which were then identified to the lowest possible taxonomic level. Individuals were counted and an abundance matrix was created. An all-taxa approach was used, targeting Annelida, Arthropoda, Bryozoa, Echinodermata, Foraminifera, Mollusca, Porifera, and Sipuncula.

## 2.4 | Sediment analysis

Grain-size analyses were carried out using a set of American Standard Test Sieve Series (ASTM) sieves with mesh sizes of  $\frac{1}{2}$  phi from 2 mm to the minimum granulometric fraction ( $<0.125$  mm), following the standard procedures suggested by the American Society for Testing and Materials and the British Standard. The samples were dried (at 80°C) for 24 h and quartered before analyses. The results were processed with a dedicated application in Microsoft Excel (Gradistat©V8).

## 2.5 | Data analysis

At each station, diversity indices, including the number of specimens ( $N$ ), taxonomic richness ( $S$ ), Shannon diversity index ( $H'$ ) and Pielou's evenness ( $J$ ) for assemblages were computed. Sample coverage and estimated richness at the same coverage to render this metric

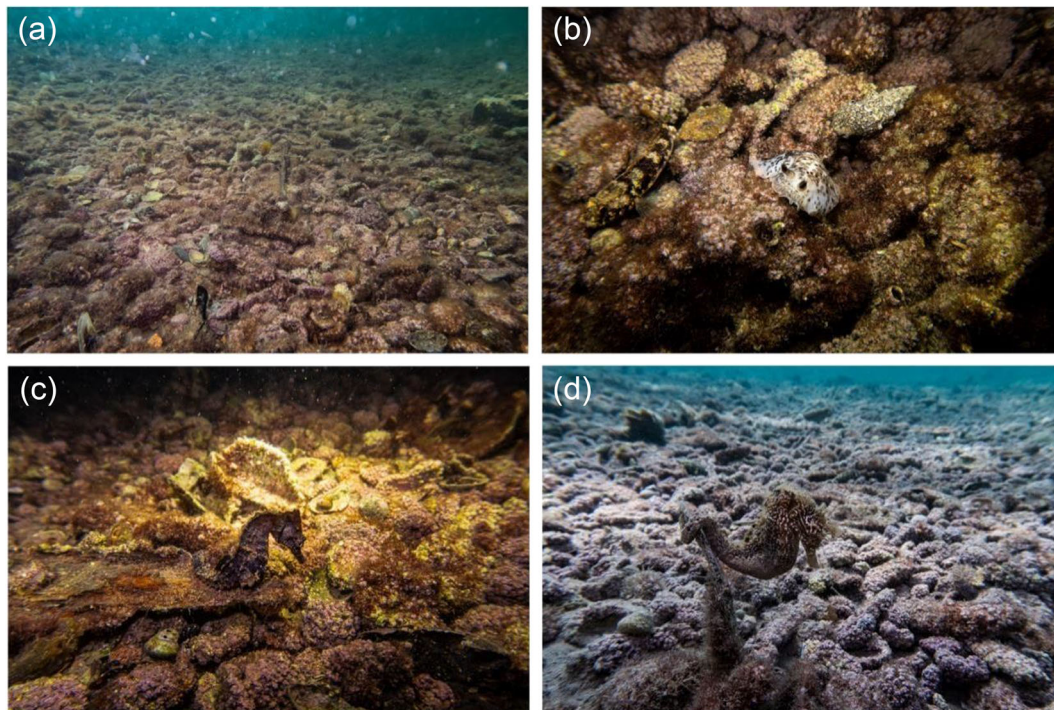
comparable among samples collected with different sampling techniques were also quantified using the R package iNEXT (Chao & Jost, 2012; Hsieh, Ma & Chao, 2016). SIMPER analyses, based on the Bray–Curtis similarity matrix, calculated from the fourth-root-transformed prey abundance data, were performed to assess dissimilarities among benthic communities at three stations and to determine the taxa that most significantly contributed to the observed dissimilarities. The analyses were performed using PRIMER 6+. In the analysis, depending upon the different taxonomic levels detected, the initially identified taxa were assigned to a major taxonomic level (classes).

