

Article

The Bryozoan *Margaretta cereoides* as Habitat-Former in the Coralligenous of Marzamemi (SE Sicily, Mediterranean Sea)

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Abstract: Although several bryozoans are considered habitat-former species, allowing colonisation by epibionts and promoting biodiversity, studies dealt so far with only some, usually constructional, species. In this context, the present study focuses on the epibiosis found on the erect mineralised but flexible species *Margaretta cereoides*, contributing with some macroalgae to the canopy formation on a coralligenous build-up collected at 36.7 m depth offshore Marzamemi (Ionian Sea, Mediterranean) in the frame of the project CRESCIBLUREEF. Focusing on bryozoans and serpulids we documented high diversity (species richness) on the investigated substrata (*M. cereoides*, *Flabellia petiolata*, *Peyssonnelia rubra*, *Osmundaria volubilis* and all other fleshy algae including *Phyllophora crispa*). Diversity, total number of colonies/specimens hosted, and number of colonies/specimens per cm² are higher on *M. cereoides* than on algae, possibly in relation with the morphology, robustness and persistence of the surface offered by the bryozoan contrasting with the flexible and ephemeral nature of most algae, often provided with chemical defenses. Bryozoan and even more serpulid epibiont diversity on *M. cereoides* is also higher than those reported for studied species in the Mediterranean and for *Flustra foliacea* from North Europe.

Keywords: epibiosis; biodiversity; serpulids; build-up; fleshy algae; Ionian Sea



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1. Introduction

Several bryozoans have often been considered relevant habitat-formers able to create 3D structures, enhancing habitat structural complexity and promoting biodiversity (e.g., Wood et al., 2012 [1]; Lombardi et al., 2014 [2]; Lombardi et al., 2020 [3]). Studies have especially been devoted to “frame builders”, i.e., species with robust skeletons developing large-sized colonies and able to produce bioconstructions by growing on each other and/or fusing their branches (see [1]; Cocito, 2004 [4] for a review). In the Mediterranean Sea, data mostly refer to *Pentapora fascialis* (Pallas, 1766) and *Schizoporella errata* (Waters, 1878) ([2,4]; Holon & Harmelin, 2013 [5] and references therein). Both species typically develop large colonies of some dm in diameter and height and exceptionally up to 80–100 cm, branched hemispherical or massive with irregular digitations, respectively (Novosel, 2005 [6]; Cocito et al., 2006 [7]; AR personal observations). Colonies often coalesce to form monospecific bioconstructions supporting high biodiversity. *Pentapora fascialis* from 8–22 m depth in the Ligurian Sea, hosted 84 species, including 27 bryozoans and 2 serpulids (Ferdegini & Cocito 1999 [8]). A lower number of epibionts (36 species, including 4 bryozoans and 3 serpulids) has been reported for *S. errata* from 0.3–2 m depth in the same area [8], and even fewer species (28, including 5 bryozoans and 1 serpulid) were observed on colonies

from Minorca examined by Maluquer (1985) [9]. High biodiversity figures have also been reported for other species with erect-rigid skeletons developing cm- to dm-sized colonies, i.e., *Myriapora truncata* (Pallas, 1766), *Smittina cervicornis* (Pallas, 1766) and *Reteporella couchii couchii* (Hincks, 1878), supporting a total of 22, 28 and 37 species, respectively (Cocito, 2009 [10]).

However, less attention has been devoted to non-constructional species, though some of them are known to develop dense assemblages of colonies hosting several epibionts [1]. For instance, this is the case for *Flustra foliacea* (Linnaeus, 1758) from around the British Isles and the North Seas of Europe (e.g., Stebbing, 1971a [11]; Connor et al., 2004 [12]), a poorly calcified species forming large (up to 15 cm high), erect, flexible colonies with irregularly ribbon-like to flabelliform bilaminar fronds. Colonies from 15–20 m off Oxwich Point, South Wales analysed by Stebbing (1971b) [13] supported a total of 42 species, including 1 serpulid and 25 bryozoans. Bitschofsky et al. (2011) [14] reported 42 bryozoan epibionts on this bryozoan after a more extensive study on 51 samples from some North Sea localities, stored in several museums and collected in a wider depth range, in a time span of about 240 years (1776 to 2008).

In the Mediterranean, habitat-forming, non-constructional bryozoans have been unreported so far except for *Cellaria salicornioides*, a species forming extensive carpets on muddy bottoms at ca. 35 m depth in the Adriatic Sea off Rovinj, Croatia, from where McKinney & Jaklin (2000) [15] listed 54 species, including 31 bryozoans and 4 serpulids. No data are so far available for *Margaretta cereoides*. This is a cheilostome species forming erect, articulated bush-like colonies, usually up to 10 (rarely 15) cm high, that attach to the substratum by means of chitinous rootlets. Branches consist of heavily calcified, jointed, slender (10–20 mm long and ca. 1 mm in diameter), straight to gently bending internodes arising laterally from the parental ones singularly or in pairs or triplets. Chitinous rootlets mostly develop in basal internodes to form bundles of anchoring rhizoids and occasionally at different heights, allowing the lateral shoring of the colony. Known from the Mediterranean and the Atlantic, *M. cereoides* is a sciaphilic species thriving in sites with sustained currents in shallow waters (from ca. 5 m down to ca. 50 m depth). In the Mediterranean, it usually occurs in shaded habitats associated with rhizomes of *Posidonia oceanica* (Linnaeus) Delile meadows, at the entrance of submarine caves, on the underlayer of algal and *Cellaria* carpets and the precoralligenous (e.g., Gautier, 1962 [16]; Ferdeghini et al., 2000 [17]; McKinney & Jackin, 2001 [18]; Di Martino & Taylor, 2014 [19]; A.R., personal observations). *Margaretta cereoides* has also been reported as a habitat-forming species developing dense meadows on a rocky plateau at 10 m depth at Lastovo Island, Adriatic Sea [6].

Several colonies of this species were observed associated with coralligenous build-ups offshore of Marzamemi (South of Siracusa, Gulf of Noto, Ionian coast of SE Sicily) during underwater surveys in the frame of the two years long project FISR 04543 “CRESCIBLUREEF”, which aimed at understanding the tempo and mode of the Coralligenous inception and development (see Rosso et al., 2022 [20]). In this area, a Coralligenous habitat was first mapped at the beginning of the 1980s (Di Geronimo in Violanti et al., 1990 [21], figure 3), and discrete build-ups were examined in the last two decades (Di Geronimo et al., 2001 [22]; 2002 [23]; Rosso & Sanfilippo, 2009 [24]). New remote acquisition and Remote Operated Vehicle (ROV) documentation confirmed the occurrence of coralligenous bioconstructions, mostly in the shape of pillars clustered or locally slightly spaced apart, arranged in two main belts approximately between 36 and 100 m in depth, seemingly in relation to the local terraced seascape (Varzi et al., 2023 [25]). Image analysis and computed axial tomography indicated that the internal framework mainly consists of coralline algae and subordinate invertebrates, mostly bryozoans and serpulids producing extensive cavities largely filled with sediment (Bracchi et al., 2022 [26]). As indicated by ROV imaging, the outer surfaces are covered with a dense canopy of soft sciaphilic algae to which subordinate erect bryozoan colonies add at a higher depth. In particular, one of the collected build-ups showed a considerable number of colonies of the bryozoan *M. cereoides* intermingled with the algae of the canopy. The Chlorophyta *Flabellia petiolata* (Turra) Nizzamudin and the Rhodophyta

Osmundaria volubilis (Linnaeus) R.E. Norris and *Peyssonnelia rubra* (Greville) J. Agardh were more abundant and obvious. In order to investigate and assess the habitat-forming role of the bryozoan *M. cereoides*, this paper aims at (1) analysing the epibiont assemblage associated with *M. cereoides* and its diversity; (2) comparing this epibiont assemblage with those found on algae in the same canopy; (3) discussing the possible differences /affinities of these epibiont assemblages in relation to the nature of their basibionts and (4) comparing the epibiont assemblage found on *M. cereoides* with those occurring on other habitat-forming bryozoans.

2. Materials and Methods

The studied build-up originates from a field of discrete columnar coralligenous bioconstructions emerging from a biogenic coarse-grained bottom characterized by abundant living maerl rhodoliths in the middle of a submarine channel (see [25,26]). This field was detected in June 2021 during a preliminary survey investigating the Coralligenous distribution in the area and the underwater characterization of the bioconstructions. The build-up (indicated with the letter E) was collected on the 3rd of August, 2021 during the second field survey of the project CRESCIBLUREEF at 36°43.454' N; 15°09.657' E, 36.7 m depth (Figure 1), with a sea bottom temperature of 18 °C, following examination of the ROV_290621_06 below the local distribution of the *P. oceanica* meadow (Figure 2A).

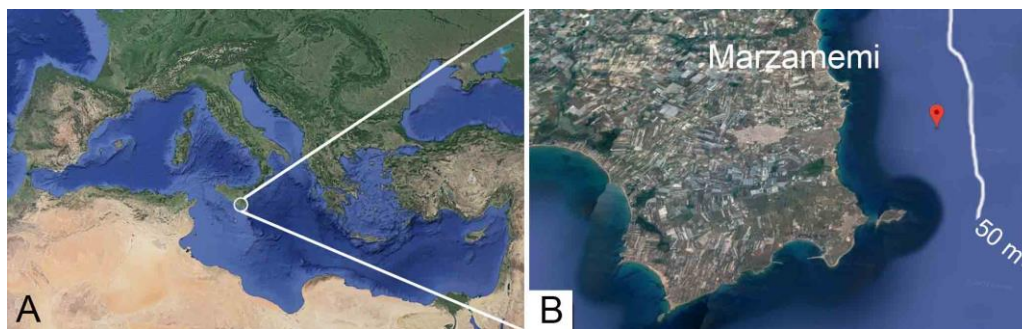


Figure 1. Location of the sampling site in the coralligenous bottoms in the western Ionian Sea: (A) within the Mediterranean Sea, and (B) right ESE of the Marzamemi village.

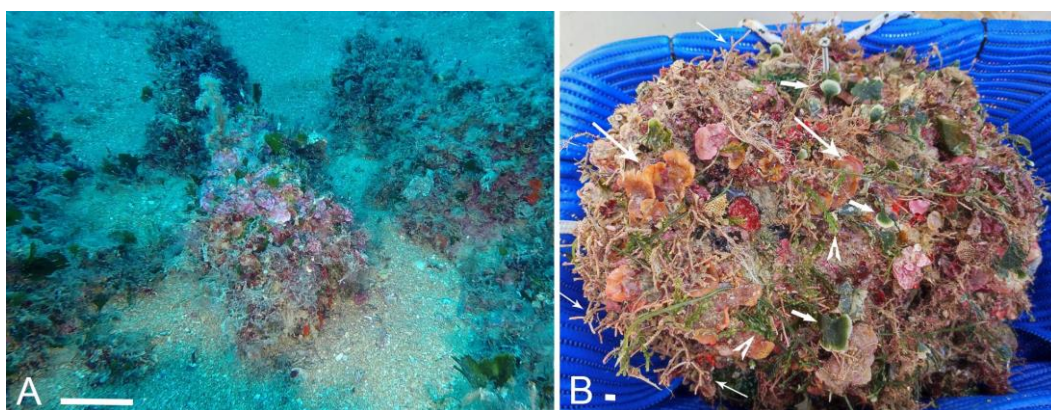


Figure 2. (A) Image from the ROV_290621_06 in a setting similar to that from where the coralligenous build-up was collected. (B) The build-up E soon after recovery, showing the dense canopy of algae and interspersed colonies of the bryozoan *Margaretta cereoides*. Arrow heads: *Caulerpa cylindracea*; Stout arrows: *Flabellia petiolata*; Big slender arrows: *Peyssonnelia rubra*; Small slender arrows: *Margaretta cereoides*. Scale bars = 10 cm.

The build-up consisting of calcareous algae and subordinate encrusting invertebrates (mainly bryozoans, serpulids and sponges) was stout and irregularly fungiform (Figure 2), with a height of 38 cm and a circumference of 52.5 cm at the top, 112 cm at an intermediate height and 71 cm at its base, corresponding approximately to ca. 34, 72 and 50 cm in main cross sections.

The surface was covered with a dense canopy including fleshy algae and colonies of the erect bryozoan *M. cereoides*. These organisms were removed manually after collection and the photogrammetric acquisition of the build-up in its original condition (see [26] for further details).

For the present investigation, the samples CBR2_4_26, CBR2_4_27, CBR2_4_28 and CBR2_4_30 were examined. They consist of the material collected from the build-up surface including soft algae, bryozoans and a mix of non-constructional organisms found on the carbonate bioconstruction (stored as sample CBR2_4_21c and not considered in the present study) but not specimens/colonies found detached from the structure, even if possibly fallen from it at any time during treatment. Materials from all these samples were preserved in alcohol and grouped for the scope of the present investigation. In the Palaeoecology laboratory of the Department of Biological, Geological and Environmental Sciences (DipBioGeo), University of Catania, large-sized elements forming the canopy were separated and examined for their epibionts focusing on skeletonized taxonomic groups. All material was examined and identified under Zeiss Discovery 8 stereomicroscopes with different magnification configurations. Selected specimens were photo-documented using a photo camera and the software imaging program ZEN 3.1 connected to a stereomicroscope. Several bryozoan colonies were analysed untreated and/or cleaned but uncoated under a Tescan Vega 2 LMU, Low Vacuum Scanning Electron Microscope (SEM) at the Microscopical Laboratory of the DipBioGeo. Images were generated using back-scattered electrons. Macroalgae were identified on the basis of diacritical morpho-anatomical characters using the most recent taxonomic literature. Observations were carried out on thalli preserved in an alcohol–seawater solution. For microscopic observations, some specimens were decalcified with 10% HNO₃ and stained with 1% aqueous aniline blue acidified with dilute HCl to highlight pit-connections, or with Lugol solution to highlight plastids under a Zeiss Axioplan (Göttingen, Germany) microscope. Sections were made with a razor blade under a Zeiss stereomicroscope.

