Biodiversity associated with a coralligenous build-up off Sicily (Ionian Sea)

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ABSTRACT

Coralligenous is one of the most important habitats of the Mediterranean Sea hosting a very high biodiversity that, however, has not been fully investigated yet. The paper addressed the study of the biodiversity of a coralligenous bioconstruction collected at a depth of 36.7 m off Marzamemi (SE Sicily, Ionian Sea). The species diversity, composition and structure of the main associated taxonomic groups were investigated in order to identify possible differences between the communities of the hard framework (mainly built by calcified corallinales) and the canopy cover. The examined build-up showed significant species diversity for almost all groups. Bryozoans were the most diversified group and, together with foraminifers, also the most abundant both on the canopy and the frame. Further groups showed high species diversity (except for serpulids) and total abundance (except for molluscs) on the canopy rather than on the frame. Due to their different nature and microenvironmental parameters, the canopy and the frame hosted different communities. Besides juvenile specimens, the canopy mostly hosted unmineralized/weakly mineralized, small-sized, short-lived species well adapted to living on ephemeral and flexible substrates. On the contrary, the rigid and persistent frame mostly hosted highly mineralized, large, long-lived species, which usually contributed to the building/strengthening of the bioconstruction. Unlike mapping and monitoring, a thorough description of coralligenous biodiversity requires accurate naked eye and microscopical analysis assisted by SEM investigation due to the small size and cryptic behaviour of several species.

KEY WORDS: bioconstruction, canopy, frame, community composition, priority habitat, Mediterranean Sea

1. INTRODUCTION

The Coralligenous is a characteristic habitat of the Mediterranean Sea, occurring in dim light conditions, mainly formed by crustose coralline algae with a secondary contribution from skeletonized invertebrates such as serpulids, bryozoans, cnidarians and vermetids (Ballesteros 2006). The frame formed by these organisms create a 3D structure increasing habitat complexity and promoting colonisation by a plethora of further species, therefore increasing biodiversity (e.g., Ballesteros 2006). Because of this, the Coralligenous is a priority habitat of the Mediterranean Sea (Habitats Directive 92/43/CE), included in the Barcelona Convention and the Marine Strategy Framework Directive (2008/56/EC) (Ballesteros 2003), and subjected to an ad hoc conservation plan (UNEP, 2017). In fact, this habitat is strongly threatened by several human activities, such as bottom trawling, anchoring, artisanal and recreational fishing (Ballesteros 2006, Piazzi 2012), by the increased expansion of

invasive algal species (Piazzi et al. 2007, UNEP 2007), and by the effects of climate change (Piazzi et al. 2012). It is considered one of the most important Mediterranean marine habitats in terms of biodiversity and productivity (Laborel 1961, 1987, Laubier 1966), likely hosting the highest number of species among the Mediterranean communities (Ballesteros 2006). Its framework, including crevices and cavities, increases available surface and microhabitats allowing colonisation by both sessile and mobile dwellers (Laborel 1961, Pérès & Picard 1964, Laubier 1966, Ros et al. 1985, Sartoretto 1996). Laborel (1961) and Laubier (1966) provided pioneering descriptions of coralligenous biodiversity, followed by several studies (e.g. Sarà 1968, Boudouresque 1973, Ros et al. 1985, Ballesteros 1993, Sartoretto 1996) and a major contribution by Hong (1980, 1982) whose extensive lists include a total of 682 species belonging to several taxonomic groups. The high diversification of invertebrate species associated with the coralligenous habitat (38 taxa from orders to phyla in Ballesteros 2006), usually coupled with very high specimen/colony abundances, allows the identification of different algal- or animal-dominated facies (see La Rivière et al. 2021; Montefalcone et al. 2021). Algal and animal communities vary among sites, geographical areas, and even within the same concretion according to different environmental conditions (Ballesteros 2006, Piazzi et al. 2022). Basso et al. (2022) observed important differences in living associations at the surface of Ligurian Coralligenous, depending on its primary substrate (sub-horizontal sedimentary seafloor *vs* rocky wall), and, within the same site, on side exposure.

Among environmental parameters, light penetration and food availability have been considered the main constraints for the development of particular algal associations (Ballesteros 2006), or animal facies dominated by gorgonians or sponges, bryozoans, and small scleractinians in eutrophic or oligotrophic conditions, respectively (Ballesteros 2006, Casas-Güell et al. 2016). Even though cnidarians are among the most evident animals of coralligenous communities, bryozoans are usually the most abundant (Ballesteros 2006). To date, the Porifera phylum is the most species-rich animal group, with over 300 species living in the coralligenous biocostructions (Bertolino et al. 2013, 2014; Longo et al. 2017). Recently, Rosso et al. (2023) showed that the bryozoan *Margaretta cereoides* can highly contribute to the canopy formation, also showing more abundant and diversified epibionts than large co-occurring algae, mostly *Flabellia petiolata, Halimeda tuna* and *Osmundaria volubilis*.

Besides the contribution to biodiversity, the different roles that bryozoans, serpulids, and, to a lesser extent, cnidarians, vermetids, and encrusting foraminifers can play in the Coralligenous accretion, owing to the diversification of their morphologies and sizes, have been only rarely addressed (Hong 1980, Di Geronimo et al. 2002, Rosso & Sanfilippo 2009). Furthermore, information about the possible preferential location of these organisms in the canopy (largely ephemeral and susceptible to rapid decay, detachment, and breakage) and the frame (more stable and persistent, even if prone to bioerosion processes) is still nearly lacking, with the exception of Hong (1980) and Harmelin (2017). The first author highlighted the abundance of millimetre-sized spirorbines on elements of the canopy, such as the green algae *H. tuna* and *F. petiolata*, and of the heavy calcified, some cm long, serpulid *Spirobranchus triqueter* on the frame. Harmelin (2017) described two different bryozoan associations representing separate facies, one again associated with the flexible alga *F. petiolata* and one typical of a hard substratum. Nevertheless, detailed lists of species characterizing the aforementioned substrates are lacking, especially separated for living (community) and dead (thanatocoenosis) components. However, the separation of these components is relevant, especially when focusing on skeletonised organisms, in order to foresee their potential preservation in the bioconstruction from a geobiological point of view. Finally, a comparison between skeletonised potentially preservable constructors and frame-associated taxa, and the epibenthos forming and/or inhabiting the canopy can help to understand the contribution of these components to the observed total present-day and past biodiversity.

As part of a wider research on Coralligenous, this paper aims to detect species contributing to the formation and colonisation of the frame and the overlying canopy, in order to understand their role in the formation of total biodiversity, focusing mainly on fleshy algae, foraminifers, scleractinians, molluscs, serpulids, barnacles,

ostracods, bryozoans and brachiopods. Results also allow comparisons with previous knowledge on Coralligenous' biodiversity in the same area.

2. MATERIALS AND METHODS

The present study is part of the FISR project CRESCIBLUREEF – "Grown in the blue: new technologies for knowledge and conservation of Mediterranean reefs", which investigates the coralligenous biodiversity associated with a discrete bioconstruction (build-up E). It was collected by scuba divers in August 2021 off Marzamemi, SE Sicily, Ionian Sea (36°43.454' N; 15°09.657' E), from a seafloor eroded by a submarine channel, at a depth of 36.7 m, with a bottom temperature of 18°C (Fig. 1). The site is characterized by sparse decimetre-sized coralligenous columnar build-ups (Di Geronimo et al. 2001, 2002) in the form of hybrid bank (Bracchi et al. 2017), that are surrounded by medium to coarse biogenic sediment (Varzi et al. 2023).

Fig. 1. Study area in the Ionian Sea, off Marzamemi, SE Sicily and location within the Mediterranean (inset). The star indicates the sampling site.