## 3 | RESULTS

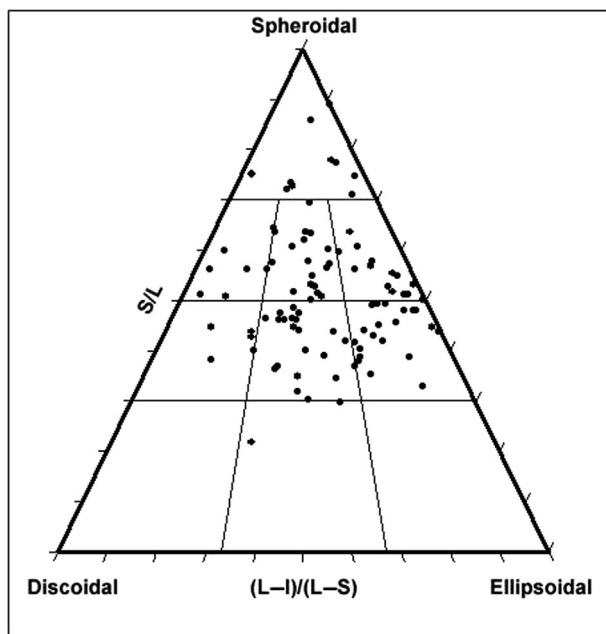
The RB extends for approximately 1.5 km along the perimeter wall of the eastern coast of the first inlet, at a depth ranging between 0.5 and 2.0 m. It has an average width of approximately 10 m and is occasionally interrupted by patches of *Cymodocea nodosa*. Although the rhodoliths at the northern station (S1) were small and sparse, covering about 50% of the bottom, their sizes at the southern station (S2) ranged from a few millimetres to approximately 6 cm, completely covering the substratum and forming a multilayered bed up to 10 cm thick. Rhodoliths were classified into three categories of the ternary diagram (Figure 2), with the spheroidal shape predominating. The facies complexity increased from north to south, with living rhodoliths increasing in abundance and being overlain in several layers at station S2 (Figure 3a–d).

Rhodoliths were formed by *Neogoniolithon brassica-florida* (Harvey) Setchell & L.R. Mason and were monospecific (Figure 4). The specimens had features that are diagnostic of the genus *Neogoniolithon*, namely: thalli with dorsiventral organization; monomeric structure consisting of a single system of branched filaments; lowermost filaments arranged in decumbent arching tiers of cells (coaxial anatomy) (Figure 4b); epithallial cells with rounded or flattened distal walls (Figure 4c); epithallial cells with primary cell wall formed by rodlike (*Mastophora*-type) crystallites (Figure 4d); meristematic cells usually as short or shorter than their immediate perithallial derivatives; cells in contiguous filaments joined by fusions (Figure 4c); secondary pit connections absent; trichocytes, if present, occurring in horizontal layers (Figure 4e), vertical series or singly; and reproductive cells produced in uniporate conceptacles. Based on reproductive morphology, the identification of specimens is consistent with the description of *N. brassica-florida* (Woelkerling, Penrose & Chamberlain, 1993; Penrose, 1996; Bressan & Babbini, 2003; Cormaci, Furnari & Alongi, 2017): sporangial conceptacle large, with roof markedly protruding above thallus surface (Figures 4f, 4g); roof of conceptacle 10–15 cells thick; pore channel lined with protruding cells; and conceptacles without central columella (Figure 4h).

Rhodolith sections showed that the algal structure grew around an inner core (both symmetrically and asymmetrically) on all exposed surfaces for approximately 2 cm (Figure 5), with a thin layer of



**FIGURE 2** Rhodolith bed and associated fauna in the Mar Piccolo of Taranto, south-eastern Italy, at a depth of 2 m near station S2, where the bed is dense and multilayered. (a) Overview of the bed. (b) Close-up showing the density of the associated fauna. (c–d) Seahorses *Hippocampus hippocampus* (c) and *Hippocampus guttulatus* (d) feeding in this habitat (photo credit M. Spoto).



**FIGURE 3** Ternary plot of the rhodoliths in the Mar Piccolo of Taranto using the shape diagram of Sneed & Folk (1958): long (L), intermediate (I), and short (S) axes of the rhodoliths.

carbonate concretion surrounding the nucleus, corresponding to the first growth stages. Small columnar algal structures grew on this layer, increasing the total exposed surface area and trapping the sediment that crept into the free spaces and making the structure compact. The