Living and dead assemblages were separated for all detected organisms. Bryozoan colonies were considered alive when they included at least some functional zooids. For serpulids, the occurrence of the worm tissues and the operculum inside the tube was checked. Bryozoan colonies were counted as units when they clearly showed the ancestrulae and/or peri-ancestrular areas. The number of targeted algae of the canopy, i.e., *Flabellia petiolata*, *Osmundaria volubilis* and *Peyssonnelia rubra*, was scored soon after detachment counting separately individual blades, either encrusted or not by epibionts. The green alga *F. petiolata* consisted of cylindrical stems of 1–3 cm arising from a stoloniferous base formed by unpigmented, irregularly branched, some centimetres long filaments, each bearing a flabellar to rhomboidal thin and extremely flexible blade, usually about 1–2 cm but up to ca. 4 cm wide in the examined material. *O. volubilis* is a red alga showing erect portions 2–7 cm high in the present samples, consisting of narrow ribbon-like, helicoidally coiled blades fixed to substrate by a discoid base. *P. rubra* is a red alga consisting of groups of roundish blades 1–3 cm in diameter attached to the substrate by pluricellular rhizoids. For *F. petiolata*, individual stems and blades were counted separately because several stems missed their blades. Each individual helicoidal and roughly circular blade was counted for *O. volubilis* and *P. rubra*, respectively. Further algae were not counted because they were decidedly smaller, or they were represented by more fragmented blades/branches. Colonies of *M. cereoides* were accurately detached from the build-up trying to avoid separation of their internodes, and their number was also compared to the clusters of basal rootlets observed still attached on the build-up surface when examined for identification of all live and dead constituent organisms (Donato et al., 2022 [27]). In order to provide an indication of the

colonisable surfaces offered to epibionts by all constituents of the canopy, we estimated their exposed surfaces following the methods reported below. Branches of *M. cereoides* and stems of *F. petiolata* were assimilated to slender cylinders of ca. 1 and 0.5 mm in diameter, respectively, and their length was measured to calculate the outer surface. Blades of *F. petiolata*, *O. volubilis* and *P. rubra* were put on a graph paper, and the covered areas were roughly measured and doubled to consider both sides.

The statistical analysis was performed with Primer 6.1.12 software (Primer-e/Quest Research Limited, Albany, New Zealand) on species (variables) vs. substrates (samples) matrixes. Diversity indexes were calculated with Primer software on the raw number of species per sample.

Material is housed in the Palaeontological Museum of the DipBioGeo, University of Catania (PMC), with bryozoans and serpulids in the CBR Rosso and Sanfilippo collections, respectively. Catalogue numbers are reported for figured species only (see below).

3. Results

The examined build-up was selected because colonies of the bryozoan *Margaretta cereoides* were obvious in the canopy (Figure 2B) among thalli of both partly calcified algae, such as *P. rubra*, and soft-bodied species. These latter were mostly represented by *F. petiolata* and *O. volubilis*, together with *Caulerpa cylindracea* Sonder, and less abundant and/or obvious species, including *Phyllophora crispa* (Hudson) P.S.Dixon, *Rytiphylaea tinctoria* (Clemente) C. Agardh and *Rhodymenia* spp. The surface of the build-up resulted from the superimposition of more or less tightly packed laminae of non-geniculate coralline algae, including *Lithophyllum stictiforme* (Areschoug) Hauck, mineralised Peyssonneliaceans and encrusting sponges [26].

A total of 82 blades of *F. petiolata* and ca. 40 further stems missing the typical enlarged blade were collected offering an estimated surface of ca. 576 cm² (Table 1). *P. rubra* and *O. volubilis* were less abundant, represented by 54 and 20 blade units and accounting for 217 and 161 cm², respectively (Table 1). *Margaretta cereoides* occurred with 87 colonies offering a surface of ca. 440 cm² (Table 1).

Besides the bryozoans and serpulids focused on in this paper, several epibionts occurred in the canopy, including abundant flesh algae and mineralised algal species largely represented by Hydrolithaceae (among which *Hydrolithon* spp.), common foraminifera mostly represented by the slightly attached species *Rosalina bradyi* (Cushman, 1915) and *Lobatula lobatula* (Walker & Jacob, 1798) and the encrusting *Miniacina miniacea* (Pallas, 1766), molluscs (mostly *Gregariella semigranata* (Reeve, 1858)), and a few brachiopod specimens belonging to *Joania cordata* (Risso, 1826) and *Argyrotheca cuneata* (Risso, 1826).

Focusing on bryozoans (Tables 1–3; Supplementary Materials Table S1; Figures 3A,B, 4, 5A–G, 6 and 7A–H,J,K) and serpulids (Tables 1 and 4; Supplementary Materials Table S2; Figures 3C,D, 5A,B,H–M and 7I,K), the total species richness was of 63 and 12 species, respectively. When examining the different substrata separately, *M. cereoides* alone hosted 47 bryozoans and 11 serpulids accounting for ca. 75% and 92% of the total diversity, respectively.

Table 1. Summary of bryozoans and serpulids found as epibionts on the engineer species of the canopy in the examined coralligenous build-up E collected offshore Marzamemi (Ionian Sea). NA: Not applicable.

| Engineer Species of the Canopy | <i>Margaretta cereoides</i> | | <i>Flabellia petiolata</i> | | <i>Peyssonnelia rubra</i> | | <i>Osmundaria volubilis</i> | | Further Fleshy Algae | | Total Canopy | |
|--|-----------------------------|-------|----------------------------|-------|---------------------------|------|-----------------------------|------|----------------------|-------|--------------|-----|
| Colonies/Thalli | 87 | | 82 + 121 Stems | | 54 | | 20 | | Several, Not Counted | | | |
| Approximate Available Surface (cm ²) | 440 | | 576 | | 217 | | 161 | | Not Estimated | | | |
| | L | D | L | D | L | D | L | D | L | D | L | D |
| Bryozoan number of species | 47 | 9 | 37 | 4 | 19 | 2 | 19 | 1 | 41 | 4 | 63 | 14 |
| Bryozoan total number of colonies | 457 | 83 | 324 | 12 | 81 | 2 | 48 | 1 | 220 | 11 | 1132 | 103 |
| Bryozoan colonies/cm ² | 1.02 | 0.18 | 0.56 | 0.02 | 0.37 | 0.01 | 0.30 | 0.01 | NA | NA | NA | NA |
| Bryozoan relative species percentages (%) | 74.60 | 14.29 | 58.73 | 6.35 | 30.16 | 3.17 | 30.16 | 1.59 | 65.08 | 6.35 | 100 | 100 |
| Bryozoan relative colony percentages (%) | 40.37 | 80.58 | 28.62 | 11.65 | 7.16 | 1.94 | 4.24 | 0.97 | 19.43 | 10.68 | 100 | 100 |
| Serpulid number of species | 11 | 9 | 8 | 3 | 3 | | 3 | | 5 | 4 | 12 | 9 |
| Serpulid total number of specimens | 158 | 161 | 139 | 3 | 19 | | 4 | | 58 | 7 | 378 | 169 |
| Serpulid specimens/cm ² | 0.36 | 0.37 | 0.24 | 0.01 | 0.09 | | 0.02 | | NA | NA | NA | NA |
| Serpulid relative species percentages (%) | 91.67 | 100 | 66.67 | 33.33 | 25.00 | | 25.00 | | 41.67 | 44.44 | 100 | 100 |
| Serpulid relative specimen percentages (%) | 41.80 | 100 | 36.77 | 1.78 | 5.03 | | 1.06 | | 15.34 | 4.14 | 100 | 100 |

Values were also elevated but lower for *F. petiolata* (59% and 67% for bryozoans and serpulids, respectively) and all soft algae considered together (65% and 42%), but decidedly lower for both *P. rubra* and *O. volubilis* (both accounting for the 30% and 25%, respectively). Figures for dead assemblages were lower but with roughly similar trends. The highest values were found for bryozoans and serpulids on *M. cereoides*, with 9 species each accounting for the 64% and 100% of the dead bryozoan and serpulid assemblages, respectively. Intermediate values were observed for *F. petiolata* (29% and 33%) and all algae together (29% and 44%), and the lowest values for *P. rubra* and *O. volubilis*, with bryozoans represented by only 2 (14%) and 1 (7%) species, respectively, whereas serpulids were missing.

A total of 1132 living and 103 dead bryozoan colonies were found (Tables 1–3 and S1). Most colonies (457 living + 83 dead, corresponding to 40.4% and 80.6% of all colonies found on the canopy of the E build-up) encrusted *M. cereoides*. Further 324 living and 12 dead colonies (corresponding to 28.6% and 11.6%, respectively) occurred on *F. petiolata*, and 220 living and 11 dead colonies (19.4% and 10.7%, respectively) on further fleshy algae grouped together. Figures were lower on both *P. rubra* and *O. volubilis*, showing 81 and 48 living colonies and related relative percentages of 7.2% and 4.2%, respectively. Only 2 and 1 dead colonies occurred on *P. rubra* (1.9%) and on *O. volubilis* (1%). *Margaretta cereoides* also showed the highest colonization values per surface unit (slightly more than 1 live colony/cm² and 0.2 dead colonies/cm²) in comparison with *F. petiolata*, *P. rubra* and *O. volubilis*, which showed colonization values of 0.56, 0.37 and 0.30 live colonies/cm² but negligible values for dead colonies.

Table 2. Relevance (numbers and relative percentages) of the different bryozoan orders (cyclostomes, ctenostomes and cheilostomes) in the epibiont assemblages found on the bryozoan *Margaretta cereoides* and main algae of the canopy of the build-up E collected offshore Marzamemi (Ionian Sea). L: living and D: dead assemblages.

| Engineer Species of the Canopy | <i>Margaretta cereoides</i> | | <i>Flabellia petiolata</i> | | <i>Peyssonnelia rubra</i> | | <i>Osmundaria volubilis</i> | | Further Fleshy Algae | | Total Canopy | |
|--------------------------------------|-----------------------------|------|----------------------------|------|---------------------------|-----|-----------------------------|-----|----------------------|-----|--------------|------|
| | L | D | L | D | L | D | L | D | L | D | L | D |
| Epibiont Bryozoan Species | | | | | | | | | | | | |
| Total number of cyclostome species | 10 | 2 | 8 | 2 | 3 | | 6 | | 9 | | 11 | 4 |
| Cyclostome species % | 21.3 | 22.2 | 21.6 | 50 | 15.8 | | 31.6 | | 22 | | 17.5 | 30.8 |
| Total number of cyclostome colonies | 97 | 4 | 80 | 4 | 10 | | 9 | | 56 | | 251 | 7 |
| Cyclostome colonies % | 21.2 | 4.82 | 24.7 | 33.3 | 12.3 | | 18.8 | | 25.5 | | 22.2 | 6.8 |
| Total number of ctenostome species | 5 | | 2 | | 2 | | 1 | | 3 | | 5 | |
| Ctenostome species % | 10.6 | | 5.41 | | 10.5 | | 5.26 | | 7.32 | | 7.94 | |
| Total number of ctenostome colonies | 38 | | 18 | | 5 | | 1 | | 5 | | 66 | |
| Ctenostome colonies % | 8.3 | | 5.6 | | 6.2 | | 2.1 | | 2.3 | | 5.8 | |
| Total number of cheilostome species | 32 | 7 | 26 | 2 | 14 | 2 | 12 | 1 | 29 | 4 | 47 | 9 |
| Cheilostome species % | 68.1 | 77.8 | 70.3 | 50 | 73.7 | 100 | 63.2 | 100 | 70.7 | 100 | 74.6 | 69.2 |
| Total number of cheilostome colonies | 322 | 79 | 226 | 8 | 66 | 2 | 38 | 1 | 159 | 11 | 815 | 96 |
| Cheilostome colonies % | 70.5 | 95.2 | 69.8 | 66.7 | 81.5 | 100 | 79.2 | 100 | 72.3 | 100 | 72.0 | 93.2 |
| Total number of bryozoan species | 47 | 9 | 37 | 4 | 19 | 2 | 19 | 1 | 41 | 4 | 63 | 13 |
| Total number of bryozoan colonies | 457 | 83 | 324 | 12 | 81 | 2 | 48 | 1 | 220 | 11 | 1132 | 103 |

Living colonies belonged to 63 species including 11 cyclostomes, 5 ctenostomes and 47 cheilostomes, accounting for 17.5, 7.9 and 75.0%, respectively (Table 2). Relationships between these taxonomic groups remained very similar when the number of colonies was considered, with cheilostomes still accounting for 72% but with a slight decrease of ctenostomes (5.8%) counterbalanced by an increase of cyclostomes (22.2%). However, both species richness and colony abundance varied if the epibionts associations found on *M. cereoides* and the different algae were considered separately. The total number of living species ranged from 19 (on both *P. rubra* and *O. volubilis*) to 47 (on the bryozoan), with an intermediate species richness found on *F. petiolata* (37 species) and further fleshy algal species considered together (41 species).