The build-up E measures 38 cm in height with a circumference of 71 cm at its base, 52.5 at the top, and a maximum circumference of 112 cm, with a total weight of 30 kg (Fig. 2). Its calcareous surface is composed of live and dead encrusting organisms that contribute to the build-up accretion through superposition and early cementation (Basso et al. 2022, Cipriani et al. 2024). This framework surface was densely covered by an algal-bryozoan canopy, that was removed soon after collection for species identification and counting. Collected samples of the canopy, named CBR2_4_26, CBR2_4_27, CBR2_4_28 and CBR2_4_30, here combined and referred to as sample CBR2_4_canopy (or simply canopy), were treated at the Palaeontology Laboratory of the Department of Biological, Geological and Environmental Sciences (DSBGA). The term "canopy" is used here to indicate the erect, habitat-forming epibenthic species covering the frame of the coralligenous build-up and the associated organisms, including both sessile and vagile strictly epiphyte taxa (e.g. ostracods, herbivore molluscs). The canopy essentially includes ephemeral organisms, mainly represented by fleshy algae and soft-

bodied animals, as well as species possessing more or less mineralised skeletons that are detachable from the frame because of their adhesion through organic structures (such as the chitinous rootlets of the bryozoan *M. cereoides*). Material was first sieved on a 63 μm mesh in order to retain all microfaunal components. After canopy removal, the carbonate core (corresponding to the sample CBR2_4_21c of Bracchi et al. (2022), here indicated as CBR2_4 frame, or simply frame) of the sampled build-up was dried and sectioned at the University of Milano-Bicocca. After photogrammetry for visual estimate of surface constituents (Bracchi et al. 2022) it was longitudinally sectioned to obtain two thick median slices orthogonal to each other, for the investigation of internal constituents and structures (Cipriani et al. 2023; 2024). The external surfaces of such four slices (named Alfa, Beta, Gamma, Delta: Fig. 2c), corresponding to about one-half of the total framework surface, were analysed for the identification and quantification of the organisms associated with the framework. Because observations were performed on about one-half of the total build-up surface, the counting of specimens/colonies was doubled.

Samples of both canopy and frame surface were examined at the microscopy laboratory of the DSBGA. Identification and photo-documentation were performed using Zeiss Discovery 8 stereomicroscopes, one equipped with an Axiocam MRC and Axiovision acquisition system with the software imaging program ZEN 3.1. A Tescan Vega 2 LMU, Low Vacuum Scanning Electron Microscope (SEM) was used for high magnification images of selected specimens. Macroalgae, preserved in an alcohol–seawater solution, were analysed at the laboratory of Phycology of the DSBGA and identified based on diacritical morpho-anatomical characters using updated taxonomic literature. Selected specimens were observed under a Zeiss Axioplan (Göttingen, Germany) microscope after decalcification with 10% HNO_3 and stained with 1% aqueous aniline blue acidified with dilute HCl to highlight pit-connections, or with Lugol solution to highlight plastids. Sections were made with a razor blade under a Zeiss stereomicroscope. Molluscs were identified at the Paleobiology laboratory of the University of Milano-Bicocca.

Detected fleshy algae, foraminifers, scleractinians, molluscs, serpulids, ostracods, barnacles, bryozoans and brachiopods were identified at the lowest possible taxonomic level (usually species) and, except for algae, counted. Counting included all recognisable young individuals/colonies for all groups. In contrast, only epilithic sponge specimens were identified pending specific sampling for sponge fauna characterisation (Bertolino, pers. observ.). Further sessile organisms, such as hydrozoans and ascidians, and motile organisms, such as echinoids, asteroids, crustaceans (except ostracods), and errant polychaetes were only identified at a high taxonomic level and preserved in alcohol 96° for future identification.

Few sessile live species and specimens found not attached to the canopy constituents were included in the listing and counting of the sample CBR2_4 canopy because they were considered simply detached and fallen down from their substrata during washing. In contrast, the negligible quantity of dead elements was excluded from counting because they largely consisted of worn, usually unidentifiable, remains of species that presumably lived outside the build-up, as obvious for some bivalve species characteristic of soft bottoms.

All species were listed, distinguishing dead and live individuals/colonies, taking into account for these latter the occurrence of: 1) at least some functional zooids in bryozoan colonies; 2) the worm and/or its operculum for serpulids; 3) soft tissues and/or articulated valves for bivalves; 4) the mollusc and the operculum for gastropods; 5) the soft tissues and the pedicle for brachiopods; 6) soft tissues and still articulated scuta for barnacles; 7) attachment to the substrate and expanded pseudopods and/or Rose Bengal colouring for foraminifera.

Shannon-Wiener index and Pielou's Evenness were calculated to synthetically describe diversity and equitability of each taxonomic group, and to highlight their contribution to the diversity of the whole association.

Literature was examined for reviews about diversity of flora and fauna associated with the Coralligenous and for information on particular areas/settings, to be compared with present results. We selected only papers providing lists of species for at least one of the high rank taxonomic groups here deal with. Comparison was made directly with a build-up collected in the same area and comparable depth and more roughly with further coralligenous assemblages.

Specimens are preserved in the following repositories: 1) Paleontological Museum of the University of Catania (PMC) in the collective CRESCIBLUREEF material of the Rosso, Sanfilippo and Sciuto collections for bryozoans, serpulids, and ostracods and foraminifera, respectively; 2) Laboratory of Phycology of the University of Catania for fleshy macroalgae; 3) Laboratory of Paleobiology of the University of Milano-Bicocca for calcareous algae and molluscs. Selected sponges are preserved at DISTAV, University of Genoa. Code numbers are provided for figured material only (see below).

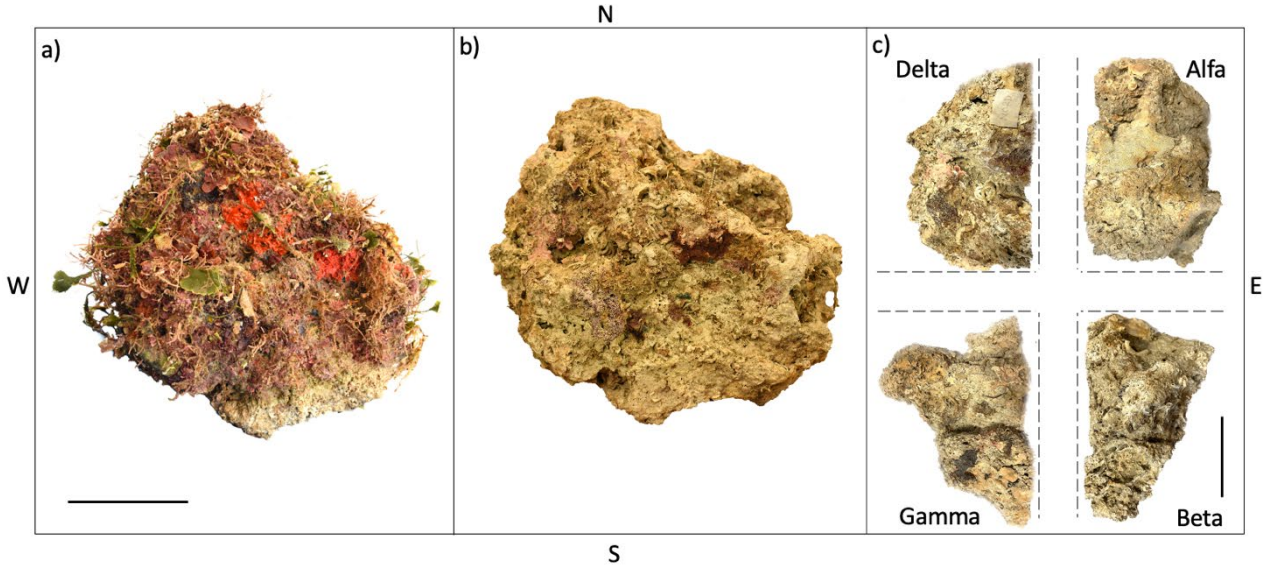

Fig. 2. The studied "build-up E" reported as CBR2_4_21c in Bracchi et al. (2022). Side view with the canopy (a) and after its removal (b). The four studied frame blocks (c) obtained after sectioning and removal of the central core slices (see text for further information). Note that each frame block is rotated 90° to show its wider lateral side. Scale bars: a; b; c: 10 cm.