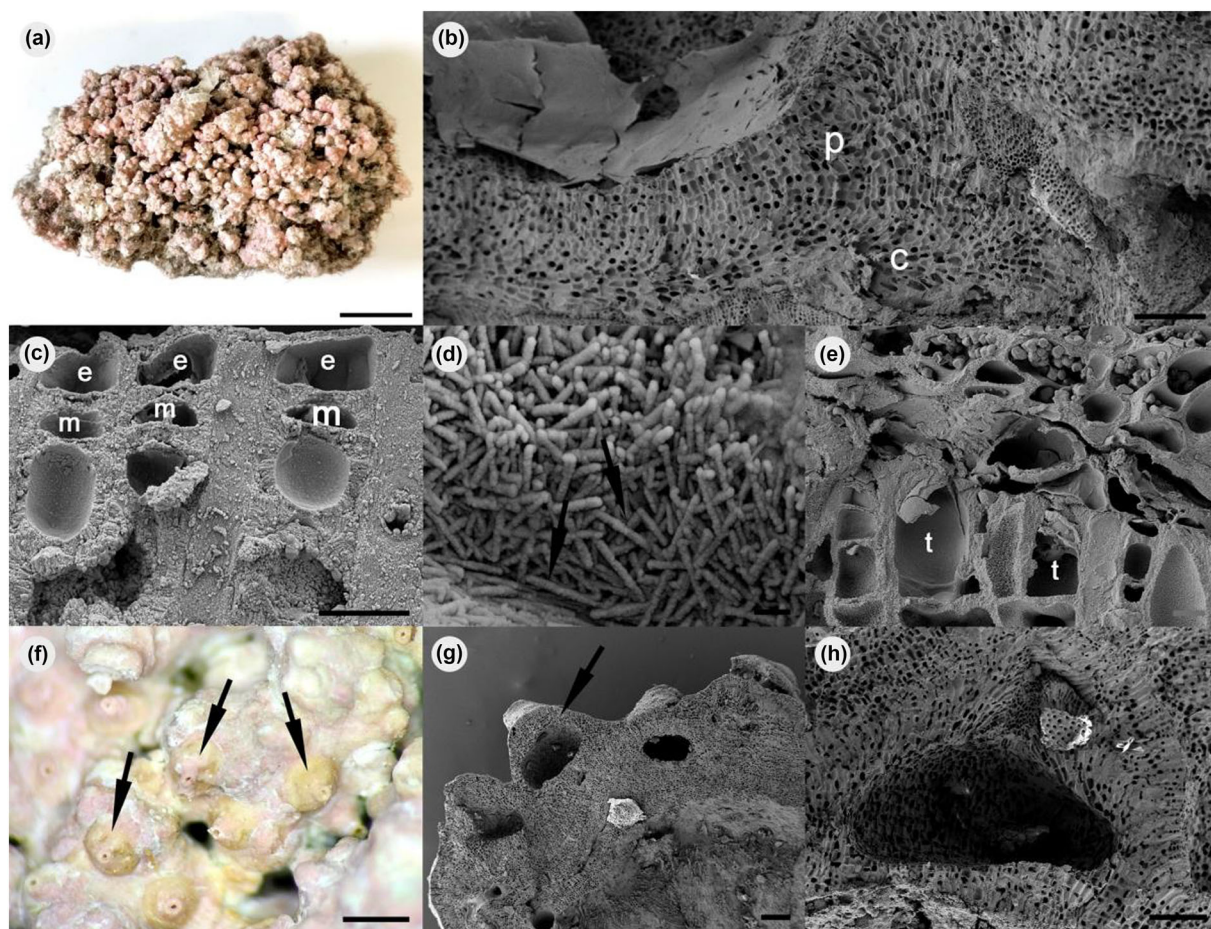
rhodolith cores were of differing origins, including limestone fragments, shells, or anthropic debris (Figure 5).

### 3.1 | Sediment characteristics

Sediments under the RB and at the control station had similar grain-size distributions and were classified as 'very coarse sand'. The distribution was polymodal: very coarse sand was the major fraction, with fine and very fine gravels as secondary components. The muddy component was negligible (<2%). The median sediment particle size ( $D_{50}$ ) of the sediments was  $1250 \pm 125 \mu\text{m}$ . The sandy fraction was mostly bioclastic (shell fragments or whole shells), whereas the gravel fraction was often of anthropogenic origin, resulting from crushed limestone, used locally as an inert component of concrete.

### 3.2 | Macrobenthic community

A total of 3,701 individual invertebrates were identified, with the highest abundance associated with rhodoliths at S1 and S2 (1,669 and 1,079 individuals, respectively) and with the lowest abundance found in the sediments below the RB (336 and 202 individuals, respectively) (Table 1). The abundance at the control station was similar to that in the sediments below the rhodoliths (415 individuals). Annelids were the most abundant invertebrates found in the sediments at all stations. At the control station, annelids accounted for 81% of the



**FIGURE 4** *Neogoniolithon brassica-florida* from Mar Piccolo of Taranto, south-eastern Italy. (a) Gross morphology (scale bar: 1 cm). (b) Section through the thallus with monomerous construction: note the coaxial ventral core (c) and the peripheral region (p) (scale bar: 100  $\mu$ m). (c) Section through the thallus showing epithelial cells (e) with rounded and flattened distal walls and short meristematic cells (m) (scale bar: 10  $\mu$ m). (d) Primary cell wall of an epithelial cell formed by rod-shaped (*Mastophora*-type) crystallites (arrows) (scale bar: 400 nm). (e) Section through the thallus showing buried trichocytes (t) (scale bar: 10  $\mu$ m). (f) Several large and protruding uniporate conceptacles (arrows) (scale bar: 1 mm). (g) Section of a multilayered rhodolith with uniporate conceptacle, with roof markedly protruding above the thallus surface (arrow) (scale bar: 200  $\mu$ m). (h) Sporangial uniporate conceptacle without central columella in vertical section (scale bar: 100  $\mu$ m).

specimens, and at stations S1 and S2, they accounted for 81% and 71% of the specimens, respectively. The most abundant taxon associated with rhodoliths was Arthropoda, which accounted for more than 80% of the assemblage at S1 and S2. Sampling was effective, with a coverage that was always greater than 0.9 (Table 1), and was greater on the RB (>0.96) than in the underlying sediments. The control station had a remarkable coverage of 0.974.