Analogously, the total number of colonies varied strongly. *Margaretta cereoides* showed the highest values with 457 colonies accounting for 40.4% of the total association, followed by *F. petiolata* (324 colonies = 28.6%) and all other algae (220 colonies = 19.4%), whereas *P. rubra* and *O. volubilis* hosted only 81 and 48 colonies, representing 7.2% and 4.2%, respectively. Some variability was also observed between the three orders (cyclostomes, ctenostomes and cheilostomes) on the different types of substrata of the canopy, with ranges of ca. 15–31%, 5–10% and 63–74% at species and of ca. 12–25%, 2–8% and 69–81% at colony level, respectively. These figures indicate comparable dominances of cheilostomes

at both species and colony level in assemblages on individual substrata and lower relative percentages (but wider variabilities) for ctenostomes (and especially for cyclostomes) as regards colony abundance relative to species richness (Figure 4).

Encrusters dominated with 41 species and 752 colonies (Table 3), invariably representing about 65% of the total assemblage, followed by erect flexible species (17 species and 289 colonies = ca. 27%), whereas erect rigid morphotypes were decidedly subordinate (5 species and 91 colonies representing 7.9% and 8.1%, respectively). Leaving out the epibiosis found on soft-bodied algae considered together, encrusting species were dominant on both *M. cereoides* and *F. petiolata* (27 and 26 species, respectively), developing 285 colonies (62% of the assemblage) on *M. cereoides* and 244 colonies (75% of the assemblage) on *F. petiolata*. In contrast, both *P. rubra* and *O. volubilis* hosted 12 species (63%), represented by 56 (69%) and 33 (69%) colonies, respectively.

Table 3. Relevance (numbers and relative percentages) of the different growth morphologies developed by epibiont bryozoans found on the bryozoan *Margaretta cereoides* and main algae of the canopy of the build-up E collected offshore of Marzamemi (Ionian Sea). Note that morphotypes have been grouped in only three main types for the sake of simplicity.

| Engineer Species of the Canopy | <i>Margaretta cereoides</i> | | <i>Flabellia petiolata</i> | | <i>Peyssonnelia rubra</i> | | <i>Osmundaria volubilis</i> | | Further Fleshy Algae | | Total Canopy | |
|--|-----------------------------|-----|----------------------------|------|---------------------------|-----|-----------------------------|-----|----------------------|-----|--------------|------|
| | L | D | L | D | L | D | L | D | L | D | L | D |
| Epibiont Bryozoan Species | | | | | | | | | | | | |
| Total number of erect flexible species | 16 | | 10 | 1 | 6 | | 4 | | 11 | | 17 | 1 |
| Erect flexible species % | 34 | | 27 | 25 | 31.6 | | 21.1 | | 26.8 | | 27 | 7.7 |
| Total number of erect flexible colonies | 133 | | 72 | 2 | 21 | | 10 | | 53 | | 289 | 2 |
| Erect flexible colonies % | 29.1 | | 22.2 | 16.7 | 25.9 | | 20.8 | | 24.1 | | 25.5 | 1.94 |
| Total number of encrusting species | 27 | 9 | 26 | 3 | 12 | 2 | 12 | 1 | 25 | 4 | 41 | 12 |
| Encrusting species % | 57.4 | 100 | 70.3 | 75 | 63.2 | 100 | 63.2 | 100 | 61 | 100 | 65.1 | 92.3 |
| Total number of encrusting colonies | 285 | 83 | 244 | 10 | 56 | 2 | 33 | 1 | 132 | 11 | 752 | 101 |
| Encrusting colonies % | 62.4 | 100 | 75.3 | 83.3 | 69.1 | 100 | 68.8 | 100 | 60 | 100 | 64.4 | 98.1 |
| Total number of erect rigid species | 4 | | 1 | | 1 | | 3 | | 5 | | 5 | |
| Erect rigid species % | 8.51 | | 2.7 | | 5.26 | | 15.8 | | 12.2 | | 7.94 | |
| Total number of erect rigid colonies | 39 | | 8 | | 4 | | 5 | | 35 | | 91 | |
| Erect rigid colonies % | 8.53 | | 2.47 | | 4.94 | | 10.4 | | 15.9 | | 8.1 | |
| Diversity (number of species) | 47 | 9 | 37 | 4 | 19 | 2 | 19 | 1 | 41 | 4 | 63 | 13 |
| Total abundance (number of colonies including undetermined ones) | 457 | 83 | 324 | 12 | 81 | 2 | 48 | 1 | 220 | 11 | 1132 | 103 |

Ranges of variability were slightly lower for rigid erect morphotypes when species were considered (3–15%), but wider for erect flexible and encrusting species that showed variations of 13% at species level and of 16–18% at colony level. The highest relative percentages of encrusters occurred on *F. petiolata* (see above), whereas erect flexible species were more diversified and abundant (16 species = 34% and 133 colonies = ca. 29%) on *M. cereoides*.

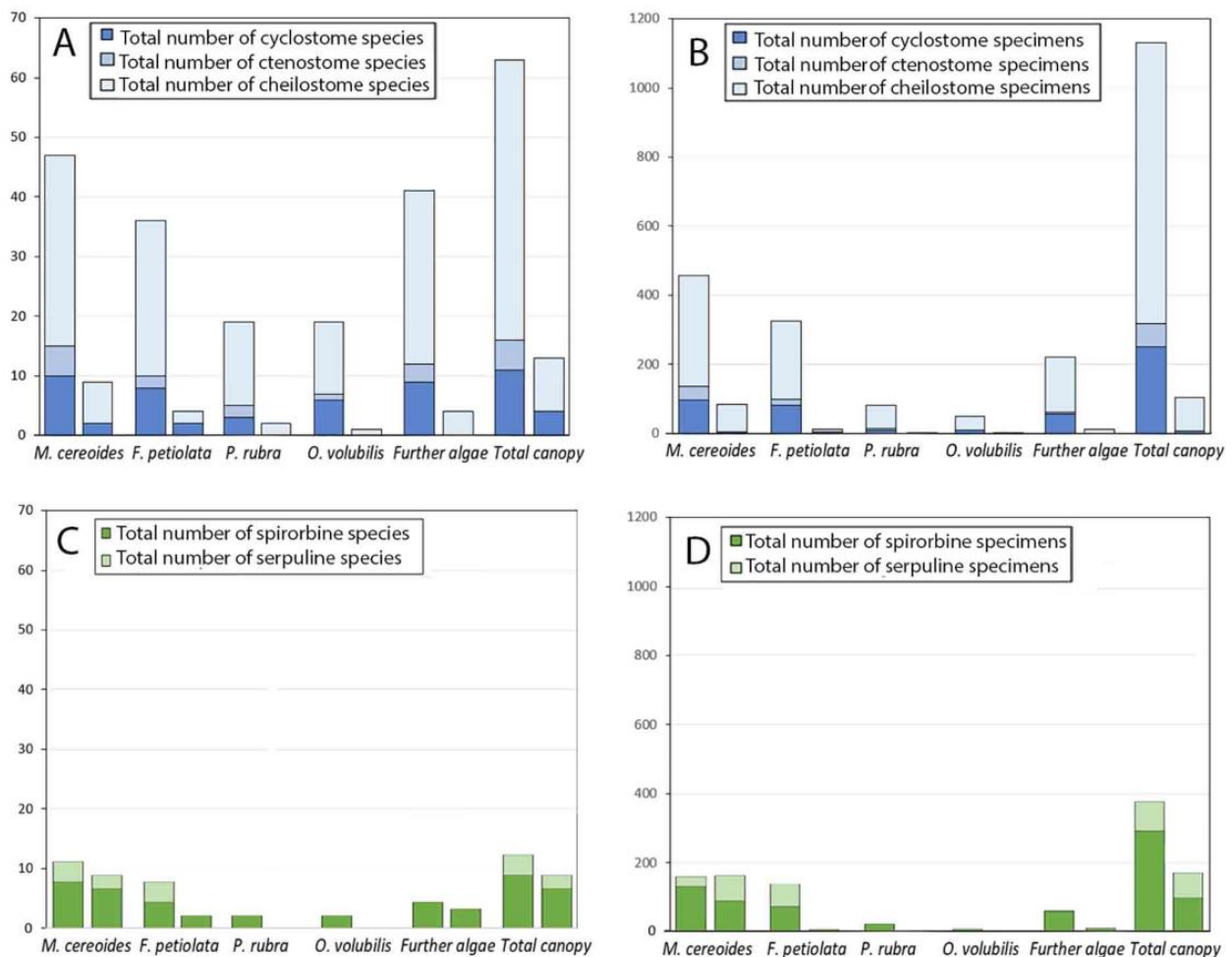


Figure 3. Relevance of taxonomic groups within bryozoan and serpulid epibiont assemblages found on the bryozoan *Margaretta cereoides* and the main algae of the canopy on the build-up E collected offshore Marzamemi (Ionian Sea). For each substrate the left column refers to living and the right one to dead assemblages. (A,B) Relevance of cyclostome, ctenostome and cheilostome bryozoans at species (A) and colony (B) level. (C,D) Relevance of serpulid and spirorbine serpulids at species (C) and specimen (D) level.

Only ca. 1/3 of the species were represented by more than 10 colonies, with only 9 species ranging from 24 to 48 colonies and 4 species exceeding 50 colonies, whereas 18 species occasionally occurred with only 1–2 colonies (Supplementary Materials Table S2). With 228 colonies, the encrusting (celleporiniform) *Celleporina caminata* (Figures 5A,C and 7J,K) dominated (mostly on *M. cereoides* and subordinately on the stems of *F. petiolata*), usually developing small (1–2 mm) pisiform colonies. The erect flexible species *Scrupocellaria delilii* (72 colonies) (Figure 7C) was also abundant on *M. cereoides* (38 colonies) and subordinately on *F. petiolata* (10 colonies) and further soft-bodied algae (16 colonies). The third most abundant species was *Mecynoezia delicatula* (64 colonies) developing small erect rigid colonies usually consisting of an extremely reduced encrusting part, often divided in 2–3 (rarely 4) branches, each giving rise to short (less than 1 cm long), erect, often fertile portions (Figures 5B and 6A). This species was common (34 colonies) on *M. cereoides* but subordinate on *F. petiolata* (8 colonies) and on other soft-bodied algae (16 colonies), *P. rubra* (4 colonies) and *O. volubilis* (2 colonies). *Aetea* cf. *truncata* developed relatively common extensive networks on almost all elements of the canopy (but subordinately on *P. rubra* and *O. volubilis*), from where some short branches sporadically developed. Further relatively abundant species were the encrusters *Copidozoum planum* (48 colonies largely on *F. petiolata* and further soft-bodied algae), usually forming small sized colonies, *Annectocyma major*

(42 colonies) and *Beania mediterranea* (40 colonies, mostly on *M. cereoides*), as well as the erect flexible *Beania cylindrica* (Figures 5G and 6F) (42 colonies, especially on *M. cereoides* and *P. rubra*). Both *Beania* species were relatively larger, with *B. cylindrica* developing erect branches up to 2 cm long. Further common species were the encrusters *Chorizopora brongnartii* (Figures 5D and 7G) (29 colonies, usually extremely small-sized, especially found on the upward facing surface of *P. rubra*) and *Turbicellepora coronopus* (26 colonies, especially on *M. cereoides*) and the erect flexible species *Crisia ramosa* (35 colonies), *Amathia delicatula* (34 colonies, especially on *M. cereoides*) and *Cabera boryi* (24 colonies, especially on *F. petiolata*).

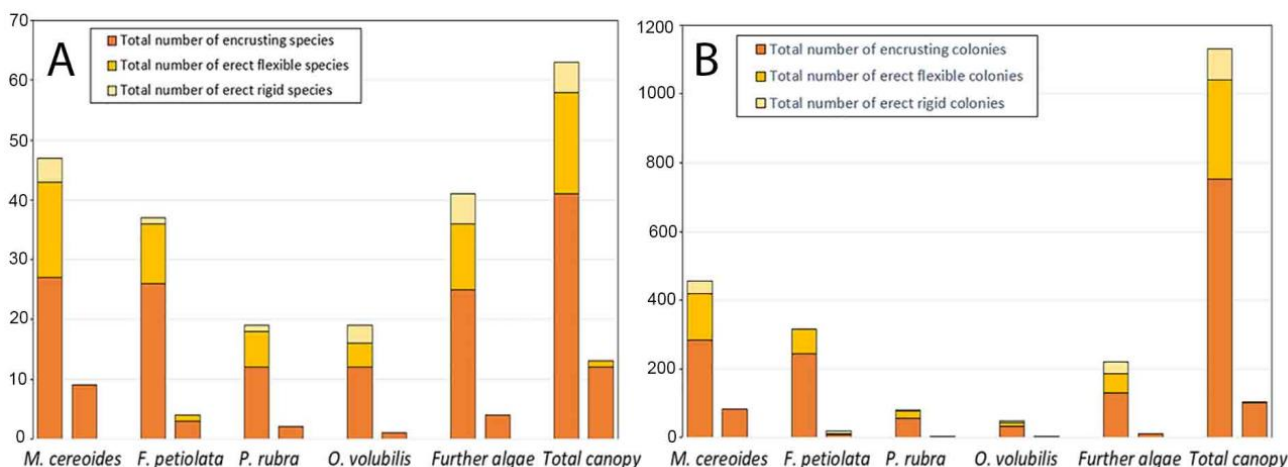


Figure 4. Species richness (A) and colony abundance (B) of encrusting, erect flexible and erect rigid morphotypes in the bryozoan epibiont living (left column) and dead (right column) assemblages found on the bryozoan *Margaretta cereoides* and the main algae of the canopy on the build-up E collected offshore Marzamemi (Ionian Sea).