3. RESULTS

A total of 242 live species belonging to bryozoans, fleshy algae, molluscs, foraminifers, serpulids, ostracods, and, subordinately to scleractinians, brachiopods and barnacles, including 5383 living specimens/colonies, were identified for the whole examined build-up (Figs 4 and 5, Table 1, S1-S7). A total of 221 living species and 3808 specimens/colonies constituted and/or occurred in the canopy, including large-sized fleshy or weakly mineralised algae (such as *Peyssonnelia rubra*), the bryozoan *M. cereoides* (with colonies up to 10, rarely 15 cm high), and their epibionts. The frame is mainly formed of encrusting, layered, foliose, and warty to lumpy growth forms of coralline algae (Woelkerling et al. 1993), which will be described in detail in a separate contribution. Sponges are common with encrusting habitus including *Eurypon cinctum*, *E. gracile*, *Phorbas fictitious, Haliclona* spp. and *Pseudosuberites sulphureus* that were recognized in a preliminary survey. The frame was colonized by 1575 specimens/colonies belonging to 105 species.

The dead assemblage (thanatocoenosis) included 163 species, of which 98 were also found alive and 3561 specimens/colonies (Table 1). The dead community was subordinate in the canopy, and largely settled on *M. cereoides*; 89 species were found, of which 54 were also alive, and 623 individuals. On the contrary, thanatocoenosis was significant on the frame with 113 species, of which 53 were also alive, and 2938 specimens/colonies (Table 2).

Fleshy algae

A total of 60 specific and infraspecific taxa (S1) were found, including 44 Rhodophyta (73%), 6 Ochrophyta (10%) and 10 Chlorophyta (17%). The most represented canopy forming species were *P. rubra, F. petiolata* (Fig. 4H), *O. volubilis*, *Phyllophora crispa* and *Rhodymenia* spp. Quite abundant was also the invasive species *Caulerpa cylindracea*, characterised by a very slender morphotype. Two calcified species, the palmelloid green

alga *Palmophyllum crassum* and the encrusting red alga *Peyssonnelia rosa-marina* were observed on the frame, with large thalli whereas smaller specimens grew on elements of the canopy.

Foraminifers

Foraminifers accounted for 33 living species with 1837 specimens (Table 1, S2). Almost all species (32 = 97.0%) occurred on the canopy with 1547 specimens (corresponding to 84.2% of the total number of specimens) (Table 2; Fig. 3). In contrast, only 15 species (corresponding to 45.5%) were present on the frame with 290 specimens (15.8%) (Table 2; Fig. 3). The community was quite diversified but not much evenly distributed, as demonstrated by the Shannon index of 1.83 and the Pielou's Evenness of 0.17 for the canopy (Table 3). A similar situation was found on the frame, where the community was quite diversified (Shannon index of 1.31) but unequally distributed (Pielou's Evenness of 0.32) (Table 3). The most significant species in terms of abundance were *Rosalina bradyi* (Fig. 4Q), *Miniacina miniacea* (Fig. 4N), *Lobatula lobatula*, *Elphidium crispum* and *Neoeponides bradyi,* which represented the 85.2% of the whole alive foraminifer community.

Relevant differences between the canopy and the frame were also observed in the composition of the community. On the canopy, the most abundant species was *R. bradyi,* with 713 specimens (including 201 juveniles), followed by *L. lobatula* with 238 specimens (of which 16 were juveniles), all - except for 2 - associated to the canopy. Other abundant species were *M. miniacea* (158, of which 10 juv.), *E. crispum* (105) and *N. bradyi* (102). Other species exclusively or mainly found on the canopy were *Planorbulina mediterranensis* (81), *Miliolinella webbiana* (49) and *Cornuspiramia adherens* (20). Less than a dozen specimens represented all other species. On the frame, the most abundant species was *M. miniacea,* (Fig. 5N) with 190 specimens, followed by *E. crispum* (48). *Adelosina mediterranensins* and *Adelosina* sp., both with 2 representatives, were exclusively detected on the frame.

The foraminifer dead community consisted of only 10 species (all also found in the living community) and 186 specimens (Table 1). The frame and the canopy hosted 7 dead species each (70% of the foraminifer dead community), with 28 specimens (15.1%) on the canopy, and 158 (84.9%) on the frame (Table 2; Fig. 3). *P. mediterranensis* (13 specimens) was the most abundant species on the canopy, and *M. miniacea* (142 specimens) dominated on the frame.

Molluscs

Molluscs were present with a total of 33 live species and 325 specimens (Table 1; S3). Molluscs showed the highest number of living juveniles (193) corresponding to about half of the community. The canopy hosted 31 species (corresponding to 93.9%) and 210 specimens (64.6%) whereas the frame hosted only 5 species (15.2%) and 115 individuals (35.4%) (Table 2; Fig. 3). The mollusc community of the canopy was rather diversified (Shannon index of 1.95) and quite equally distributed (Pielou's Evenness of 0.20) (Table 3). On the contrary, the community of the frame was not much diversified (Shannon index of 0.59) but quite evenly distributed (Pielou's Evenness of 0.55) (Table 3). The most abundant species were *Gregariella semigranata* (Fig. 5M) and *Bittium latreillii,* which represented the 46.5% of the living community.

On the canopy, the bivalve *G. semigranata* was the most abundant species with 76 specimens (of which 65 juv.), followed by the gastropod *B. latreillii* with 75 specimens (all juv.). Slightly abundant were *Striarca lactea* (8, of which 6 juv.) and *Pusillina incospicua* (6, of which 3 juv.), while other species were represented by very few specimens. Among them are the vermetids *Thylacodes arenarius* (2) and *Vermetus granulatus* (1) mostly found as epibionts on mineralised bryozoans (Fig. 4O, P). Some byssate bivalves including *Musculus costulatus* (4 juv.) and *Glans trapezia* (1 juv.) and several species of herbivore gastropods (e.g., *Williamia gussoni*: 5, of which 2 juv. Specimens) were found only on the canopy.

On the frame, the dominant species was *G. semigranata* with 100 (of which 1 juv.) specimens, followed by far *Hiatella arctica* with 10 specimens (all juv.). Species typical of hard substrates, such as the boring bivalves *Rocellaria dubia* (1 juv.) and *Sphenia binghami* (2, 1 juv.), also occurred with few specimens.

Thanatocoenosis included 68 species (of which 20 were also found alive) and 232 specimens (Table 1). On the canopy 43 species (63.2%) and 144 specimens (62.1%) were found, while on the frame 32 species (47.1%) with 88 specimens (37.9%) were registered (Table 2; Fig. 3). On the canopy, the most abundant species was *G. semigranata* (34, of which 21 juv.), followed by *B. latreillii* (21, of which 15 juv.). On the frame, the gastropod *G. semigranata* was the most abundant species (10, of which 3 juv.) followed by *Pusillina inconspicua* (8, of which 4 juv.) and the vermetid *V. granulatus* (7) (Fig. 5L).

Serpulids

Serpulids accounted for 21 living species and 802 specimens (Table 1, S4). The canopy hosted 17 species (81%) and 564 specimens (70.3%), while the frame hosted 17 species (81%) and 238 specimens (29.7%) (Table 2; Fig. 3), with 13 shared species.

The community on the canopy was moderately diversified (Shannon index of 1.62) and not equally distributed (Pielou's Evenness of 0.22) (Table 3). On the frame, it was more diversified (Shannon index of 2.16) and also better distributed (Pielou's Evenness of 0.51) (Table 3). The most significant species were *Josephella marenzelleri* (Fig. 4H) and *S. triqueter* (Fig. 4F, G), constituting the 58.9% of the whole serpulid living community.