A total of 158 taxa were identified (see supplementary Table S1 for the a detailed list), with most (84%) specimens classified to species level. Taxonomic richness, standardized by coverage, showed that the rhodoliths had high diversity (51 and 75 species at S1 and S2, respectively), whereas the sediments at S1 and C were much poorer (29 and 24 species, respectively). The taxonomic richness in the sediments at S2 was remarkably high and was comparable with that of the RB.

Both rhodolith and sediment invertebrates had the highest Shannon diversity index ( $H'$ ) at S2, whereas the lowest  $H'$  was

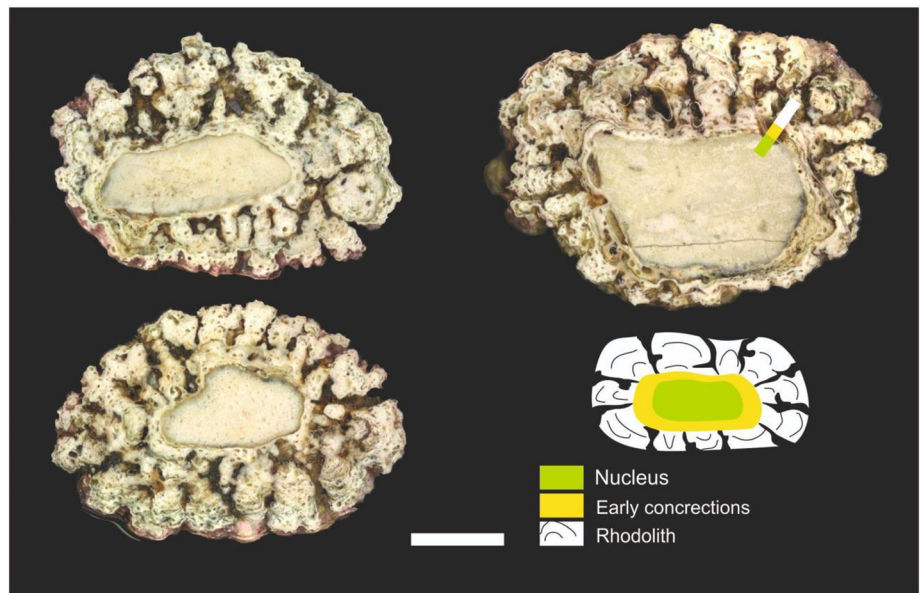
observed at the control station. Evenness was generally low to moderately high (always <0.7) and was higher in the sediments than in the rhodoliths, suggesting stronger dominance patterns in the RB.

SIMPER analysis (Table 2) indicated a higher dissimilarity between the benthic community associated with rhodoliths at S1 and S2 than between C and S2, with respect to the sediment community. The observed dissimilarity in rhodoliths was explained by the presence of Polyplacophora, Gastropoda, and Clitellata, and by Clitellata, Gymnolaemata, Polyplacophora, and Polychaeta, with regard to sediment samples.

### 3.3 | Polychaete assemblage

A total of 72 Polychaeta taxa (62 at the species level, four at the genus level, one at the subfamily level, and five at the family level) were identified, belonging to 19 different families. Polychaetes from the RB

**FIGURE 5** Sections of rhodoliths impregnated in epoxy resin to show their growth. Note the occurrence of asymmetrical (upper row) and symmetrical (lower row, left) morphologies. A growth scheme (not to scale) is shown at the bottom right. Scale bar: 2 cm.



**TABLE 1** Abundance ( $N$ ), observed species richness ( $S_{\text{obs}}$ ), estimated species richness ( $S_{\text{est}}$ ), at a coverage of 0.963 (Chao & Jost, 2012, Shannon index  $H'$ , and Pielou's evenness  $J$  of the invertebrate assemblages on two rhodolith beds, the sediments below, and at the control station C.