The highest number of species with living colonies (48) occurred on *M. cereoides*, and most of them (29) were shared with *F. petiolata* and other constituents of the canopy. Further 7 species were shared with other algae, and 11 were only found on *M. cereoides*. Among them *Bugulina cf. fulva* (Figure 6C), with 6 colonies, was the most abundant. In contrast, out of the 18 species never found on *M. cereoides*, 4 occurred only on *F. petiolata*, each with 1 to 4 colonies.

When looking at dead bryozoans still attached on their substrata, the total number of species (14) and colonies (103) was remarkably low, but two species (*Schizobrachiella sanguinea* and *Plesiocleidochasma mediterraneum*) were added that were not present in the living population. A single species (*C. caminata*) with 72 colonies accounts for more than 70% of the dead assemblage, whereas all other species were present with 1–3 colonies, except for *Turbicellepora coronopus* with 5 colonies. Most species and colonies were found on *M. cereoides* (78% and 76% of the dead assemblage, respectively) and subordinately on the stems of *F. petiolata* or on the thalli of the relatively robust *Phyllophora crispa*. In all instances, however, the number of colonies per cm² was almost negligible.



Figure 5. Microscope images of bryozoan and serpulid epibionts on the canopy of the E Build-up collected offshore Marzamemi (Ionian Sea). (A): *Celleporina caminata* and *Miniacina miniacea* on a *Flabellia petiolata* stem. PMC. Rosso Collection I. H. B. 98a1. (Scale bar: 2 mm). (B) Bryozoans and serpulids clustered on a soft algae PMC Rosso Collection I. H. B. 59b. (Scale bar: 5 mm mm). (C) Young *Celleporina caminata* on *Margaretta cereoides*, PMC. Rosso Collection I. H. B. 98a2. (Scale bar: 2 mm). (D) *Chorizopora brongniartii* on a fleshy algae. PMC. Rosso Collection I. H. B. 99a1. (Scale bar: 500 μ m). (E) *Microporella bicollaris* on a fleshy algae. PMC. Rosso Collection I.H.B. 96a. (Scale bar: 2 mm). (F) *Arthropoma ceciliae* on *M. cereoides*. PMC. Rosso Collection I. H. B. 100a. (Scale bar: 2 mm). (G) *Beania cylindrica* on *M. cereoides*. PMC. Rosso Collection I. H. B.101a. (Scale bar: 2 mm). (H) *Serpula vermicularis* on *M. cereoides*. PMC. Sanfilippo Collection I. H. Pol.-2a. (Scale bar: 2 mm). (I) *Josephella marezellieri* on *Caulerpa cylindracea*. PMC. Sanfilippo Collection I. H. Pol-3a. (Scale bar: 2 mm). (J) *Filograna* sp. on *Flabellia petiolata*. PMC. Sanfilippo Collection I. H. Pol-4a. (Scale bar: 5 mm). (K) *Neodexiospira pseudocorrugata* on *F. petiolata*. PMC. Sanfilippo Collection I. H. Pol-5a1. (Scale bar: 1 mm). (L) *Spirobranchus triqueter* and several *Simplaria pseudomilitaris* on *M. cereoides*. PMC. Sanfilippo Collection I. H. Pol-6a. (Scale bar: 5 mm). (M) *S. pseudomilitaris* on *M. cereoides*. PMC. Sanfilippo Collection I. H. Pol-7a. (Scale bar: 1 mm).

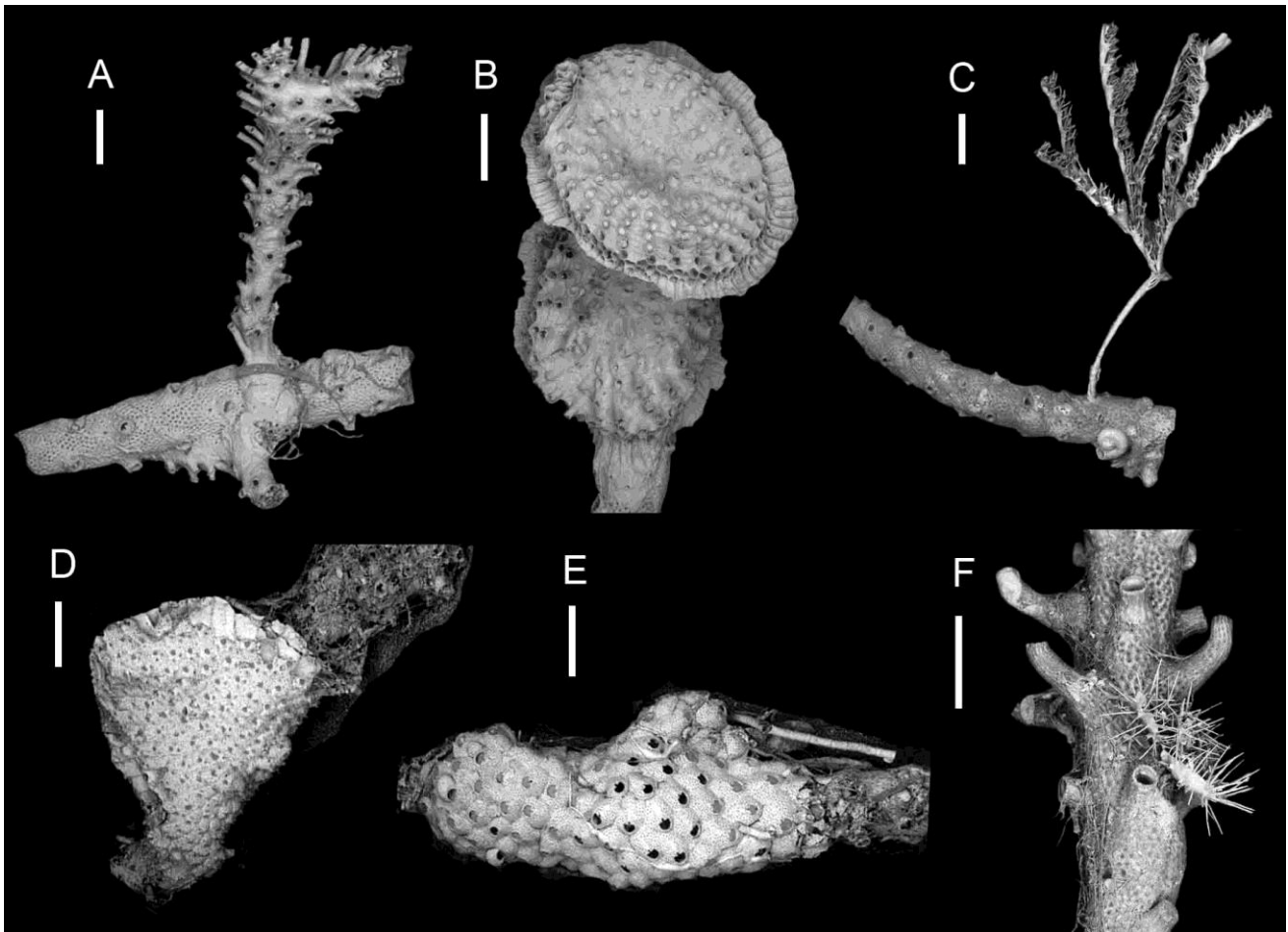


Figure 6. SEM images of bryozoans epibiont on *Margareta cereoides* found in the studied E Build-up collected offshore Marzamemi (Ionian Sea). **(A)**: *Mecynoecia delicatula* fertile colony. PMC. Rosso Collection I. H. B-59b. (Scale bar: 1 mm). **(B)** *Plagioecia patina*. The upper colony is peripherally budded from the lower one. PMC. Rosso Collection I. H. B-102a. (Scale bar: 1 mm). **(C)** *Bugulina* cf. *fulva*. PMC. Rosso Collection I.H. B-103a. (Scale bar: 1 mm). **(D)** Large colony of *Schizomavella* (*Schizomavella*) *linearis*. PMC. Rosso Collection I. H. B-104a. (Scale bar: 1 mm). **(E)** *Arthropoma ceciliae*. PMC. Rosso Collection I. H. B-100a. (Scale bar: 1 mm). **(F)** *Beania cylindrica*. PMC. Rosso Collection I. H. B-101a. (Scale bar: 1 mm).

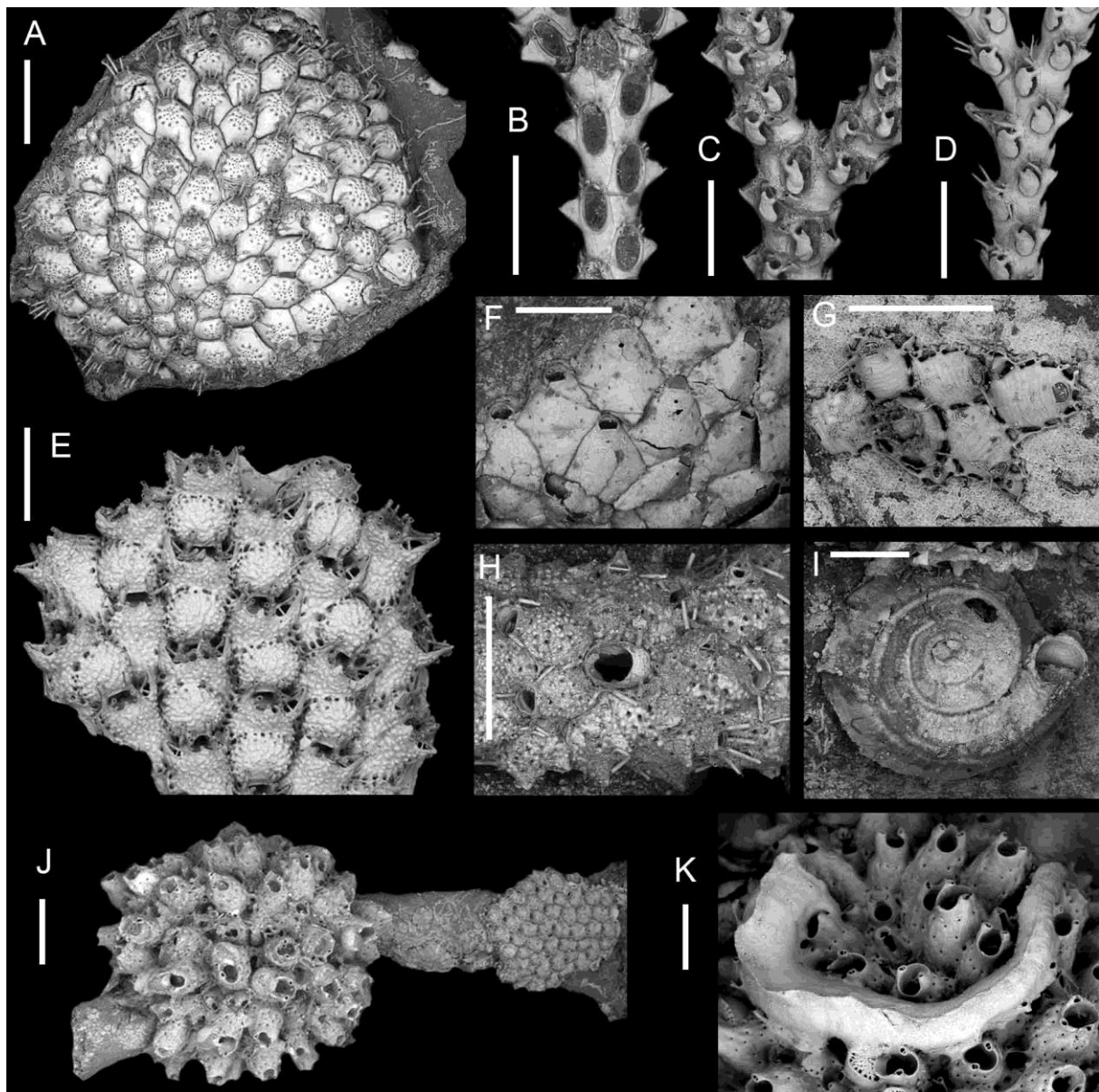


Figure 7. SEM images of bryozoans and a serpulids epibiont on the canopy of the E Build-up collected offshore of Marzamemi (Ionian Sea). (A): *Puellina gattyae* on a fleshy alga. PMC. Rosso Collection I. H. B-105a. (Scale bar: 500 μm). (B) *Scrupocellaria scruposa* PMC. Rosso Collection I. H. B-106a. (Scale bar: 500 μm). (C) *Scrupocellaria delilii*, PMC. Rosso Collection I. H. B-107a. (Scale bar: 500 μm). (D) *Scrupocellaria* cf. *incurvata*. PMC. Rosso Collection I. H. B-108a. (Scale bar: 500 μm). (E) *Escharoides mamillata* detached from *Flabellia petiolata*. PMC. Rosso Collection 109a. (Scale bar: 500 μm). (F) *Haplopoma* cf. *impressum* on *F. petiolata*. PMC. Rosso Collection I. H. B-110a. (Scale bar: 500 μm). (G) *Chorizopora brongniartii* on *Peyssonnelia rubra*. PMC. Rosso Collection I. H. B-99a2. (Scale bar: 500 μm). (H) *Microporella modesta* on *M. cereoides*. PMC. Rosso Collection I. H. B-86f. (Scale bar: 500 μm). (I) *Neodexiospira pseudocorrugata* on *F. petiolata*. PMC. Sanfilippo Collection I. H. Pol. 5a2. (Scale bar: 500 μm). (J) *Celleporina caminata* and *Cribrilaria hincksi* on a *F. petiolata* stem. PMC. Rosso Collection I. H. B-70b. (Scale bar: 500 μm). (K) Small specimen of *Spirobranchus triqueter* on *Celleporina caminata*. PMC. Rosso Collection I. H. B-98a3. (Scale bar: 500 μm).