On the canopy, *J. marenzelleri* (255) was the most abundant species, followed by *S. triqueter* (Fig. 5H) with 109 specimens (of which 8 juv.). Here, spirorbines such as *Janua heterostropha* (50, of which 2 juv.), *Neodexiospira pseudocorrugata* (Fig. 4L) (18, of which 5 juv.) and *Simplaria pseudomilitaris* (Fig. 4K) (14, of which 8 juv.) were well represented, whereas *Spirorbis cuneatus* (whit only 1 specimen) was exclusively found on the canopy.

Also on the frame, *J. marenzelleri* dominated the community (64 specimens), followed by *S. triqueter* (Fig. 5H) (44), *Metavermilia multicristata* (24), *Placostegus crystallinus* (Fig. 5G) (12), *Serpula concharum* (10), *Hydroides pseudouncinata* (Fig. 5E, F) (10), whereas further species were represented by less individuals. Though represented by few specimens, *Semivermilia crenata* (8) and *Spiraserpula massiliensis* (4) were exclusively detected on the frame.

Serpulid dead community included 28 species (of which 14 were also detected alive) with 2186 specimens (Table 1). On the canopy, 20 species (71.4%) with 324 specimens (14.8%) were detected, while on the frame 27 species (96.4%) with 1862 specimens (85.2%) were found (Table 2; Fig. 3). The most abundant species on the canopy was *Filograna* sp. (Fig. 4I) (101, of which 2 juv.), followed by *S. pseudomilitaris* (75). On the frame, *J. marenzelleri* showed the highest number of individuals (326), followed by *S. triqueter* (270, of which 10 juv.).

Ostracods

Ostracods were present with 7 living species and 60 individuals (Table 1, S5). All species were found on the canopy with 56 specimens (93.3% of specimens). On the frame, only 1 species (14.3%) with 4 specimens (6.7%) was found (Table 2; Fig. 3).

Ostracod community was quite diversified (Shannon index of 1.78) and equally distributed (Pielou's Evenness of 0.52) on the canopy but insufficient for any calculation on the frame (Table 3).

On the canopy, the species *Aurila speyeri* (Fig. 4R) was the most abundant (23 specimens + juv.) followed by *Xestoleberis dispar* (12 specimens), *Bairdia conformis* (7 specimens) and *Loxoconcha gibberosa* (7 specimens + juv.).

On the frame, only 4 living specimens (6.7%) of *A. speyeri* were found in the crevices.

Dead community included only disarticulated valves of 9 species, mostly represented in the living community except for *Loxoconcha tumida* and *Urocythereis favosa*.

Bryozoans

Bryozoans showed 84 alive species with 2281 colonies (Table 1, S6). The canopy hosted 70 species (83.3%) and 1409 colonies (61.8%) while the frame hosted 62 species (73.8%) and 872 colonies (38.2%) (Table 2; Fig. 3).
The community on the canopy was diversified (Shannon index of 5.95) but not very evenly distributed (Pielou's Evenness of 0.29) (Table 3). On the frame, it showed a higher level of diversification (Shannon index of 13.46) and a pretty good distribution (Pielou's Evenness of 0.51) (Table 3).
On the canopy, the most abundant species was *Celleporina caminata* (Fig. 4J) with 268 colonies (of which 36 juv.), followed by *M. cereoides* with 101 colonies (of which 3 juveniles). Quite abundant were *Scrupocellaria delilii* (98, of which 1 juv.) *Mecynoecia delicatula* (Fig. 4E) (82, of which 2 juv.) *Aetea truncata* (63), *Copidozoum planum* (56), *Beania cylindrica* (50), *Crisia ramosa* (47), *Beania mediterranea* (47) and *Annectocyma major* (42). In contrast, *Amathia delicatula* (40), *Walkeria tuberosa* (16) and *Escharoides mamillata* (Fig. 4B) (16, of which 5 juv.) were well represented exclusively on the canopy. Further species were subordinate and preferentially found on the rigid substratum offered by the bryozoan *Margaretta cereoides* (e.g., *Arthropoma cecilii*: Fig. 4A) or the fleshy algae (e.g., *Chorizopora brongniartii*: Fig. 4C).
On the frame, the most abundant species were *C. caminata* and *Calyptotheca rugosa* (Fig. 5C), both with 38 colonies followed by *Plesiocleidochasma mediterraneum* (Fig. 5L) (32), *Beania hirtissima* (30), *Copidozoum planum* (28), *S. delilii* (28), *Beania mediterranea* (24) and *M. delicatula* (24, of which 6 juv.). *Onychocella marioni* (24), *Schizotheca fissa* (14), *Cribrilaria radiata* (12) and *Ellisina gautieri* (12), were among the most abundant species exclusively found on the frame. Although numerically subordinate *Hippopleurifera punlchra* formed large colonies (Fig. 5A, B, H).
Dead community included 52 species (of which 35 were also found alive) and 939 colonies (Table 1). A total of 17 species (32.7%) with 123 colonies (13.1%) and 42 species (80.8%) with 816 colonies (86.9%) were counted on the canopy and the frame, respectively (Table 2; Fig. 3). *C. caminata,* with 90 colonies (of which 1 juv.), was the dominant species on the canopy, followed by *Turbicellepora coronopus* (5). On the frame, the most abundant species was *C. planum* (46).

Minor taxa

Brachiopods, barnacle cirripeds and scleractinians counted few species and specimens comparing to the other investigated taxa, overall accounting for 4 living species and 78 specimens (Table 1, S7). All species were present on the canopy with 22 specimens, while only 3 species with 56 specimens were found on the frame (Table 2; Fig. 3).
In particular, brachiopods included 3 alive species and 48 specimens. On the canopy 3 species and 20 specimens, while on the frame by 2 species and 28 specimens represented them. *Joania cordata,* (Fig. 5P) with 12 specimens (of which 5 juv.) dominated the canopy, followed by *Argyrotheca cuneata* (Fig. 5K) with 7 specimens (of which 4 juv.) and by *Megathiris detruncata* (1 specimen). On the frame, *A. cuneata* with 22 individuals dominated on *J. cordata* (6, of which 4 juv.).
Barnacles were represented only by *Verruca spengleri,* for both the canopy and the frame. Only 2 individuals were found on the canopy, while 28 specimens settled on the frame (Fig. 5J).
Scleractinians were represented by 2 species, *Caryophyllia* sp. and *Paracyathus pulchellus* (Fig. 5O), each with only 2 specimens attached on the frame.
Thanatocoenosis included 5 species (of which 3 found also alive) with 18 specimens (Table 1). On the canopy, only 2 species and 4 specimens were counted, while on the frame all the 5 species and 14 specimens were detected (Table 2; Fig. 3). On the canopy, only brachiopods were found with the species *A. cuneata* and *J. cordata* (2 specimens each). On the frame, the same brachiopods were registered with 2 and 4 specimens, respectively, plus 4 specimens of *V. spengleri* and 2 each of the cnidarians *Caryophyllia* sp. and *P. pulchellus*.

Table 1. Taxonomic groups found in the community of the studied build-up E (canopy and frame together) reported separately for live and dead species and specimens/colonies.

Taxa	**Species**				**Specimens/colonies**			
	Live	%	Dead	%	Live	%	Dead	%
Fleshy algae	60	24.8	NA		NA		NA	
Foraminifers	33	13.6	10	6.1	1837	34.1	186	5.2
Molluscs	33	13.6	68	41.7	325	6	232	6.5
Serpulids	21	8.7	28	17.2	802	14.9	2186	61.4
Ostracods	7	2.9	NA		60	1.1	NA	
Bryozoans	84	34.7	52	31.9	2281	42.4	939	26.4
Minor taxa	4	1.7	5	3.1	78	1.4	18	0.5
Total	**242**	**100**	**163**	**100**	**5383**	**100**	**3561**	**100**

Table 2. Numbers of live and dead species (a) and live and dead specimens/colonies of all taxonomic groups identified on the studied build-up E, reported separately for canopy and frame.