Type	Station	$N$ (total)	$N$ (mean $\pm$ SD)	$S_{\text{obs}}$ (total)	$S_{\text{obs}}$ (mean $\pm$ SD)	$S_{\text{est}}$ (SC = 0.963)	Coverage	$H'$	$J$
Sediments	C	415	138.3 $\pm$ 44.7	29	16.7 $\pm$ 2.1	24	0.974	1.482	0.440
	S1	336	112.0 $\pm$ 78.3	44	22.7 $\pm$ 7.6	29	0.947	2.544	0.672
	S2	202	67.3 $\pm$ 18.2	42	19.0 $\pm$ 9.2	54	0.916	2.354	0.630
Rhodoliths	S1	1,669	556.3 $\pm$ 664.4	77	44.7 $\pm$ 4.9	51	0.981	1.728	0.398
	S2	1,079	359.7 $\pm$ 33.3	79	42.3 $\pm$ 7.0	75	0.966	2.379	0.544

were dominated by the syllids, which alone accounted for almost 30% of the individuals sampled and 34% of the taxonomic diversity. *Syllis gracilis* was the most common species, in accordance with its endolithic lifestyle. On rhodoliths, the families Hesionidae, Dorvilleidae, and Ophelidae were the most represented, with *Oxydromus pallidus* being the most abundant species. *Myxicola* cf. *aesthetica* was another abundant taxon living in the matrix of rhodoliths and was the only sabellid species.

*Cirrophorus nikebianchii*, *Cirriformia tentaculata*, and *Tharyx killariensis* accounted for 67% of the sampled individuals, with *C. nikebianchii* accounting for 56%. Syllidae, Cirratulidae, and Dorvilleidae were the dominant families, accounting for 18%, 15%, and 13% of the total number of species, respectively; Capitellidae and Lumbrineridae also showed relatively high diversity.

The rhodolith assemblages showed higher diversity than the sediment owing to the presence of taxa that typically occur on both hard and soft substrata (e.g. *Polyopthalmus pictus* and *Armandia cirrhosa*, respectively). The assemblages from the sediment below the rhodoliths showed large similarities with those from the control station, as both were dominated by *C. nikebianchii* and oligochaetes. However, they had a higher number of species because of the presence of taxa from the families Cirratulidae, Dorvilleidae, and Capitellidae, which were absent at

the control station, where Spionids dominated the species diversity. The most species-rich group at all three stations was the Syllids, which had the highest number of species and genera in rhodoliths and sediments, and were the second largest group at the control station, although different species occurred in the different samples. The non-indigenous component is also well represented, with a total of five species: one Lumbrineridae, two Capitellidae, and two Spionidae.

### 3.4 | Molluscan assemblage

Overall, 28 molluscs were found, all identified to species level. The poorness of the southern station S2 (with two individuals, representing two species in the sediment and among the rhodoliths) was in contrast to the much more diverse molluscan assemblages at the C and S1 stations. The gastropod family Trochidae was the most diverse (14.3%) and abundant (35.4% of the molluscan assemblage), with *Steromphala albida* being the most abundant species, especially on rhodoliths.

The rhodolith assemblage contained a few infaunal bivalves (possibly living in tiny sediment-filled crevices of the rhodoliths), several sessile epibenthic bivalves (e.g. Mytilidae and Anomiidae),

**TABLE 2** The output of SIMPER analyses carried out on the benthic community composition. Taxa included in this table were responsible for 80% cumulative dissimilarity among different samples (sediments at S1, S2, and C; rhodoliths at S1 and S2). Dissimilarity values between sediments and rhodoliths at the stations were not reported. The similarity value of the sediments versus the rhodoliths was close to 96%; the contribution of taxa to the dissimilarity has not been reported here.

Groups	SIMPER % dissimilarity	% contribution of taxa
Sediments vs Rhodoliths	95.44	Malacostraca (37.13), Foraminifera (14.44), Clitellata (13.38), Gymnolaemata (10.09), Ostracoda (7.51)
Rhodoliths S1 vs Rhodoliths S2	80.82	Polyplacophora (29.80), Gastropoda (25.41), Clitellata (19.04), Malacostraca (10.73)
Sediments C vs Sediments S2	63.97	Clitellata (22.00), Gastropoda (20.55), Ostracoda (18.49), Polychaeta (13.17), Foraminifera (10.04)
Sediments S1 vs Sediments S2	57.17	Clitellata (24.64), Gymnolaemata (22.31), Polyplacophora (19.26), Malacostraca (9.89), Gastropoda (9.60)
Sediments C vs Sediments S1	57.12	Gymnolaemata (22.69), Polyplacophora (19.59), Ostracoda (15.58), Foraminifera (9.59), Clitellata (9.47), Polychaeta (5.72)

several gastropods, such as the grazers Trochidae and Cerithiidae, and some predatory neogastropod species. In the sediments, there were some infaunal bivalves and gastropods (e.g. Nassariidae), but also numerous epibenthic gastropods (Trochidae and Cerithiidae).