Table 4. Relevance (numbers and relative percentages) of the two serpulid subfamilies in the epibiont assemblages found on the bryozoan *Margaretta cereoides* and main algae of the canopy of the build-up E collected offshore of Marzamemi (Ionian Sea). L: living and D: dead assemblages.

| Engineer Species of the Canopy | <i>Margaretta cereoides</i> | | <i>Flabellia petiolata</i> | | <i>Peyssonnelia rubra</i> | | <i>Osmundaria volubilis</i> | | Further Fleshy Algae | | Total Canopy | |
|--------------------------------------|-----------------------------|------|----------------------------|-----|---------------------------|---|-----------------------------|---|----------------------|-----|--------------|------|
| | L | D | L | D | L | D | L | D | L | D | L | D |
| Epibiont Serpulids | | | | | | | | | | | | |
| Total number of serpuline species | 8 | 7 | 5 | 3 | 3 | | 3 | | 5 | 4 | 9 | 7 |
| Serpuline species % | 72.7 | 77.8 | 62.5 | 100 | 100 | | 100 | | 100 | 100 | 75 | 77.8 |
| Total number of spirorbine species | 3 | 2 | 3 | | | | | | | | 3 | 2 |
| Spirorbid species % | 27.3 | 22.2 | 37.5 | | | | | | | | 25 | 22.2 |
| Total number of species | 11 | 9 | 8 | 3 | 3 | | 3 | | 5 | 4 | 12 | 9 |
| Total number of serpuline specimens | 129 | 87 | 71 | 3 | 19 | | 4 | | 57 | 7 | 292 | 95 |
| Serpuline specimens % | 81.6 | 54.0 | 51.1 | 100 | 100 | | 100 | | 98.3 | 100 | 77.2 | 56.2 |
| Total number of spirorbine specimens | 29 | 74 | 68 | | | | | | 1 | | 86 | 74 |
| Spirorbine specimens % | 18.4 | 46.0 | 48.9 | | | | | | 1.72 | | 22.8 | 43.8 |
| Total number of specimens | 158 | 161 | 139 | 3 | 19 | | 4 | | 58 | 7 | 378 | 169 |

Serpulids occurred with 378 living specimens and 169 empty tubes (Tables 1 and 4; Supplementary Materials Table S2). Like for bryozoans, the highest number of specimens (158 living and 161 dead) occurred on *M. cereoides*, accounting for 41.8% and 95.3% of the living and dead assemblages, respectively. Further 139 living and 3 dead specimens (36.8% and 1.8%, respectively) encrusted *F. petiolata* and 58 living and 7 dead specimens (15.3% and 4.1%, respectively) were found on other fleshy algae considered together. Only few living specimens (but no dead ones) occurred on *P. rubra* and *O. volubilis*, accounting for 5% and 1.1% of the observed assemblage, respectively.

Serpulids were absent on several *M. cereoides* colonies and algal thalli, and the number of specimens per cm² reached 0.36 on *M. cereoides* but lowered remarkably to 0.24 on *F. petiolata*. Figures were quite negligible on *P. rubra* (0.09) and *O. volubilis* (0.02). Serpulines decidedly prevailed at both species (73%) and specimen (82%) level with values ranging from 63 to 100% at species level and from 51 to 98% at specimen level. Serpulines also strongly prevailed on each considered constituent of the canopy, except on blades of *F. petiolata*, where spirorbines reached 68 specimens, accounting for 49% of the whole population.

The most abundant species was the serpuline *Josephella marenzelleri* (Figure 5I), which occurred with 144 specimens, representing ca. 38% of the assemblage as a whole and 37% on *M. cereoides* (59 specimens) (Supplementary Materials Table S2). Specimens of this species possessing a characteristic minute flexible tube were usually clustered. In contrast, specimens of *Spirobranchus triqueter* (Figures 5L and 7K), a serpuline species having large sized heavily mineralised tubes, were often found coiled around the internodes of *M. cereoides* and the stems of *F. petiolata*. This species occurred with 72 specimens in the whole assemblage (19%), 50 of which were on *M. cereoides* (32%). The third most abundant species (50 specimens) was the spirorbine *Janua heterostropha*, representing only 13% of the whole assemblage, but more than 35% on *F. petiolata*, on which blades this minute spirorbine was particularly abundant, sometimes with clustered juvenile specimens.

Analogously, tubes of *Filograna* sp. (Figure 5J) were mostly found on *F. petiolata*, though dead specimens were also abundant on *M. cereoides*. A further spirorbine, *Simplaria pseudomilitaris* (Figure 5L,M), occurred with 20 specimens (5%), mostly on *M. cereoides* (16 = 10%). Among further species only the spirorbine *Neodexiospira pseudocorrugata* (Figures 5K and 7I) and the serpuline *Serpula vermicularis* (Figure 5H) were relatively abundant, with a total of 16 and 10 specimens, respectively, accounting for 4% and less than 3%. Like the congener, *N. pseudocorrugata* was especially found (15 specimens) on blades of *F. petiolata*, where it accounted for ca. 11%.

Among the 12 living species, all but one occurred on *M. cereoides* and 8 on *F. petiolata*, whereas only 3 species were found on both *P. rubra* and *O. volubilis*.

Dead serpulid assemblage was relatively scant with 9 species and 169 specimens, almost all (158) found on the colonies of *M. cereoides*. Few dead specimens only sporadically occurred on *F. petiolata* and other fleshy algae, such as *Phyllophora crispa* and *Rhodymenia* sp. All species except *Filogranula calyculata* (only represented by one dead specimen) also occurred in the living assemblages, though sometimes on different elements of the canopy (see *Filograna* sp.). The most represented species was *S. pseudomilitaris* (42% of the serpulid dead assemblage), followed by *S. triqueter* and *Filograna* sp. (20% and 17%), whereas *J. marenzelleri* was subordinate (slightly more than 10%) and all other species rare.

4. Discussion

4.1. Diversity

Almost all bryozoan and serpulid species reported on *M. cereoides* are typical inhabitants of shelf habitats in the Mediterranean, including some newly described species, such as *Microporella modesta* (Di Martino et al., 2020) (Figure 7H) and *M. bicollaris* (Di Martino & Rosso, 2021) (Figure 5E), except for *Protula* sp., whose taxonomic status needs some investigation. Furthermore, specimens of *Serpula vermicularis* show a peculiar ornamentation consisting of spines on the central keel, making them similar to those already found in submarine caves from the eastern Mediterranean and identified as *S. vermicularis* forma *echinata* (Sanfilippo et al., 2017a [28]). This finding confirms the occurrence of a morphologically distinguishable population of *S. vermicularis*, whose distribution and taxonomic status deserve further investigation.

Unlike algae occurring with at least two non-indigenous species (*C. cylindracea* and *C. taxifolia* v. *distichophylla*), both bryozoans and serpulids are only represented by species considered native to the basin. Both bryozoans and serpulids occurring on *M. cereoides* represent a relevant part of the total number of species so far known from the Mediterranean for these two taxonomic groups. Bryozoans on the examined *M. cereoides* colonies and the whole build-up represented 8.5% and more than 11%, respectively, of the 556 bryozoan species reported by Rosso and Di Martino (2016) [29]. Analogously, serpulids accounted for the 16% and more than 17% of the 69 species obtained summing up those reported by Castelli et al. (2008) [30] for the western basin and by Ben-Eliahu and Fiege (1996) [31] and Çinar et al. (2006, 2021) [32,33] for the eastern Mediterranean.

Bryozoans found on *M. cereoides* also account for the 21.9% of the total diversity so far known for the coralligenous habitat (219 species reported in [29]), a figure relatively close to the 28.8% accounted to by the whole assemblage of the canopy in the examined build-up. Serpulids are usually merged within polychaetes in literature and summaries are not available for them. However, the 11 species found only on *M. cereoides* outnumber the 6 and 10 species reported by Casellato and Stefanon (2008) [34] and by Laubier (1966) [35] for the Adriatic Sea and the Marseille area, respectively, and parallel the 11 species reported from 90-100 m deep coralligenous assemblages in the Gulf of Noto by [24].

The Margalef index ($d = 10.4$) also indicates a high diversification for bryozoan and serpulid living assemblages (Table 5). Figures are also elevated for *M. cereoides* and *F. petiolata* considered separately (8.9 and 7.2, respectively) and for further algae considered together (8.5), but lower at 5.4 and 4.6 for *O. volubilis* and *P. rubra*, respectively, although still indicating a good species richness.

The high values of both J' (ranging from 0.7 to 0.9) and H' (ranging from 2.6 to 3.3) indexes indicate a relatively equilibrated distribution of epibionts on available substrata.

Table 5. Margalef (d), Pielou (J') and Shannon (H') indexes for bryozoan and serpulid living assemblages found on the bryozoan *Margaretta cereoides* and on algae of the canopy of the build-up E collected offshore Marzamemi (Ionian Sea).

| | <i>M. cereoides</i> | <i>F. petiolata</i> | <i>P. rubra</i> | <i>O. volubilis</i> | Further Algae | All Canopy |
|------|---------------------|---------------------|-----------------|---------------------|---------------|-------------|
| d | 8.979201569 | 7.234201966 | 4.633102932 | 5.424673103 | 8.568186705 | 10.39512588 |
| J' | 0.727544638 | 0.844863311 | 0.869820647 | 0.942942333 | 0.828398275 | 0.771925758 |
| H' | 2.990844237 | 3.216109475 | 2.688652546 | 2.914674783 | 3.223977221 | 3.363055763 |

4.2. Habitat-Forming Role of *M. cereoides* and Algae in the Canopy of the Studied Coralligenous Build-Up

Data reported above clearly points to the relevance of *M. cereoides* as a substratum, at least for bryozoans and serpulids. This relevance is also supported by the high figures in diversity (species richness), total number of colonies/specimens hosted and number of colonies/specimens per cm² observed on *M. cereoides* in comparison with the algal constituents found in the canopy developed on the E build-up collected off Marzamemi in the Ionian Sea.

Comparisons of the epibiosis developed on algal and animal substrata, especially bryozoans, are missing in the literature. However, in an investigation aimed to highlight variation in species richness of epifaunal bryozoan assemblages and their composition in relation with different algal functional groups and related structural complexity on an array of filamentous to large laminar (Laminariales including *Macrocystis*) algae of SW Atlantic, Liuzzi and Lopez Gappa (2010) [36] found no significant differences except between filamentous and foliose algae. Analogously, Hayward (1980) [37] found that besides a small number of primary epibiont species, i.e., species directly depending on the host algal substratum as a resource and hence establishing species-specific and even obligate associations with their hosts, other epiphytes (which he indicated as “secondary epiphytes”) simply are opportunistic eurytopic species settling on any kind of available algal substrate. Hayward [37], however, suggested that epibionts settle on particular plant species in relation to particular physical factors, including the size of the colonisable surface and its texture and rigidity. Differences in the colonization pattern between laminar corallinales and fleshy algae has also been remarked by Gallardo et al. (2021) [38] for macroalgae collected at 15 m depth off Mataró, NE Spain. These authors assessed that the nature (soft vs. hard consistency of the thallus) and the architecture (branched or crusted and convoluted) of macroalgae can limit the size and abundance of the epibiont invertebrates and can condition the populations of organisms that settle on them.

Comparisons of the present situation with data from the literature are difficult due to the different investigated geographical and ecological settings, the taxonomic and even ecological and functional groups dealt with and the approaches used. After examination of museum collections of algae originating from a wide geographical area, for instance, [36] found a remarkably low total diversity of 36 epibiont bryozoans on 36 encrusted algal genera.

Notwithstanding the relatively low differentiation of algal basibiont morphologies and the single sample and site, in the examined situation, epibiont species richness was comparably higher (63 bryozoans) and differences between substrata more remarkable. This is also indicated by the statistical analysis (Figure 8) that groups more tightly *P. rubra* and *O. volubilis*, the two substrata with the lower relevance of both bryozoan and serpulid epibionts. This comparably low occurrence of epibionts could be related to the possible presence of antifouling substances produced by these algae, discouraging epibiont settlement (see Ryland, 1959 [39]; Steinberg and de Nys, 2002 [40]).