Taxa		**Canopy**					**Frame**					**Total**	
		Live	%	Dead	%	Total	Live	%	Dead	%	Total	Live	Dead
Species	Fleshy algae	60	100	NA		60	2	3.3	NA		2	60	NA
	Foraminifers	32	97.0	7	70	32	15	45.5	7	70	16	33	10
	Molluscs	31	93.9	43	63.2	56	5	15.2	32	47.1	33	33	68
	Serpulids	17	81	20	71.4	22	17	81	27	96.4	27	21	28
	Ostracods	7	100	NA		7	1	14.3	NA		1	7	NA
	Bryozoans	70	83.3	17	32.7	73	62	73.8	42	80.8	80	84	52
	Minor taxa	4	100	2	40	4	3	75	5	100	5	4	5
	Total	**221**		**89**		**254**	**105**		**113**		**164**	**242**	**163**
Specimens	Foraminifers	1547	84.2	28	15.1	1575	290	15.8	158	84.9	448	1837	186
	Molluscs	210	64.6	144	62.1	354	115	35.4	88	37.9	203	325	232
	Serpulids	564	70.3	324	14.8	888	238	29.7	1862	85.2	2100	802	2186
	Ostracods	56	93.3	NA		56	4	6.7	NA		4	60	NA
	Bryozoans	1409	61.8	123	13.1	1532	872	38.2	816	86.9	1688	2281	939
	Minor taxa	22	28.2	4	22.2	26	56	71.8	14	77.8	70	78	18
	Total	**3808**		**623**		**4431**	**1575**		**2938**		**4513**	**5383**	**3561**

Table 3. Shannon-Wiener (H') and Pielou's Evenness (J') indices for the living communities of the studied groups of build-up E. Indices were not calculated for minor taxa due to the very low numbers of species and specimens.

Taxa	**Canopy**		**Frame**	
	H'	J'	H'	J'
Foraminifers	1.83	0.17	1.31	0.32
Molluscs	1.95	0.20	0.59	0.55
Serpulids	1.62	0.22	2.16	0.51
Ostracods	1.78	0.52	NA	NA
Bryozoans	5.95	0.29	13.46	0.51

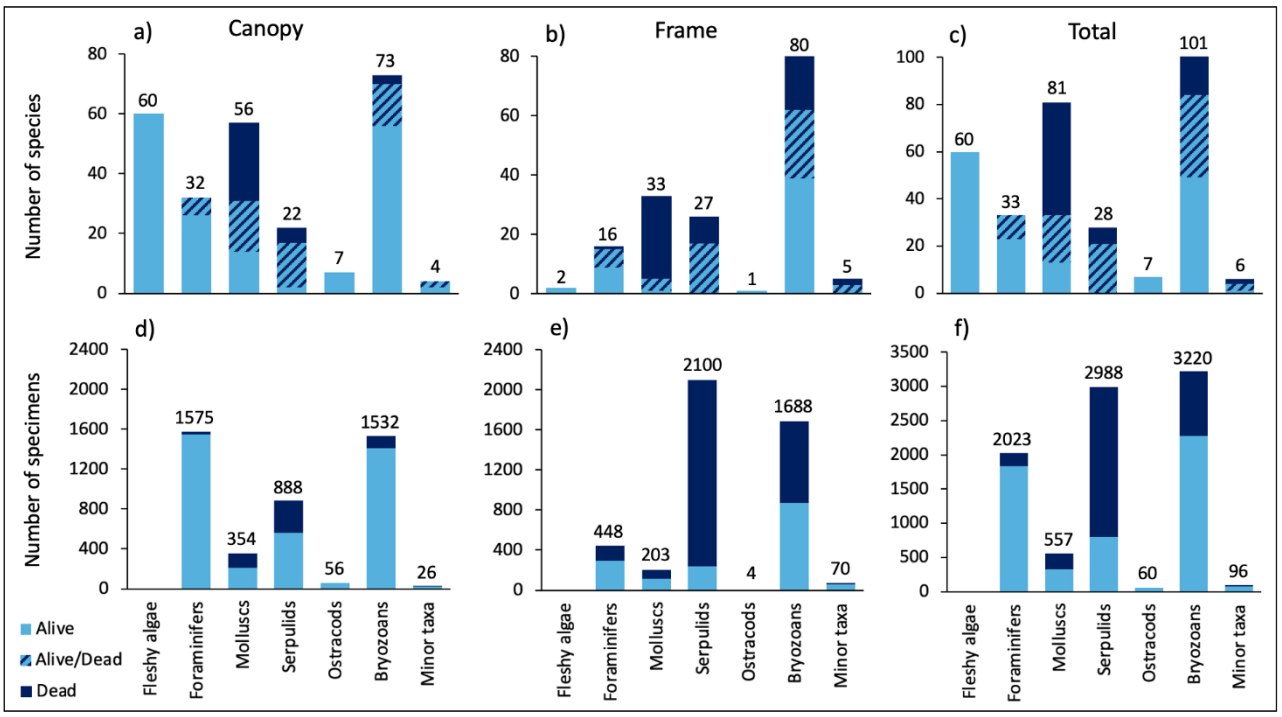

Fig. 3 Total number of species (a, b, c) and specimens/colonies (d, e, f) for each taxon identified on the studied build-up E in the canopy and the frame, respectively. Species found only alive, simultaneously with alive and dead specimens/colonies, and only with dead specimens/colonies are reported with different colours. Minor taxa include scleractinians, cirripeds and brachiopods. Note that several species occurred both in the canopy and the frame: see Table 2 and the text for further information and consequently the total number of species for each taxonomic group is less than the sum of species found in the canopy and the frame.