Four non-indigenous species were present (*Arcuatula* cf. *senhousia*, *Cerithium scabridum*, *Malleus regula*, and *Pinctada radiata*), but with few individuals. This is the first record of *Cerithium scabridum* in this basin. In contrast, all bivalves have been previously recorded in the area (Mastrototaro, Matarrese & D'Onghia, 2003; Stasolla et al., 2014; Kousteni et al., 2019).

### 3.5 | Crustacean community

Thirty-four taxa of crustaceans were found. The overwhelming majority of species (86%) and individuals (97%) occurred in association with rhodoliths. A poorer assemblage, both in terms of taxonomic richness and abundance, was found in the sediments (43% of species and 2% of individuals), with even lower levels at the control station, where only the amphipod *Centraloecetes dellavallei* was abundant (0.5% of total abundance). Most crustaceans were peracarids, with amphipods and isopods dominating in number of species (16 and eight, respectively) and individuals (661 and 1664, respectively), whereas cumaceans and tanaids were found with fewer

individuals. Decapods (six species with 16 individuals) and ostracods (numerous individuals) also occurred. The most abundant species in the rhodolith assemblage were the isopods *Carpas stebbingi* and *Paranthurus japonica*, the amphipods *Apolochus neapolitanus*, *Elasmopus rapax*, *Maera grossimana*, and the tanaid *Chondrochelia savignyi*, which were also the main components of the underlying sediments; other abundant species, such as the isopod *Cymodoce truncata* and the amphipods *Apocorophium acutum* and *Quadrimaera inaequipes* were exclusive of the rhodolith assemblage. Some less abundant and rare species were also shared between rhodoliths and sediment, for example, *M. grossimana* and *Periculodes aequimanus*, whereas the decapod *Brachynotus gemmellari* and the cumacean *Iphinoe trispinosa*, which only occurred in the sediments, were replaced by the congeneric *Brachynotus foresti*, and *Iphinoe serrata* and *Iphinoe tenella*, respectively, on the rhodoliths. Four non-indigenous species were found in the rhodolith assemblage, that is, the isopods *P. japonica*, *Mesanthura* cf. *romulea*, *Paracerceis sculpta*, and the amphipod *Caprella scaura*. *Paranthurus japonica* accounted for 9% of the total fauna and was the only non-indigenous species in the sediments. This species was first recorded at Mar Piccolo of Taranto (Lorenti et al., 2016), whereas specimens of the genus *Mesanthura* were recently detected in the nearby Mar Grande of Taranto (Lorenti, Dappiano & Gambi, 2009). In contrast, *P. sculpta* and *C. scaura* are long-established non-indigenous species (Forniz & Maggiore, 1985; Sconfietti & Danesi, 1996; Eleftheriou et al., 2011). Remarkably, amphipod and isopod juveniles and brachyuran megalopa larvae were abundant, suggesting the persistence of their populations over time.

### 3.6 | Sponge assemblage

A total of 13 Porifera taxa were recorded associated with rhodoliths, nine of which were identified at the species level and four at the genus level. All taxa identified belonged to the class Demospongiae, with Haplosclerida being the most represented order (with eight taxa). The remaining taxa belonged to the orders Clionaida (one taxon), Dictyoceratida (one species), Poecilosclerida (one species), and Suberitida (two species). The assemblage consisted of small insinuating or encrusting massive sponges found between layers of coralline thalli or overgrowing rhodoliths. Only one small specimen (*Cliona* sp.) of a boring sponge was found. Most of the rhodolith samples examined harboured a single sponge taxon (86.7%), whereas two or three demosponge taxa were identified in only a few samples.

The most common sponges found in rhodolith samples belonged to the order Suberitida: *Hymeniacidon perlevis*, followed by *Pseudosuberites mollis*. The Haplosclerida *Oceanapia isodictyiformis* and *Haliclona* (*Haliclona*) *michelei* were common as well, whereas the remaining taxa were found only once or twice.

Overall, the sponge assemblage at both sampling stations was similar in terms of taxa number (eight in S1 and nine in S2), with the exceptions of Clionaida and Dictyoceratida (*Dysidea fragilis*), which were only found at S2, and Poecilosclerida (*Mycale* (*Aegogropila*) *contarenii*), which was only found at S1.



## 4 | DISCUSSION

### 4.1 | Structure and associated diversity of the rhodolith bed

The RB in Mar Piccolo of Taranto occurs between 0.5 and 2.0 m in depth, and is the third RB discovered in such shallow waters in the Mediterranean Sea (Calvo, Drago & Sortino, 1980; Mazzola & Vizzini, 2005; CAR/ASP-PNUE/PAM, 2011). The RB investigated extends over an area of approximately 5 ha, with the estimated rhodolith cover ranging between 15% and 100%, and occurring in both single and multiple layers. Such distribution, coverage, and structure are typical of true beds (Steller et al., 2003; Basso et al., 2016).