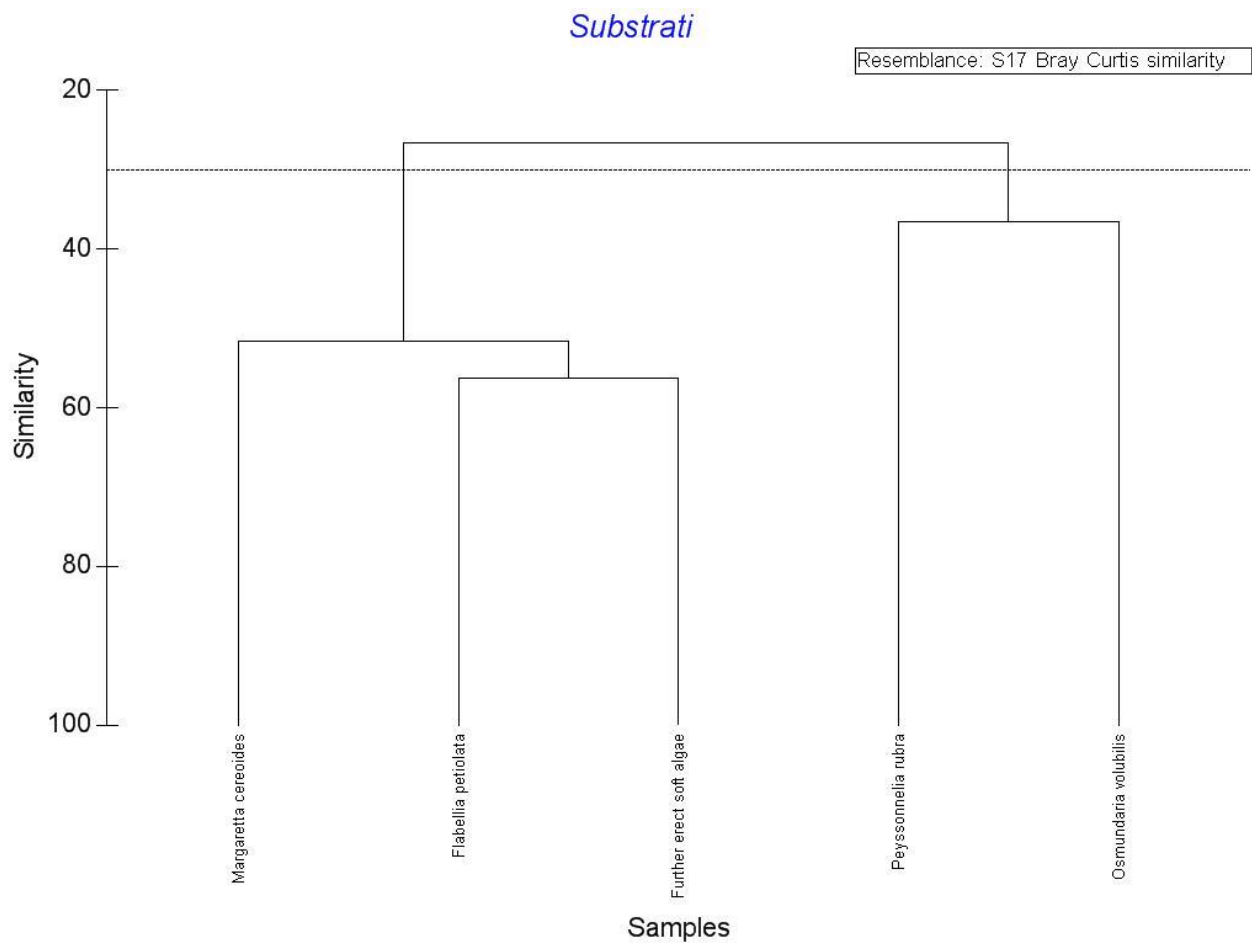


Figure 8. Bray–Curtis similarity dendrogram of substrates, treated as samples; two groups are defined at 30% BC level (hatched line).

Though generalisation is difficult, red and brown algae have been reported as the most chemically prolific (da Gama et al., 2014 [41]). *P. rubra* was one of the species missing epibionts in all habitats from where it was collected in a study by Uriz et al. (1991) [42]. The particular texture of both surfaces and mostly of the downward facing one, characterized by a mat of rhizoids and entangled sediment, could be unsuitable/unpleasant for the settlement of epibiont species. Indeed, only 1/3 of the bryozoan species and $\frac{1}{4}$ of the serpulid species, representing ca. 11% and 6% of the total bryozoan and serpulid living assemblages, respectively, were found on these two algae. The number of colonies/specimens was very low for bryozoans and negligible for serpulids, with entire fronds not fouled at all. Species were usually occasional and only some of the most abundant were relatively common except for *C. brongniartii*, a slightly mineralised, encrusting bryozoan that was preferentially found (more than 50% of its colonies) on the upward-facing surfaces of *P. rubra*. The location of this species, often found on the upward-facing surfaces of algal substrata, could be related with its relative tolerance to light, also indicated by its occurrence/abundance at shallow depths and on buoyant and drifted substrata (e.g., [16]; Koćak and Aydin-Önen, 2014 [43]; Dick and Grischenko, 2017 [44]; Subías-Barata et al., 2022 [45]; A.R., personal observations). In contrast, *F. petiolata*, a green alga that resulted as non-toxic in all seasons in a study on antifouling algal toxicity of Mediterranean species by Martì et al. (2004) [46], hosted a comparably higher number of species (37 bryozoans and 8 serpulids) and colonies/specimens (324 bryozoans and 139 serpulids). An amount of 41 bryozoan and 5 serpulid species (with 220 colonies and 58 specimens) were present on further algae, largely represented by fronds of *Phyllophora crispa*. Whereas no data is available for epibionts on *F. petiolata*, extensive surveys on epibionts growing on *P. crispa*

from several samples collected in different sites and seasons around the Giglio Island (Tuscany Archipelago, NE Tyrrhenian Sea) allowed (Rossbach et al., 2022 [47]) to recognize a number of bryozoan species belonging to 43 different families and ([47] and Rossbach et al., 2021 [48]) to list 9 serpulid taxa, roughly comparable to figures observed in the present study. As far as we know, together with the record of 54 bryozoan epibiont species on 100 fronds of the large-sized *Laminaria rodriguezii* Bornet, 1888 (colonisable surface of ca. 10 m²) from ca. 60 m depth at the Apollo Bank (Ustica, S Tyrrhenian Sea), these represent examples of the highest bryozoan diversity associated with algae documented from the Mediterranean.

The highest number of bryozoan and serpulid species, along with the highest number of colonies/specimens per cm², was observed on *M. cereoides* rather than on other elements of the canopy. This points to the habitat-forming relevance of this bryozoan in the studied build-up, in agreement with the possible “bioconstructional” role suggested for populations of this species in relatively deep, high energy settings of the Columbian Caribbean by Yepes-Narváez (2020) [49]. *Margaretta cereoides* alone hosts almost 75% and 92% of bryozoan and serpulid species diversity, respectively, providing suitable colonisable surface for most of the detected species, some missing on other substrata.

Algal thalli are fleshy and flexible. This implies that epibionts must be specifically adapted to cope with these characteristics, exhibiting small sizes that can be functional to avoid early detachment. As reported by [37], a weak or incomplete calcification can also help to overcome substrate flexibility, with particular species selecting fronds of the most suitable algal substrates and showing particular distribution patterns on them. Besides unmineralised ctenostomes, in the present instance, we observed some cheilostome bryozoans, such as *Escharoides mamillata* and further species like *Prenantia cheilostoma*, which consisted of only few zooids often lacking basal calcification. Analogously, the small spirorbines *Janua heterostropha* and *N. pseudocorrugata*, characterized by reduced or missing basal calcification, were nearly exclusively found (sometimes clustered) on the extremely flexible blades of *F. petiolata* and less frequently on other algae. Tiny and flexible tubes also allowed the success of the serpulid *J. marenzelleri* not only on *F. petiolata* but also on further algae, including *C. cylindracea* (Figure 5I). Similar adaptations were recorded for bryozoans and serpulid assemblages associated with fleshy algae at 5–25 m depth in the Ciclopi Island Marine Protected Area ([28]; Rosso et al., 2019 [50]). The absence/reduction of basal calcification could also allow further functions. Manríques and Cancino (1996) [51] demonstrated that it favors the uptake of algal exudates by particular epibiont bryozoan species preventing zooid degeneration, and Muñoz et al. (1991) [52] reported on the interchange of metabolic substances between the host and the epibionts. This adaptation is also possibly useful for reducing the impact of depressing photosynthetic activity, enhancing the durability of the ephemeral algal fronds and delaying/avoiding the consequent frond loss (Taylor and Wilson, 2003 [53] and references therein), an adverse event for epibionts. Competition for space seems relatively low to absent on algal fronds, probably because of their rapid degradation and turnover constantly providing new colonisable surfaces.

In contrast, the preference for *M. cereoides* seems related to the different nature of the colonisable surface offered by the bryozoan, i.e., a more consistent (harder) and relatively more persistent surface, in comparison with the algal species usually lasting for one year or less (see McKinney and Jackson, 1989 [54]). Indeed, even if data relating to life histories of all species considered in this study are lacking, we can expect these algae to be more ephemeral than *M. cereoides* whose colonies, presumably growing for several years, include mineralised internodes thickened by secondary calcification during aging, with basal internodes usually more heavily covered by epibionts. Algae probably have shorter life histories although some parts, and especially the stems of *F. petiolata*, often persist for some time after degradation/consumption of the blades, as observed in the present instance. Internodes of *M. cereoides* and stems of *F. petiolata* share a slender cylindrical, i.e., filiform, shape offering epibionts a 3D-space instead of the 2D-space provided by ribbon-like to laminar algal blades.

It is also worth noting that some of the largest bryozoan colonies and most of the largest serpulid tubes were found on *M. cereoides*. These include the encrusting unilaminar bryozoans *Arthropoma cecilia* (Figures 5F and 6E), *Schizomavella (S.) linearis* (Figure 6D), *Copidozoum planum*, *Plagioecia patina* (Figure 6B) and *Hippoporina pertusa*, as well as the encrusting unlayered celleporiform species *C. caminata* (Figures 5A,C and 7J) and *Turbicellepora coronopus*, and also some serpulids, especially *S. triqueter* (Figure 5L) and *S. vermicularis* and the elevated, heavily skeletonized spirorbine *Simplaria pseudomilitaris* (Figure 5M). In addition, large, erect and flexible colonies, such as *Bugulina cf. fulva* (Figure 6C), preferred *Margaretta* internodes to settle on. Instead, until present, *M. cereoides* has only occasionally been reported as a substratum for a few bryozoan species, i.e., the celleporids *Turbicellepora robusta* (Lopez de la Cuadra and Garcia Gomez, 2001 [55]) and *C. caminata* [6], this latter species being the most abundant in the present sample.

Whatever the exploited substratum, epibionts are often represented by young colonies/specimens. This could be partly explained by the sampling season (August), a period when almost all species are fertile in the Mediterranean Sea (e.g., [16] for bryozoans and Kupriyanova et al., 2001 [56] for serpulids), and it is possible to find recently settled generations at their early developmental stages and as juveniles, often growing on newly produced algal blades. Some of the detected serpulids, such as *S. triqueter*, *S. vermicularis* and spirorbine species, are known as pioneer species (Fava et al., 2016 [57]). With some exceptions, especially on *M. cereoides* basal articles and some *F. petiolata* stems and more occasionally on some algae (Figure 5B,J,L), colonies/specimens are often largely spaced from each other, leaving uncovered large available surfaces (cf. densities of colonies/specimens per square centimeter on different substrata in Table 1). Though small and presumably young, however, bryozoan colonies were often fertile, including gonozooids and oecia, sometimes in zooids not far from the ancestrula in encrusting cheilostomes. Early fertility has often been considered as typical of r-strategist species with opportunistic life histories as an adaptation for exploiting unstable habitats, with ephemeral substrata and/or reduced to unpredictable resource supply ([54]; Taylor, 2020 [58]; Harmelin and Rosso, in press [59]) and already reported for assemblages colonising infralittoral algal communities (e.g., [50]).

The number of dead bryozoan species and colonies, as well as the proportionally higher serpulid species and specimens, was low in comparison to the living assemblage, and only two bryozoan and no serpulid species were added in the thanatocoenoses (dead assemblages). This parallels what usually occurs on hard surfaces of cave walls (e.g., [19]) but contrasts with expectation due to the usual increase in both species and colony/specimen numbers produced by the accumulation of skeletal remains on sedimentary bottoms (e.g., Kidwell and Bosence, 1991 [60] and Rosso, 1996 [61] for bryozoans). However, on a coralligenous build-up, the canopy largely consisted of ephemeral (often short living) substrata, and even “perennial” algae usually lose their fronds during fall or undergo to periodic frond consumption and/or degeneration. The highest number of dead bryozoan colonies and especially of serpulid specimens was observed on *Margaretta* and the stems of *Flabellia*, which often persist after the decay of the fan-shaped fronds. This high number of epibionts and especially of dead colonies/specimens on such substrata appears correlated with both their hardness and longevity, sometimes encompassing/exceeding the epibiont’s life span. The relatively low number of observed dead colonies/specimens could also result from their ease detachment from the substratum, possibly favoured by both the smallness of the adhesion surface after the reduction of basal mineralisation (see above) and the possible pellicular shedding of algal epithelial cells, a strategy adopted by some algae to avoid epibiont overgrowth (see Nylund and Pavia, 2005 [62]). These detached colonies/specimens could contribute carbonate bioclasts to the sediments accumulating within crevices and cavities in the coralligenous build-up and in the surrounding soft bottoms. This process also affects *Margaretta* colonies and internodes that can be detached from their substratum after death and deterioration of chitinous joints and rootlets, with internodes accumulating in the neighboring biodetritic bottoms, as observed in samples collected in the northern sector of

the Gulf of Noto at 45 m depth, possibly close to coralligenous build-ups in the area ([61]; Rosso, 1989 [63]).