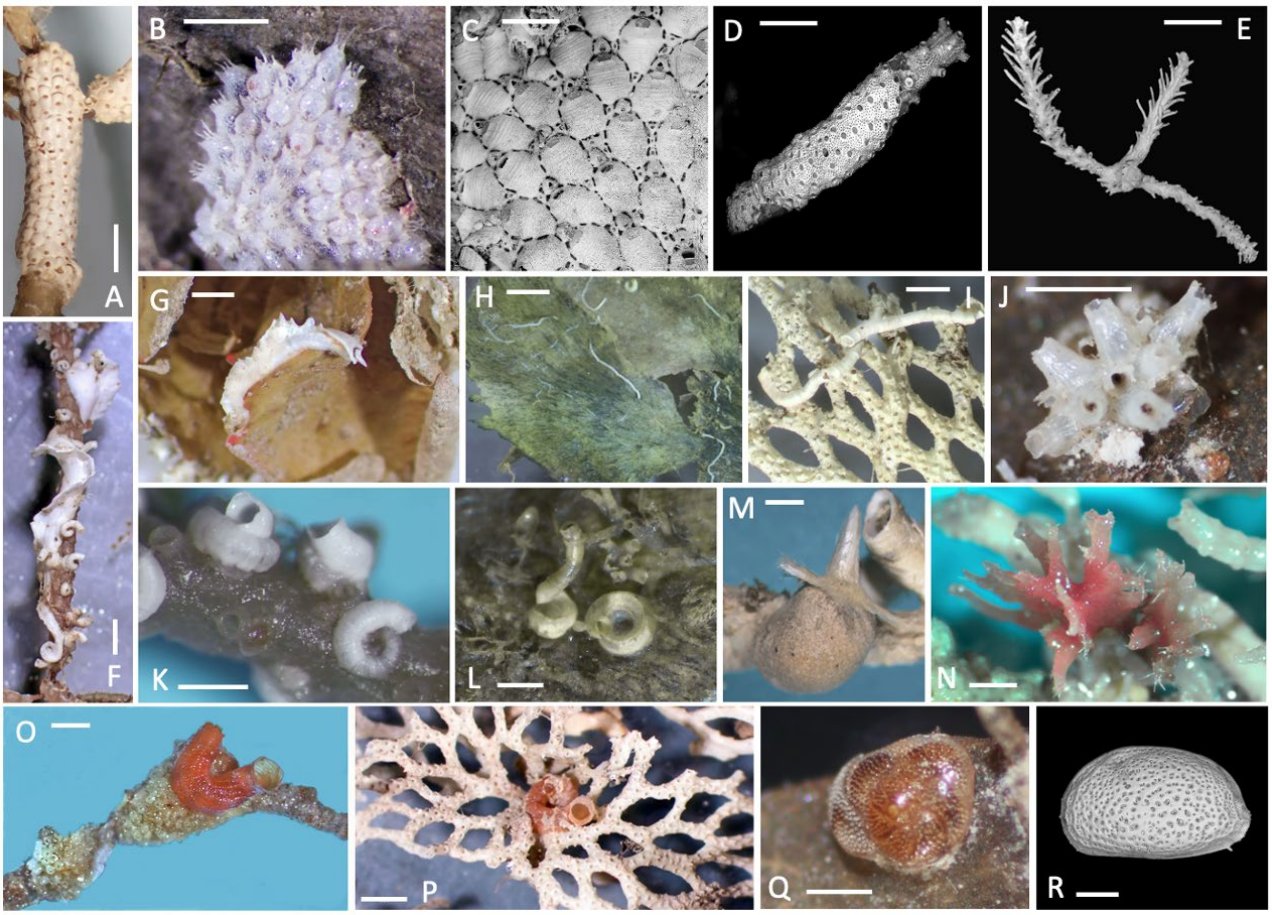

Fig. 4. Species typically observed on the canopy documented through transmitted light microscopy except for D-E and R photographed through SEM. (A) The encrusting bryozoan *Arthropoma cecilii* on the bryozoan *Margaretta cereoides*. PMC Rosso Collection I.H.B100a. (B) The bryozoan *Escharoides mamillata* on the alga *Flabellia petiolata*. PMC Rosso Collection I.H.B-109a. (C) The bryozoan *Chorizopora brongniartii* on the alga *F. petiolata*. PMC Rosso Collection I.H.B99a1. (D) The bryozoan *Schizobrachiella sanguinea* on *M. cereoides*. PMC Rosso Collection I.H.B-112a. (E) The bryozoan *Mecynoecia delicatula* on *M. cereoides*. PMC Rosso Collection I.H.B59b. (F) The serpuline *Spirobranchus triqueter* and the spirorbine *Simplaria pseudomilitaris* on *M. cereoides*. PMC Sanfilippo Collection I.H.Pol-6a. (G) The serpuline *S. triqueter* on *Peyssonnelia rubra.* PMC Sanfilippo collection I.H.Pol-6a. (H) The serpuline *Josephella marenzelleri* on *F. petiolata*. PMC Sanfilippo collection I.H.Pol-3a. (I) The serpuline *Filograna* sp. on a *Reteporella* colony. PMC Sanfilippo collection I.H.Pol-2a. (J) Young colony of the bryozoan *Celleporina caminata* on the stem of a *F. petiolata* thallum. PMC Rosso Collection I.H.B-98a4. (K) Several *S. pseudomilitaris* spirorbid specimens on *M. cereoides*. PMC Sanfilippo collection I.H.Pol-7a. (L) The spirorbin *Neodexiospira pseudocorrugata* on *F. petiolata*. PMC Sanfilippo collection I.H.Pol-5a. (M) A sponge of the genus *Sycon* on a serpulid. Bertolino CBR Collection, University of Genova. (N) The arborescent foraminifer *Miniacina miniacea* on filamentous algae. PMC Sciuto Collection I.H.For-1a. (O) Epibiosis of the gastropod *Vermetus granulatus* on celleporid bryozoan colonies, all growing on the stem of *F. petiolata*. PMC Rosso CBR collective bryozoan collection. (P) The vermetid gastropod *V. granulatus* on a colony of the reteporiform bryozoan *Reteporella sudbournensis*. PMC Rosso Collection I.H.B-113a. (Q) The foraminifer *Rosalina bradyi* on *F. petiolata*. PMC Sciuto Collection I.H.For-2a. (R) The ostracod *Aurila speyeri*. PMC Sciuto collection I.H. O-43a. Scale bar: A, D, H, O: 2 mm; B, E, F, G, I, J, K, L, M, N: 1 mm; C: 500 μm; Q, R: 200 μm.