The rhodolith-forming species from Mar Piccolo is *N. brassica-florida*, an Atlantic boreal species, widely reported from the Mediterranean Sea (Bressan & Babbini, 2003). It is one of the most common rhodolith-forming species (Chimienti et al., 2020; Del Rio et al., 2022), and also contributes to the formation of vermetid reefs (Chemello, 2009).

The rhodoliths from Mar Piccolo showed some peculiarities, including the monospecificity of the large boxworks, which are otherwise rather multispecific (Basso, 1998; Basso, Nalin & Nelson, 2009).

The possibility of growth on different types of nuclei is well known (Horta et al., 2016). The cores of Mar Piccolo rhodoliths consisted of bivalve and gastropod shells or sea urchin tests, but anthropogenic debris such as glass fragments, calcareous breccias, and concrete fragments were also frequently observed. The shape of the rhodoliths varied, including small pralines, boxworks, and elongated or spherical formations. Although there is no clear interpretation of the relationship between rhodolith shape and water energy (Aguirre, Braga & Bassi, 2017; Braga, 2017; O'Connell et al., 2020), large boxwork rhodoliths seem consistent with a lower hydrodynamic regime (Basso, 1998; Basso, Nalin & Nelson, 2009; Sañé et al., 2016). However, the higher frequency of spherical shapes suggests that, in the Mar Piccolo, tidal currents or their combination with wind and coastal conformation (Dominik et al., 2023) ensure the regular overturning of rhodoliths. Disturbance by large living organisms (bioturbation) has also been shown to play a primary role in overturning rhodoliths, where hydrodynamic forces are insufficient to move them (Marrack, 1999; Millar & Gagnon, 2018).

The RBs usually occur in environments characterized by negligible sedimentation rates and a lack of nutrient inputs (Basso et al., 2017). The RB at Mar Piccolo is therefore noteworthy, as this eutrophic and confined water body has a high sedimentation rate (De Pascalis et al., 2016); this was also confirmed by the polychaete assemblage of the sediments, which are dominated by species typical of areas with high organic content (Bestwick, Robbins & Warren, 1989). In the deeper parts of Mar Piccolo, the rhodoliths are absent, probably because of the shift from sandy to muddy bottom, which may lead to their burial (Steller & Foster, 1995). The conditions for the growth of rhodoliths occur because of the low local sedimentation rate, compared with the depocentral area of the Mar

Piccolo basin, which is dominated by silt that is rich in organic substances (Valenzano et al., 2018). The presence of traction currents, even weak ones, induces particle size selection by the removal of the finest particles, as demonstrated by the grain-size analysis conducted in the present research. The same currents are episodically responsible for the motion of rhodoliths at the sea bottom. Therefore, the localized occurrence of rhodoliths on a small surface area of the basin could be explained in terms of basin conformation and the presence of a riparian wall that surrounds a restricted sector of the basin.

The basin is historically one of the best-studied areas in Italy because of the presence of one of the oldest marine biological institutes in the country (Istituto Sperimentale Talassografico 'Attilio Cerruti' in Taranto). Previous studies, mostly focused on anthropogenic hard substrata and associated fauna, have reported more than 730 species of invertebrates (including tunicates) (e.g. Parenzan, 1969; Tursi, Pastore & Panetta, 1974; Gherardi & Lepore, 1981; Panetta, 1981; Tursi et al., 1984; Tursi et al., 1985; Gherardi, Lepore & Sciscioli, 1993; Longo et al., 2004; Mastrototaro, D'Onghia & Tursi, 2008). Against this background, it is interesting that our study allowed the inclusion of 79 (+11%) previously unreported species for the basin.

The diversity described in this study (i.e. 158 taxa) was higher than that recorded for RBs and underlying sediments in California at depths of 2–20 m (i.e. 52 and 30 taxa, respectively) (Steller et al., 2003), but is comparable with that of deep RBs (50–90 m) off the Maltese Islands (i.e. 188 invertebrate taxa) (Deidun et al., 2022) and the shallow subtidal fringing reef RBs in Moorea French Polynesia (i.e. 177 cryptofaunal taxa) (Abrecht et al., 2022).

The presence of rhodoliths appears to be particularly valuable in a basin like Mar Piccolo, where hard substrata are mostly of anthropogenic origin and are vertical (e.g. concrete walls or poles for mussel farming), whereas natural substrata are rare, so that the bottom is almost entirely sandy or muddy. As structurally complex substrata, the RBs facilitate the presence of a biodiverse benthic community by providing shelter and protection (Amado-Filho et al., 2010; Yanovski et al., 2017; Otero-Ferrer et al., 2019; de Cerqueira Veras et al., 2020).