4.3. Bryozoan and Serpulid Assemblages on *M. cereoides* and other Large Habitat-Forming Bryozoans

Margaretta cereoides has been reported at least once as a habitat-forming species at 10 m depth in central Adriatic Sea [6], and its “bioconstructional” role has been remarked by [49] in the Columbian Caribbean. However, no study has so far been performed on the associated epibiont community in these areas or elsewhere, and only occasional information is available about particular epibiont species on colonies from the Balearic and the Adriatic seas ([6,55]: see above). Therefore, the present study is the first thorough analysis of the epibiont community associated with *M. cereoides*, indicating that this species hosts a remarkable diversity.

Indeed, few studies have been so far devoted at investigating epibiont communities on habitat-forming bryozoans in general, unlike for other taxa, especially *P. oceanica* (e.g., Mazzella et al., 1989 [64]; Nesti et al., 2009 [65]; Di Martino and Taylor, 2014 [66] for a review about bryozoan epibionts), some fleshy algae (e.g., [47,50]; Di Geronimo et al., 1990 [67]) and reef-forming organisms, including coralligenous algae and mesophotic benthic animals (e.g., [24] Harmelin, 2017 [68]; Giampaolletti et al., 2020 [69]; Pica et al., 2022 [70], focusing particularly on bryozoans). In European seas, the most investigated species is possibly *F. foliacea*. Almost 60 epibiont species have been reported from the northern seas [13,14] on this laminar weakly calcified bryozoan, which grows for up to 10–12 years, developing large colonies usually 10–15 cm high (Ryland, 1976) [71]. Bryozoans on *F. foliacea* represent ca. 2/3 of the epibionts and largely consist of weakly calcified and articulated species (Supplementary Materials Table S3). It is suggested that this prevalence could be related to both the flexible nature of the colonies (possibly also enhanced by seasonal growth discontinuities) and the species distribution in habitats with moderately strong to strong energy (Hiscock, 1983) [72]. In contrast, studied Mediterranean habitat-forming bryozoans mostly show erect, rigid colonies and are often associated with the Coralligenous. However, only data about total biodiversity, ranging from 22 to 37 species, are available for some species, i.e., *M. truncata*, *S. cervicornis*, *A. calveti* and *R. couchii couchii* ([10]: see introduction). Lists of bryozoan species (summarized in Supplementary Materials Table S3) are only available for *S. errata* and *P. fascialis*, supporting 28–36 and 84 epibiont species, respectively. In these last cases [8,9], bryozoans account for a large proportion of epibiont diversity, with a total of 7 species found on *S. errata* and 26 species on *P. fascialis* (ca. 1/3 of the assemblage). Serpulids occurring with 4 and 2 species, respectively, seem to be proportionately more diversified, taking into consideration that their total number in the Mediterranean is comparably very low (see above).

The only flexible bryozoan species so far analysed for epibionts in the Mediterranean is *C. salicornioides*, sharing with *M. cereoides* the cellariiform growth morphology of the colonies that consists of mineralised segments articulated by chitinous joints. However, colonies of *C. salicornioides* are smaller and branches are slender and straight, and they bifurcate only occasionally, producing a single distal branch but not lateral branches in a whorl pattern. McKinney and Jaklin (2000) [15] listed 54 epibiont species on *C. salicornioides*, forming dense meadows at ca. 35 m depth in the Adriatic Sea. Epibiont assemblage largely consisted of bryozoans (31 species) and subordinately by annelids (7 species, including 4 serpulids). McKinney and Jaklin (2000) [15] also noted a pattern of distribution of epibionts with the highest cover on basal segments and a spatial partition between erect flexible, encrusting and erect rigid colonies dominating on distal, intermediate and proximal (deep) segments, respectively. Though not quantitatively investigated, the number of species and colonies, as well as their coverage, was higher on proximal (oldest) segments on the examined *M. cereoides* colonies.

If we compare bryozoan and serpulid species richness on these habitat-forming bryozoan species, it appears that *M. cereoides* hosts a relevant biodiversity (Supplementary

Materials Table S3). With 11 species, serpulids decidedly outnumber the 1–4 species reported for other substrata. Some species, i.e., *S. vermicularis*, *Spirobranchus triqueter* (usually reported as *Pomatoceros triqueter*) (e.g., [8]) and *S. polytrema*, were shared. In contrast, *Filograna implexa* and *Hydroides dianthus* were missing on *M. cereoides*. However, *F. implexa* could possibly be the same species here reported as *Filograna* sp., and the absence of *H. dianthus* could be related to its shallower depth range (Bianchi and Morri, 2011 [73]; Zibrowius, 1973 [74]; Ben-Eliahu and ten Hove, 2011 [75]).

Bryozoans on *M. cereoides* accounted for 48 species, exceeding the 31 species reported on *C. salicornioides*, making it the most diverse basibiont for bryozoans in the Mediterranean, also outnumbering the 42 species reported for *F. foliacea* from the northern seas by [14]. Despite some differences, as many as 23 species were shared between *M. cereoides* and further Mediterranean basibiont bryozoans, but only 5 of them were also present on *F. foliacea*. Three of these species are cyclostomes (*Diplosolen obelius*, *Disporella hispida*, *P. patina*) whereas only two, i.e., *Schizomavella* (*S.*) *linearis* and *S. scrupea*, are cheilostomes (out of the 32 cheilostome species reported). A further two species (*Celleporina hassalli* and *C. brongniartii*) have been reported for *F. foliacea* but not for Mediterranean basibionts other than *Margaretta* from off Marzamemi. The large divergence in the composition of the epibiont community on *F. foliacea* in comparison with bryozoan habitat-forming species from the Mediterranean was expected due to the different geographical provenance areas. At the present state of knowledge, however, and due to the scant number of studies, it is difficult to understand if the species found so far that are associated only with a particular basibiont are actually actively selective or if their occurrence is purely occasional. In contrast, the shared taxa could be more eurytopic, as observed for bryozoan species epibiont on algal and plant species (see [36]).

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/jmse11030590/s1>, Table S1. List of bryozoan species occurring as epibionts on the bryozoan *Margaretta cereoides* and on algae of the canopy of the studied build-up E collected offshore Marzamemi (Ionian Sea); Table S2. List of serpulid species occurring as epibionts on the bryozoan *Margaretta cereoides* and on algae of the canopy of the studied build-up E collected offshore Marzamemi (Ionian Sea); Table S3. List of bryozoan and serpulid species epibiont on some habitat-forming bryozoans from the Mediterranean and the North Europe seas.

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References

- Wood, A.C.L.; Probert, P.K.; Rowden, A.A.; Smith, A.M. Complex Habitat Generated by Marine Bryozoans: A Review of Its Distribution, Structure, Diversity, Threats and Conservation. *Aquat. Conserv.* **2012**, *22*, 547–563.
- Lombardi, C.; Taylor, P.D.; Cocito, S. Bryozoan Constructions in a Changing Mediterranean Sea. In *The Mediterranean Sea: Its History and Present Challenges*; Goffredo, S., Dubinsky, I., Eds.; Springer: Dordrecht, The Netherlands, 2014; pp. 373–384.
- Lombardi, C.; Taylor, P.D.; Cocito, S. Bryozoans: The ‘Forgotten’ Bioconstructors. In *Perspectives on the Marine Animal Forests of the World*; Rossi, S., Bramanti, L., Eds.; Springer Nature: Cham, Switzerland, 2020; pp. 193–217.
- Cocito, S. Bioconstruction and Biodiversity: Their Mutual Influence. *Sci. Mar.* **2004**, *68*, 137–144.
- Holon, F.; Harmelin, J.-G. Bryozoan Reef, an Unknown Mediterranean Habitat? *Int. Bryozool. Assoc. Bull.* **2014**, *10*, 10–11.
- Novosel, M. Bryozoans of the Adriatic Sea. In *Denisia 16*; Neue Serie 28; Landesmuseen: Zurich, Switzerland, 2005; pp. 231–246.
- Cocito, S.; Novosel, M.; Pasarić, Z.; Key, M.M., Jr. Growth of the Bryozoan *Pentapora fascialis* (Cheilostomata, Ascophora) around Submarine Freshwater Springs in the Adriatic Sea. *Linzer Biol. Beitr.* **2006**, *38*, 15–24.
- Ferdegghini, F.; Cocito, S. Biologically Generated Diversity in Two Bryozoan Buildups. *Biol. Mar. Mediterr.* **1999**, *6*, 191–197.
- Maluquer, P. Algunas Consideraciones sobre la Fauna Asociada a las Colonias de *Schizoporella errata* (Waters, 1878) del Puerto de Mahón (Menorca, Baleares). *Publ. Dept. Zool. Barc.* **1985**, *11*, 23–28.
- Cocito, S. Le Biocostruzioni a Briozoi. *Biol. Mar. Mediterr.* **2009**, *16*, 19–30.
- Stebbing, A.R.D. The Epizoic Fauna of *Flustra foliacea* (Bryozoa). *J. Mar. Biol. Ass. UK* **1971**, *51*, 283–300.
- Connor, D.W.; Allen, J.H.; Golding, N.; Howell, K.L.; Lieberknecht, L.M.; Northen, K.O.; Reker, J.B. *The Marine Habitat Classification for Britain and Ireland. Version 04.05 Infralittoral Rock Section*; JNCC: Peterborough, UK, 2004.
- Stebbing, A.R.D. Growth of *Flustra Foliacea* (Bryozoa). *Mar. Biol.* **1971**, *9*, 267–273.
- Bitschofsky, F.; Forster, S.; Scholz, J. Regional and Temporal Changes in Epizoobiontic Bryozoan-Communities of *Flustra foliacea* (Linnaeus, 1758) and Implications for North Sea Ecology. *Estuar. Coast. Shelf Sci.* **2011**, *91*, 423–433.
- McKinney, F.K.; Jaklin, A. Spatial Niche Partitioning in the *Cellaria* Meadow Epibiont Association, Northern Adriatic Sea. *Cah. Biol. Mar.* **2000**, *41*, 1–17.
- Gautier, Y.V. Recherches Écologiques Sur Les Bryozoaires Chilostomes En Méditerranée Occidentale. *Rec. Trav. Stat. Mar. Endoume* **1962**, *38*, 1–434.
- Ferdegghini, F.; Acunto, S.; Cocito, S.; Cinelli, F. Variability at Different Spatial Scales of a Coralligenous Assemblage at Giannutri Island (Tuscan Archipelago, Northwest Mediterranean). In *Island, Ocean and Deep-Sea Biology, Developments in Hydrobiology*; Jones, M.B., Azevedo, J.M.N., Neto, A.I., Costa, A.C., Martins, A.M.F., Eds.; Springer: Dordrecht, The Netherlands, 2000; Volume 152, pp. 27–36.
- McKinney, F.K.; Jaklin, A. Sediment Accumulation in a Shallow-Water Meadow Carpeted by a Small Erect Bryozoan. *Sediment. Geol.* **2001**, *145*, 397–410.
- Rosso, A.; Di Martino, E.; Sanfilippo, R.; Di Martino, V. Bryozoan Communities and Thanatocoenoses from Submarine Caves in the Plemmirio Marine Protected Area (SE Sicily) Bryozoans from Submarine Caves. In *Bryozoan Studies 2010, Proceedings of the 15th IBA Conference, Kiel, Germany, 2–7 August 2010*; Ernst, A., Schäfer, P., Scholz, J., Eds.; Lecture Notes in Earth System Sciences; Springer: Berlin/Heidelberg, Germany, 2013; Volume 143, pp. 251–269.
- Rosso, A.; Altieri, C.; Bazzicalupo, P.; Bertolino, M.; Bracchi, V.A.; Bruno, F.; Cipriani, M.; Costa, G.; D’Alpa, F.; Donato, G.; et al. Bridging Together Research and Technological Innovation: First Results and Expected Bearings of the Project CRESCIBLUREEF on Mediterranean Coralligenous. In Proceedings of the 4th Mediterranean Symposium on the Conservation of the Coralligenous and Other Calcareous Bio-Concretions, Genova, Italy, 20–21 September 2022; p. 108.
- Violanti, V.; di Geronimo, I.; Saccà, R. Foraminiferal Thanatocoenoses from the Gulf of Noto (Southeastern Sicily). *Boll. Mus. Reg. Sci. Nat. Torino. Spec. Vol.* **1990**, 773–799.
- Di Geronimo, I.; Di Geronimo, R.; Improta, S.; Rosso, A.; Sanfilippo, R. Preliminary Observation on a Columnar Coralline Build-up from off SE Sicily. *Biol. Mar. Mediterr.* **2001**, *8*, 229–237.
- Di Geronimo, I.; Di Geronimo, R.; Rosso, A.; Sanfilippo, R. Structural and Taphonomic Analysis of a Columnar Coralline Algal Build-up from SE Sicily. *Geobios* **2002**, *35*, 86–95.
- Rosso, A.; Sanfilippo, R. The Contribution of Bryozoans and Serpuloideans to Coralligenous Concretions from SE Sicily. In *UNEP-MAP-RAC/SPA, Proceedings of the First Symposium on the Coralligenous and Other Calcareous Bio-Concretions of the Mediterranean Sea, Tabarka, Tunisia, 15–16 January 2009*; Pergent-Martini, C., Bricchet, M., Eds.; RAC/SPA Publication: Tunis, Tunisia, 2009; pp. 123–128.
- Varzi, A.G.; Fallati, L.; Savini, A.; Bracchi, V.A.; Bazzicalupo, P.; Rosso, A.; Sanfilippo, R.; Bertolino, M.; Muzzupappa, M.; Basso, D. Geomorphological Mapping of Coralligenous Reefs Offshore Southeastern Sicily (Ionian Sea). *J. Maps* **2023**. [[CrossRef](#)]
- Bracchi, V.A.; Bazzicalupo, P.; Fallati, L.; Varzi, A.G.; Savini, A.; Negri, M.P.; Rosso, A.; Sanfilippo, R.; Guido, A.; Bertolino, M. The Main Builders of Mediterranean Coralligenous: 2D and 3D Quantitative Approaches for Its Identification. In *Crustose Coralline Red Algae Frameworks and Rhodoliths: Past and Present*; Frontiers: London, UK, 2022; Volume 16648714, p. 41.
- Donato, G.; Sanfilippo, R.; Sciuto, F.; D’Alpa, F.; Serio, D.; Bracchi, V.A.; Bazzicalupo, P.; Negri, P.; Guido, A.; Bertolino, M.; et al. Biodiversity of a Coralligenous Build-up off Marzamemi (SE Sicily, Ionian Sea). In *UNEP SPA/RAC, Proceedings of the 4th Mediterranean Symposium on the Conservation of the Coralligenous and Other Calcareous Bio-Concretions, Genova, Italy, 20–21 September 2022*; pp. 151–152.