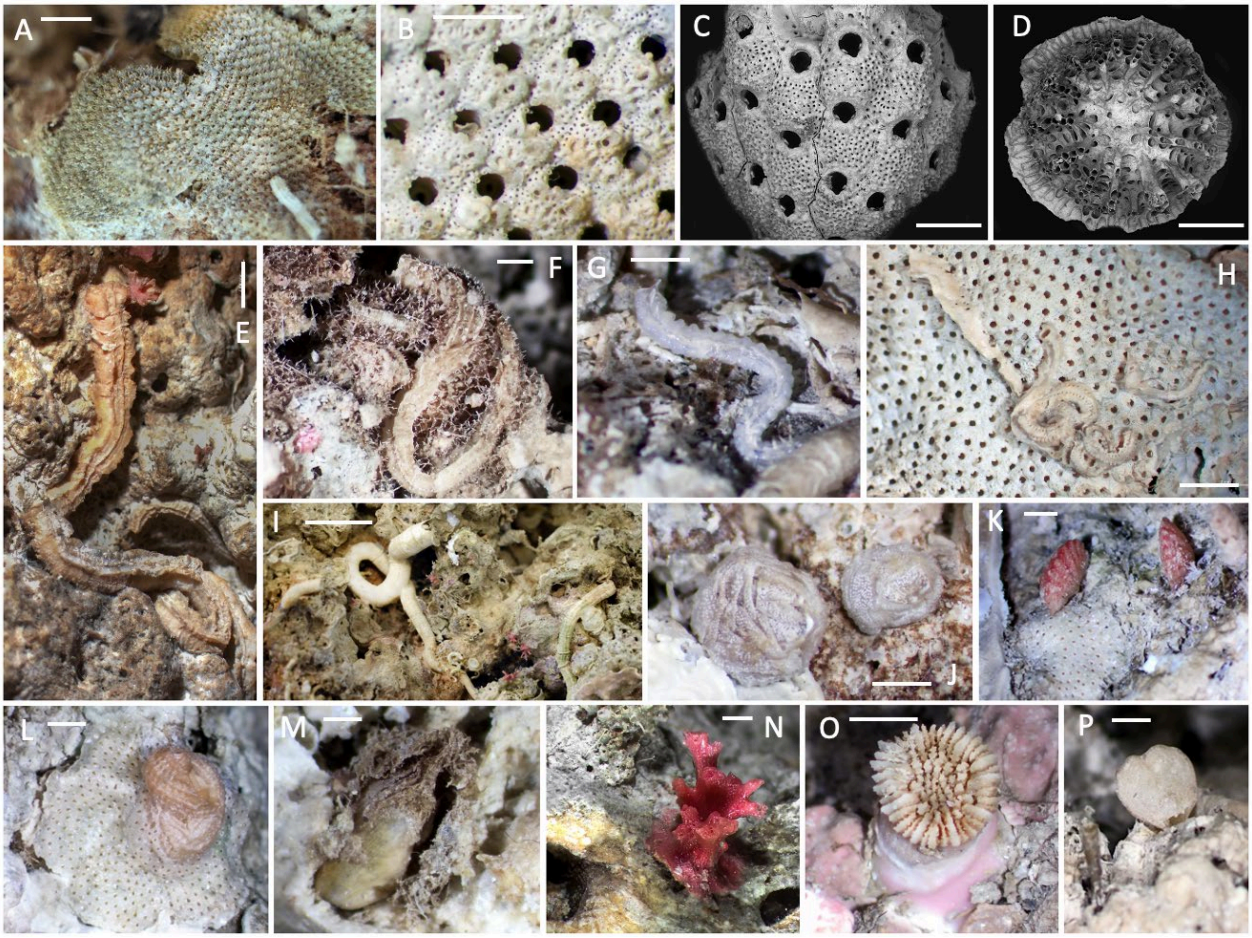

Fig. 5. Species typically observed on the frame documented through transmitted light microscopy except for C and D photographed through SEM. All material in the Basso CBR collection, University of Milano-Bicocca, except for bryozoan colonies in C and D. (A, B) The encrusting bryozoan *Hippopleurifera pulchra* forming some square centimeters large colonies, also detectable through photogrammetry. (C) The bryozoan *Calyptotheca rugosa* PMC. Rosso Collection I.H.B-114a. (D) A hemispheric colony of the bryozoan *Disporella hispida* PMC. Rosso Collection I.H.B-56b. (E) The serpulid *Hydroides pseudouncinata*. (F) The serpulid *H. pseudouncinata* covered by a sponge. (G) The serpulid *Placostegus crystallinus*. (H) The serpulids *Spirobranchus polytrema* and *S. triqueter* on the bryozoan *H. pulchra.* (I) General aspect of the frame surface. (J) The barnacles *Verruca spengleri*. (K) The brachiopods *Argyrotheca cuneata*. (L) The bryozoan *Plesiocleidochasma mediterraneum* overgrowing the vermetid *V. granulatus*. (M) The bivalve *Gregariella semigranata* in its sectioned nest partly formed by algal laminae. (N) The foraminifer *M. miniacea.* (O) The coral *Paracyathus pulchellus*. (P) The brachiopod *Joania cordata*. Scale bar: A, I: 1 cm; B, D, F, G, K, L, M, N, P: 1 mm; C: 500 µm; E, H, O: 2 mm.

4. DISCUSSION

The Coralligenous habitat is one of the most complex and diverse habitats of the Mediterranean Sea (Ballesteros 2006), but the knowledge of its biodiversity is possibly still incomplete, at least for particular still under-investigated taxa, and especially regarding the contribution of biota associated with the canopy and the frame. In this context, the data provided in this research implement available knowledge, adding detailed information on the biodiversity associated with a coralline-dominated coralligenous bioconstruction from a still understudied geographical region of the western Ionian Sea, at about 37 m depth. Several taxonomic groups are contemporaneously investigated, and compositional and structural differences between the canopy

and the frame are highlighted for the first time, also providing insights about relevant changes between their living and dead communities, focusing on the skeletonised component species, which are potentially preservable in the build-up or its neighbourhood.

4.1. Total biodiversity

Comparison of the biodiversity associated with the studied build-up and other individual coralligenous bioconstructions is almost impossible because many papers deal with single or a few taxonomic groups (e.g. Boudouresque 1973, Zabala 1986, García-Raso 1988, 1989, Bertolino et al. 2013, 2014, 2017a,b, Harmelin 2017, Casoli et al. 2019). Even comparing the biodiversity of single taxa associated with the present and other Coralligenous is difficult because data are usually provided for investigated sites or geographical areas and not for individual structures (Ballesteros 2006 and references therein). Moreover, the different features and ecological complexity of Coralligenous, its large bathymetric range and related wide array of environmental parameters, as well as different sampling and analysis techniques, increase the difficulties in finding comparative studies and evaluations (e.g., Rosso & Sanfilippo 2009).

A proper comparison can possibly be made with a previously studied columnar build-up collected from the same site at comparable depth (Di Geronimo et al. 2001, 2002). Di Geronimo et al. (2001, 2002) only identified bryozoans, serpulids, vermetids and foraminifers, apart from calcareous/fleshy algae and sponges, which occurred with far less abundance compared to the present results. Foraminifers and serpulids counted few species and specimens, and bryozoans were represented only by a dozen species in the Di Geronimo et al. (2001, 2002) build-up, while in the studied coralligenous bioconstruction they are the most abundant and diversified taxonomic group. These differences indicate strong variability between bioconstructions at the studied site off Marzamemi, as expected due to the high spatial heterogeneity widely reported for the Coralligenous elsewhere (Ballesteros 2006), one of the features prompting its inclusion among habitats worthy of protection (Habitats Directive 1992). Such high biodiversity and variability between build-ups were observed in other examined bioconstructions from the very same area and roughly the same depth range (ca 33-37 m), leading to the identification of an unprecedented number of species for foraminifers (130 taxa) and ostracods (22 species) associated with this habitat but 61-69 and 12-15 species per build-up, respectively (Sciuto et al. 2023). Analogously, serpulids are present with 36 species and from 14 to 26 species per build-up (Sanfilippo et al. in press) exceeding those previously reported in Di Geronimo et al. (2001) and Rosso & Sanfilippo (2009). Preliminary lists of bryozoans also hint at significant species richness (more than one hundred) and variability (Rosso et al. in prep.).

Comparison is more difficult when considering extensively investigated sites (including the analysis of several samples, even from several sampling stations). However, the present results for some groups still point to relatively high biodiversity values. Bryozoans, with 84 species, exceed the 67 species identified in the Coralligenous occurring along the Les Albères coasts (Laubier 1966), but not the nearly 130 species found along the Provençal coasts (Harmelin 1976) and the 171 species in the Medes Islands (Zabala 1986, Ballesteros 2006), as reported in Rosso & Sanfilippo (2009). Serpulids, with 21 species, outnumber the 6 species reported from the North Adriatic (Amoureux & Katzmann 1971, Casellato & Stefanon 2008), the 10 species from the Les Albères coast (Laubier 1966) and are comparable with the 22 species inventoried between 10 and 30 m depth at Giglio Island in NE Tyrrhenian Sea (Casoli et al. 2016).

Extending the comparison to data so far known for the coralligenous habitat from the entire Mediterranean, the diversity of serpulids is high when compared with the 36 species reported from four build-ups in the same area and almost 36 species altogether reported across the Mediterranean basin (Sanfilippo et al., in press). Other groups such as bryozoans (84 species) show one of the highest species richness and represent 38% of the 219 species so far reported for Coralligenous-associated bryozoans at Mediterranean scale (Rosso & Di Martino 2016), thus pointing to a relevant share. Though based on comparably lower values, brachiopods (3 species) account for the 37% of the 8 brachiopods species reported by Logan (1979). Ostracods, for which only 11 species were cited though not listed in Hong (1982) and Ballesteros (2006), the 7 species found in the examined build-up represent 32% of the 22 ostracods species so far known as associated with the

Coralligenous, all listed for the first time by Sciuto et al. (2023) from a group of four examined build-ups in the studied area. Though still well represented, foraminifers with 33 species out of the 130 reported in Sciuto et al. (2023) represent 25% of the foraminiferal diversity found in the Coralligenous from the same area. On the contrary, other investigated groups show lower to exiguous diversities. Molluscs represent 6% out of the 519 species known for the Coralligenous (Poursanidis & Koutsoubas 2015, Casoli et al. 2019), and scleractinians represent just 5% of the 43 species reported so far (Ballesteros 2006 and references therein).
As indicated by Ballesteros (2006), most of the algal species adapted to life in deep waters have been found in the Coralligenous. However, the floristic richness of the Coralligenous varies greatly in relation to the structure and type of the concretion, the geographical area, and the depth. Considering that the results of this study refer to a column sampled in a single season and that calcareous red algae Corallinophycidae were not included, the 60 species of macroalgae identified (excluding encrusting species) in this study represent a relatively high algal biodiversity, especially when compared with studies conducted in larger areas or aimed at the census of macroalgal flora such as Piazzi et al. (2004) and Costanzo et al. (2021) in which 99 and 92 species of macroalgae (including encrusting algae) are reported, respectively.
The data show that the build-up E supports a high biodiversity, as also demonstrated by Shannon Diversity and Pielou's Evenness (Tab. 3) calculated for each taxonomic group to synthetically evaluate which of them mostly contribute to the total diversity. Even if the distribution of species abundances (equitability) is not very uniform, species diversity ranges from moderate to high values and bryozoans clearly play a predominant role in this respect. Moreover, these values are still underestimated considering that further possible species found in the thanatocoenosis could be added. Several dead specimens of the canopy, having been found still attached to algal thalli were probably still alive shortly before our collection, and are likely part of the resident dwellers of this bioconstruction.