However, the high heterogeneity in Mar Piccolo RBs could be explained by the co-presence, even at a reduced spatial scale, of other habitats with vegetal cover or communities associated with mussel farming that can generate functionally and structurally consistent diversity owing to the presence of species that share multiple habitats and guarantee the complexity of the system. In this scenario, the RBs represent a crucial node for the connectivity of different habitats owing to the higher number of species present and shared with neighbouring habitats (de Juan et al., 2023).

Thirteen non-indigenous species have been found in the RB. Some of them seem to be recent introductions, such as the bivalve *Malleus regula* (Kousteni et al., 2019). The gastropod *Cerithium scabridum*, already found along the Adriatic coasts of southern Italy (Albano & Trono, 2008) and in the Taranto area

(Trono & Macrì, 2013), is a new report from Mar Piccolo. The polychaetes *Lumbrineris perkinsi*, *Mediomastus capensis*, *Prionospio depauperata*, and *Prionospio pulchra*, as well as the crustacean *Mesanthura romulea*, have been previously reported from the Mar Grande of Taranto (Gherardi & Lepore, 1981; Lorenti, Dappiano & Gambi, 2009; Borghese et al., 2023). Some non-indigenous species, such as the amphipod *C. scaura*, reported from Mar Piccolo since 2007 (Eleftheriou et al., 2011), have proven to be an important food source for seahorses at this site (Lazic et al., 2022). Furthermore, several other known prey species of seahorses (Kitsos et al., 2008; Gurkan et al., 2011; Ape et al., 2019; Lazic et al., 2021; Lazic et al., 2022) have also been recorded in this habitat.

## 4.2 | Importance of the RB for conservation

The RBs are of high conservation interest worldwide, as they provide habitat for some rare or commercially important invertebrates and fish species (Riosmena-Rodríguez, Nelson & Aguirre, 2017; Pereira & da Gama Bahia, 2021), and serve as nurseries and feeding grounds for several species (e.g. Costa et al., 2020). Several cryptic and burrowing fishes, such as gobies and blennies, can be abundant, and the juveniles of large fishes have also been reported to use RBs as feeding areas (Hall-Spencer et al., 2003).

Shallow RBs are threatened worldwide by numerous human activities, including eutrophication, fishing, and aquaculture (Gibson et al., 2006; Riul et al., 2008). It is remarkable that in a basin such as Mar Piccolo, historically exposed to numerous human pressures, suitable ecological conditions exist for a shallow RB harbouring taxonomically and functionally highly diversified assemblages.

Species of major conservation concern occur in the RBs of Mar Piccolo. Many blennies, Gobidae, seahorses (*Hippocampus guttulatus* and *Hippocampus hippocampus*), and pipefishes (*Syngnathus acus* and *Syngnathus tenuirostris*), among others, were observed foraging in RBs (Figure 2c–d), thus suggesting that this habitat may also play a crucial role in the survival of syngnathids, which is especially important given their reported decline (Caldwell & Vincent, 2012; Pierri et al., 2021). These fishes have peculiar life-cycle traits, and their survival appears to be closely linked to a healthy habitat with numerous hiding and feeding opportunities. As they usually feed on small invertebrates hiding in the sediments and at the water–sediment interface, complex and non-uniform substrata with high species diversity, such as RBs, could provide an optimal habitat.

Finally, the importance of preserving these ecologically sensitive systems in European waters is recognized by European Union legislation (Council Directive 92/43/EEC, 1992) and international conventions (Convention for the Protection of the Mediterranean Sea against Pollution, 1976; Bern Convention, 1996; OSPAR Convention, 1998) (Barbera et al., 2003; Gibson et al., 2007). Under the Marine Strategy Framework Directive (MSFD 2008/56/EC), which aims to achieve a ‘good environmental status’ (GES) for all marine waters, the RBs in the Mediterranean Sea have been included among the habitats of special interest.

## AUTHOR CONTRIBUTIONS

Cataldo Pierri conceived the research. Cataldo Pierri and Tamara Lazic contributed to the study conception and design. Miriam Ravisato and Roberta Trani carried out the sorting of the samples. Massimo Moretti, Roberta Trani, and Stefania Lisco analysed the samples. Caterina Longo, Paolo G. Albano, Annalisa Falace, Maria F. Gravina, Matteo Putignano, and Sara Kaleb conducted the taxonomic analyses. Cataldo Pierri and Paolo G. Albano conducted the statistical analyses. Cataldo Pierri, Michele Gristina, Tamara Lazic, Roberta Trani, Stefania Lisco, and Paolo G. Albano wrote the first draft of the article. Marco Dadamo contributed to acquiring funding. All authors contributed extensively to the research, interpreted and discussed the results, and approved the final version for publication.

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## CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interest associated with this work.

## DATA AVAILABILITY STATEMENT

The quantitative data upon which the study is based are available as supplementary material.

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## SUPPORTING INFORMATION

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