28. Sanfilippo, R.; Rosso, A.; Guido, A.; Gerovasileiou, V. Serpulid Communities from Two Marine Caves in the Aegean Sea, Eastern Mediterranean. *J. Mar. Biol. Assoc. UK* **2017**, *97*, 1059–1068.
29. Rosso, A.; Di Martino, E. Bryozoan Diversity in the Mediterranean Sea: An Update. *Medit. Mar. Sci.* **2016**, *17*, 567–607.
30. Castelli, A.; Bianchi, C.; Cantone, G.; Çinar, M.; Gambi, M.; Giangrande, A.; Iraci Sareri, D.; Lanera, P.; Licciano, M.; Musco, L.; et al. Annelida Polychaeta. In Relini G. Checklist of the Flora and Fauna in Italian Seas. *Biol. Mar. Medit.* **2008**, *15* (Suppl. S1), 323–373.
31. Ben-Eliahu, M.N.; Fiege, D. Serpulid Tube-Worms (Annelida: Polychaeta) of the Central and Eastern Mediterranean with Particular Attention to the Levant Basin. *Senckenberg. Marit.* **1996**, *28*, 1–51.
32. Çinar, M.E.; Bilecenoglu, M.; Öztürk, B.; Can, A. New Records of Alien Species on the Levantine Coast of Turkey. *Aquat. Invasions* **2006**, *1*, 84–90. [[CrossRef](#)]
33. Çinar, M.E.; Bilecenoglu, M.; Yokeş, M.B.; Öztürk, B.; Taşkin, E.; Bakir, K.; Doğan, A.; Açık, Ş. Current Status (as of End of 2020) of Marine Alien Species in Turkey. *PLoS ONE* **2021**, *16*, e0251086.
34. Casellato, S.; Stefanon, A. Coralligenous Habitat in the Northern Adriatic Sea: An Overview. *Mar. Ecol.* **2008**, *29*, 321–341.
35. Laubier, L. Le Coralligène Des Albères-Monographie Biocénotique. *Ann. Inst. Oceanogr.* **1966**, *43*, 137–316.
36. Liuzzi, M.G.; Lopez-Gappa, J. Algae as Hosts for Epifaunal Bryozoans: Role of Functional Groups and Taxonomic Relatedness. *J. Sea Res.* **2011**, *65*, 28–32.
37. Hayward, P.J. Invertebrate Epiphytes of Coastal Marine Algae. *Shore Environ.* **1980**, *2*, 761–787.
38. Gallardo, D.; Oliva, F.; Ballesteros, M. Marine Invertebrate Epibionts on Photophilic Seaweeds: Importance of Algal Architecture. *Mar. Biodivers.* **2021**, *51*, 16.
39. Ryland, J.S. Experiments on the Selection of Algal Substrates by Polyzoan Larvae. *J. Exp. Biol.* **1959**, *36*, 613–631.
40. Steinberg, P.D.; de Nys, R. Chemical Mediation of Colonization of Seaweed Surfaces. *J. Phycol.* **2002**, *38*, 621–629. [[CrossRef](#)]
41. Gama, B.A.P.; Plouguerné, E.; Pereira, R.C. The Antifouling Defence Mechanisms of Marine Macroalgae. In *Advances in Botanical Research*; Elsevier: Oxford, UK, 2014; Volume 71, pp. 413–440. ISBN 0065-2296.
42. Uriz, M.J.; Martin, D.; Turon, X.; Ballesteros, E.; Hughes, R.; Acebal, C. An Approach to the Ecological Significance of Chemically Mediated Bioactivity in Mediterranean Benthic Communities. *Mar. Ecol. Prog. Ser.* **1991**, *70*, 175–188. [[CrossRef](#)]
43. Koçak, F.; Aydin-Önen, S. Epiphytic Bryozoan Community of *Posidonia oceanica* (L.) Delile Leaves in Two Different Meadows at Disturbed and Control Locations. *Mediterr. Mar. Sci.* **2014**, *15*, 390–397. [[CrossRef](#)]
44. Dick, M.H.; Grischenko, A.V. Rocky-Intertidal Cheilostome Bryozoans from the Vicinity of the Sesoko Biological Station, West-Central Okinawa, Japan. *J. Nat. Hist.* **2017**, *51*, 141–266.
45. Subías-Baratau, A.; Sanchez-Vidal, A.; di Martino, E.; Figuerola, B. Marine Biofouling Organisms on Beached, Buoyant and Benthic Plastic Debris in the Catalan Sea. *Mar. Pollut. Bull.* **2022**, *175*, 113405.
46. Martí, R.; Uriz, M.J.; Turon, X. Seasonal and Spatial Variation of Species Toxicity in Mediterranean Seaweed Communities: Correlation to Biotic and Abiotic Factors. *Mar. Ecol. Prog. Ser.* **2004**, *282*, 73–85. [[CrossRef](#)]
47. Rossbach, F.I.; Casoli, E.; Plewka, J.; Schmidt, N.; Wild, C. New Insights into a Mediterranean Sea Benthic Habitat: High Diversity of Epiphytic Bryozoan Assemblages on *Phyllophora crispa* (Rhodophyta) Mats. *Diversity* **2022**, *14*, 346.
48. Rossbach, F.I.; Casoli, E.; Beck, M.; Wild, C. Mediterranean Red Macro Algae Mats as Habitat for High Abundances of Serpulid Polychaetes. *Diversity* **2021**, *13*, 265.
49. Yepes-Narváez, V. Environmental Ecology of Marine Bryozoans (Phylum Bryozoa) and Ascidiaceans (Tunicata: Ascidiacea) under Multistressor Scenarios. Ph.D. Thesis, The Manchester Metropolitan University, Manchester, UK, 2020; 288p.
50. Rosso, A.; Sanfilippo, R.; Sciuto, F.; Serio, D.; Catra, M.; Alongi, G.; Viola, A.; Leonardi, R. Preliminary Information on Bryozoans Associated with Selected Infralittoral Algae Communities from Eastern Sicily (Mediterranean). *Australas. Palaeontol. Mem.* **2019**, *52*, 115–129.
51. Manriquez, P.H.; Cancino, J.M. Bryozoan-Macroalgal Interactions: Do Epibionts Benefit? *Mar. Ecol. Prog. Ser.* **1996**, *138*, 189–197. [[CrossRef](#)]
52. Muñoz, J.; Cancino, J.M.; Molina, M.X. Effect of Encrusting Bryozoans on the Physiology of Their Algal Substratum. *J. Mar. Biolog. Assoc. UK* **1991**, *71*, 877–882. [[CrossRef](#)]
53. Taylor, P.D.; Wilson, M.A. Palaeoecology and Evolution of Marine Hard Substrate Communities. *Earth Sci. Rev.* **2003**, *62*, 1–103.
54. McKinney, F.K.; Jackson, J.B.C. *Bryozoan Evolution*; Unwin Hyman: Boston, MA, USA, 1989; p. 238.
55. López de la Cuadra, C.M.; García-Gómez, J.C. New and Little-Known Ascophoran Bryozoans from the Western Mediterranean, Collected by 'Fauna Iberica' Expeditions. *J. Nat. Hist.* **2001**, *35*, 1717–1732.
56. Kupriyanova, E.K.; Nishi, E.; ten Hove, H.; Rzhavsky, A.V. Life-History Patterns in Serpulimorph Polychaetes: Ecological and Evolutionary Perspectives. *Oceanogr. Mar. Biol. Ann. Rev.* **2001**, *39*, 1–101.
57. Fava, F.; Ponti, M.; Abbiati, M. Role of Recruitment Processes in Structuring Coralligenous Benthic Assemblages in the Northern Adriatic Continental Shelf. *PLoS ONE* **2016**, *11*, e0163494.
58. Taylor, P.D. *Bryozoan Paleobiology*; John Wiley & Sons: Hoboken, NJ, USA, 2020; ISBN 1118455002.
59. Harmelin, J.-G.; Rosso, A. On Some "Hemicyclopora" and "Escharella" Species (Bryozoa, Cheilostomatida) from the Atlantic-Mediterranean Region. Re-Examination of Their Generic Status and Description of New Species and a New Genus. *Zookeys* **2023**, in press.

60. Kidwell, S.M.; Bosence, D.W.J.; Allison, P.A.; Briggs, D.E.G. Taphonomy and Time-Averaging of Marine Shelly Faunas. In *Taphonomy: Releasing the Data Locked in the Fossil Record*; Allison, P.A., Briggs, D., Eds.; Plenum: New York, NY, USA, 1991; pp. 115–209.
61. Rosso, A. Popolamenti e Tanatocenosi a Briozoi di Fondi Mobili Circolitorali del Golfo di Noto (Sicilia, Italia). *Nat. Sicil.* **1996**, *20*, 189–225.
62. Nylund, G.M.; Pavia, H. Chemical versus Mechanical Inhibition of Fouling in the Red Alga *Dilsea aarnosa*. *Mar. Ecol. Prog. Ser.* **2005**, *299*, 111–121. [[CrossRef](#)]
63. Rosso, A. Contributo alla Conoscenza di Alcuni Popolamenti, Tanatocenosi e Tafocenosi a Briozoi di Alcuni Fondi Mobili Circolitorali. Ph.D. Thesis, University of Messina, Messina, Italy, 1989. Volume 331.
64. Mazzella, L.; Scipione, M.B.; Buia, M.C. Spatio-temporal Distribution of Algal and Animal Communities in a *Posidonia oceanica* Meadow. *Mar. Ecol.* **1989**, *10*, 107–129. [[CrossRef](#)]
65. Nesti, U.; Piazzini, L.; Balata, D. Variability in the Structure of Epiphytic Assemblages of the Mediterranean Seagrass *Posidonia oceanica* in Relation to Depth. *Mar. Ecol.* **2009**, *30*, 276–287.
66. Di Martino, E.; Taylor, P.D. A Brief Review of Seagrass-Associated Bryozoans, Recent and Fossil. *Studi Trentini Sci. Nat.* **2014**, *94*, 79–94.
67. Di Geronimo, I.; Giacobbe, S.; Rosso, A.; Sanfilippo, R. Popolamenti e Tanatocenosi del Banco Apollo (Ustica, Mar Tirreno Meridionale). 1990, pp. 697–729. Available online: https://www.researchgate.net/publication/283302225_Popolamenti_e_tanatocenosi_del_Banco_Apollo_Ustica_Mar_Tirreno_meridionale (accessed on 7 February 2023).
68. Harmelin, J.-G. Bryozoan Facies in the Coralligenous Community: Two Assemblages with Contrasting Features at Port-Cros Archipelago (Port-Cros National Park, France, Mediterranean). *Sci. Rep. Port-Cros Natl. Park* **2017**, *31*, 105–123.
69. Giampaolletti, J.; Cardone, F.; Corriero, G.; Gravina, M.F.; Nicoletti, L. Sharing and Distinction in Biodiversity and Ecological Role of Bryozoans in Mediterranean Mesophotic Bioconstructions. *Front. Mar. Sci.* **2020**, *7*, 581292.
70. Pica, D.; Berning, B.; Calicchio, R. Cheilostomatida (Bryozoa) from the Ionian Apulian Coast (Italy) with the Description of New Species. *Eur. Zool. J.* **2022**, *89*, 371–422.
71. Ryland, J.S. Physiology and Ecology of Marine Bryozoans. *Adv. Mar. Biol.* **1977**, *14*, 285–443.
72. Hiscock, K. Water Movement. In *The Ecology of Shallow Sublittoral Benthos*; Earll, R., Erwin, D.G., Eds.; Sublittoral Ecology; Clarendon Press: Oxford, UK, 1983; pp. 58–96.
73. Bianchi, C.N.; Morri, C. The Battle Is Not to the Strong: Serpulid Reefs in the Lagoon of Orbetello (Tuscany, Italy). *Estuar Coast. Shelf Sci.* **2001**, *53*, 215–220.
74. Zibrowius, H. Remarques sur Trois Espèces de Serpulidae Acclimatées en Méditerranée: *Hydroides Dianthus* (Verrill, 1873), *Hydroides dirampha* Mörch, 1863, et *Hydroides elegans* (Haswell, 1883). *Rapp. Comm. Int. Mer. Médit.* **1973**, *21*, 683–686.
75. Ben-Eliahu, M.N.; ten Hove, H.A. Serpulidae (Annelida: Polychaeta) from the Suez Canal—From a Lessepsian Migration Perspective (a Monograph). *Zootaxa* **2011**, *2848*, 1–147. [[CrossRef](#)]

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