4.2. Frame and canopy contribution to coralligenous biodiversity

Canopy and frame differ for several characteristics including the nature of substrates, light and hydrodynamism intensity, and sediment contiguity (e.g., Ballesteros 2006).
The dense algal-bryozoan canopy significantly increases the availability of colonisable surfaces, continuously providing virgin, albeit ephemeral, space and offering various typologies of substrates. These range from rigid to highly flexible, encompassing the 3D-space provided by the internodes of *M. cereoides,* the stems of *F. petiolata,* and certain filiform algae, as well as the 2D-space provided by the fronds and laminar algal blades, including *F. petiolata*, *O. volubilis* and *H. tuna* (see Rosso et al. 2023). Different textures are also offered, ranging from smooth to rough articulated surfaces. Furthermore, organisms can choose between more illuminated or shaded microhabitats and benefit from a gradient of hydrodynamic conditions. Owing to the dominance of ephemeral and flexible substrata, the canopy is mostly colonized by uncalcified and weakly calcified species, as well as by species exhibiting small-sized specimens/colonies, all features useful to avoid early detachment (Rosso et al. 2023), and also with a short life-span and early development (Harmelin 2017).
The present results suggest that among sessile organisms, several bryozoans, foraminifers and spirorbines seem well adapted to thrive in such ecological conditions. The dominance of small, unilaminar, and short-lived bryozoan colonies on the flexible and non-perennial substrate represented by *F. petiolata* has been also highlighted by Harmelin (2017). Encrusting foraminifers and spirorbines, with reduced or missing calcification along the attaching surface, live almost exclusively as epibionts on algae (Langer 1993, Rosso et al. 2023). Brachiopods, usually reported as common inhabitants of small crevices of the bioconstruction (Logan 1979), are another group well represented on the canopy, as also reported by Rosso et al. (2023). However, it is noteworthy that they exclusively include juveniles and small-sized species, such as *Joania cordata* which showed a double number of specimens on the canopy rather than on the frame.
On the other hand, the frame consisting of a hard structure rich in cavities and crevices prone to be often filled with sediment, and offering rough surfaces and dark/semi-dark microenvironments, is mostly colonized by large, usually well calcified, sciaphilic epifaunal species to which some infaunal (boring and insinuating) organisms add. Among them, bryozoans, serpulids and also the foraminifer *M. miniacea* prevail, according to

observations by Harmelin (2017) and Zabala (1986) for bryozoans, Rosso & Sanfilippo (2009) for serpulids, and Laborel (1987) for *M. miniacea*. Notwithstanding the available surface (hard to be estimated and not evaluated in the present instance) is possibly less extensive in comparison to the canopy, the frame hosts high number of dead species and a very high abundance of dead specimens/colonies, more than quadruplicated if compared with the canopy. Furthermore, since bryozoans and serpulids and to a lesser extent foraminifers are mineralised and cemented on the frame, they become part of the coralligenous bioconstruction contributing to its accretion (Hong 1980, Rosso & Sanfilippo 2009, Basso et al. 2022) as also demonstrated with microfacies analysis of the internal coralligenous structure of the same build-up (Cipriani et al. 2024). Scleractinian cnidarians, some molluscs, barnacles and brachiopods are also typical, but subordinate, constituents of the frame. Among molluscs, the nestling species *G. semigranata,* whose peculiar adaptation has been investigated by Sanfilippo et al. (2024), largely prevails. It is of note that several infaunal bivalve species, commonly found on soft substrates outside the bioconstruction, are herein retained as contributors to the frame biodiversity because they colonize (almost temporarily) its sediment-filled cavities and participate to the trophic dynamics of the bioconstruction.

4.3. **Assessing biodiversity**

The study of the Coralligenous represents a complicate issue due to the complex structure of this habitat. Three main methods have been employed to study coralligenous communities, each showing both advantages and disadvantages in achieving specific goals (Bianchi et al. 2003): collection of samples, photographic methods and visual census approaches (Bianchi et al. 2003, Kipson et al. 2011, Sartoretto et al. 2017, Piazzi et al. 2019). For the current build-up, the assessment of biodiversity involved identifying species through close inspection of collected material, whereas the constructional role of organisms at high taxonomic ranks was surveyed using photogrammetric analysis on its outer surface (Bracchi et al. 2022). Besides calcareous algae and mineralised Peyssonneliales, the examination of samples led to the recognition of species belonging to fleshy algae and 10 other high-level taxonomic groups of organisms, ranging from family to phylum level, namely Foraminifera, Porifera, Cnidaria, Mollusca, Serpulidae, Crustacea (including Ostracoda and Cirripedia), Bryozoa, Brachiopoda and Ascidiacea. Most of these groups consisted entirely of or included skeletonised species, some of which were evident and/or voluminous, while others were small but with a distinctive aspect, such as the foraminifer *M. miniacea*. Photogrammetry (Bracchi et al. 2022) allowed the detection of the same high rank groups (with annelids actually consisting of serpulids, and crustaceans including barnacles but not ostracods) but it did not capture cryptic and small-sized organisms, such as brachiopods and the only small ascidians present. Reliant on surface coverage, the photogrammetry technique overestimated some taxonomic groups and underestimated others, such as bryozoans and serpulids, or even overlook further ones, such as foraminifers, despite their abundances, as already remarked for submarine caves (e.g., Rosso et al. 2013). Direct observation allowed locating and identifying small specimens hidden within the complex structure of both the canopy and the frame. The elements of the canopy (especially large algal fronds such as the laminar *F. petiolata*) cover the frame, concealing organisms attached to the surface, and often fold back hiding all epibionts on the opposite side of the blades. This has been also remarked by Casoli et al. (2021), who noted that even relatively large organisms, such as the erect ascidian *Halocinthia papillosa,* were obscured by larger organisms like *Peyssonnelia* spp. or *Reteporella grimaldi* when observed in situ. Furthermore, the numerous holes and crevices of the framework host cryptic organisms, especially bryozoans, serpulids and brachiopods, that colonise these anfractuosities often in great quantity (Ballesteros 2006). Due to the small-scale spatial variability of the Coralligenous (Morri et al. 1999, Piazzi et al. 2009), a direct analysis of several, as small as possible samples from nearby areas and even slightly different settings are necessary to comprehensively describe its biodiversity.

In the last years, the use of digitalized methodologies (including photogrammetry, photo quadrats and photo mosaicking) to investigate species, communities and habitat has highly increased (Piazzi et al. 2019 and references therein, Casoli et al. 2021, 2024) greatly enhancing our knowledge. However, these techniques pose significant issues when used to assess biodiversity at low taxonomic ranks, especially at the species level.

Indeed, identification at species level is feasible for large organisms or those with very distinct diagnostic features, but impossible for most algae and for small organisms, like almost all foraminifers, molluscs, and bryozoans whose identification relies increasingly on micrometric details (e.g., Rosso et al. 2013). Nevertheless, underwater photo analysis of large areas can integrate data obtained from small collected samples (Rosso et al. 2019) and can be valuable for assessing the ecological quality of coralligenous habitats for monitoring purposes (Casoli et al. 2021).

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