



Bryozoan diversity in the Marzamemi (SE Sicily, SW Ionian Sea) and Mediterranean coralligenous habitats

Antonietta Rosso^{1,2} · Gemma Donato¹ · Rossana Sanfilippo^{1,2} · Francesco Sciuto^{1,2} ·
Valentina Alice Bracchi^{2,3} · Adriano Guido⁴ · Mara Cipriani⁴ · Daniela Basso^{2,3}

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Abstract

Although coralligenous is considered a priority habitat for conservation within European directives largely considering its complex 3D structure promoting spatial and ecological heterogeneity and related high biodiversity, detailed information on species richness and composition is still scant, at least for some taxonomic groups, including bryozoans, notwithstanding their ecological relevance within the habitat. Focusing on the bryozoan community associated with six build-ups sampled between 33 and 37 m depth offshore Marzamemi (SE Sicily, SW Ionian Sea), this study contributes to improve knowledge on coralligenous bryozoan biodiversity, from a locality in the still understudied eastern Mediterranean. A total of 127 species were recorded, raising to 145 and 257 species the coralligenous bryozoan diversity currently known for Marzamemi and the entire Mediterranean, respectively, the latter representing a high proportion (44%) of the overall Mediterranean bryozoan diversity (588 species). Heterogeneity was detected at small spatial scale, among build-ups in the Marzamemi area, and at the Mediterranean scale through comparison with the scant existing literature, which mostly focused on the western basin. Facies differentiation and related ecological heterogeneity, rather than geographic distance, are considered the main drivers. Finally, our results emphasise the critical importance of microscopic and SEM examination of specimens for species detection.

Keywords Taxonomy · Coralligenous build-ups · Microhabitats · Heterogeneity · Species inventory · Biodiversity drivers

Introduction

Coralligenous habitat represents one of the most important marine habitats in the Mediterranean Sea. It develops mainly in the circalittoral zone along continental shelves through the constructional activity of crustose coralline algae with

a secondary contribution of skeletonised invertebrates such as bryozoans, serpulids, vermetids, and cnidarians (Ballesteros 2003, Ballesteros 2006; UNEP-MAP-RAC/SPA, 2008, 2016). Coralligenous bioconstructions can display different morphologies, including build-ups occurring either as discrete bioconstructions or as tabular banks sensu Bracchi et al. (2017). These bioconstructions create complex 3D structures that enhance habitat complexity and increase biodiversity, contributing to seafloor heterogeneity and potentially influencing local hydrodynamics (e.g. Ballesteros 2006). This structural heterogeneity allows several different assemblages to coexist in a reduced space. Indeed, the 3D growth of coralline algae creates external surfaces that host relatively photophilic hard bottom-related organisms also typical of shallower waters, together with variably sized, sheltered and darkish cavities available for sciaphilic species, also shared with dark, either cave or bathyal, habitats. Depending on their location in the build-up and on micro-environmental conditions, cavities can contain sediment resulting from both autochthonous bioclastic production and the baffling and deposition of allochthonous particles,

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✉ Antonietta Rosso
rosso@unict.it

✉ Gemma Donato
gemma.donato@phd.unict.it

¹ Department of Biological, Geological, and Environmental Sciences (DSBGA), University of Catania, Catania, Italy

² Consorzio Nazionale Interuniversitario per le Scienze del Mare – CoNISMa, Rome, Italy

³ Department of Earth and Environmental Sciences (DISAT), University of Milano-Bicocca, Milan, Italy

⁴ Department of Biology, Ecology, and Earth Science (DiBEST), University of Calabria, Rende, Italy

providing suitable conditions for sediment related species, mainly of circalittoral affinity but also typical of deep waters that may shift upwards (Hong 1980, UNEP-MAP-RAC/SPA, 2008). The coexistence of such distinct communities has recently been demonstrated for molluscs by Bracchi et al. (2025).

Owing to this high microhabitat heterogeneity, coralligenous habitat is considered one of the major biodiversity hotspots in the Mediterranean Sea (Ballesteros 2006). For these reasons, it is addressed by several conservation and monitoring frameworks, including the EU Habitat Directive (Council Directive 92/43/EEC 1992) and the Marine Strategy Framework Directive (MSFD 2008/56/EC), as well as the Integrated Monitoring and Assessment Program (IMAP) of the Barcelona Convention Ecosystem Approach and subsequent updates (Montefalcone et al. 2021). However, coralligenous is currently one of the most endangered habitats, prone to environmental changes including direct anthropogenic impact with physical disturbance and degradation produced by human-related activities such as fishing, recreational scuba diving, waste discharge, and industrial pollution, as well as to climate change and related increasing temperatures and acidification all producing threats to its biodiversity (Bavestrello et al. 1997; Montefalcone et al. 2017; Betti et al. 2019; Garrabou et al. 2022). In this context, effective conservation and management require reliable baseline information on coralligenous biodiversity and its spatial variability. However, despite European and national efforts, such information remains fragmentary (e.g. Kipson et al. 2022) and usually scattered in scientific literature.

Current monitoring therefore often relies on rapid assessments finalised at obtaining estimates of coralligenous structure and biodiversity using non-destructive protocols based mostly on seascape morphology and on the presence/absence of selected macrobenthic species detected by photographic surveys (e.g. Kipson et al. 2011; Piazzini et al. 2019; Di Camillo et al. 2023; Astruch et al. 2025, and references therein). However, such an approach is unable to capture the actual biodiversity, especially for bryozoans. In fact, photographic surveys typically record only a few large-sized species, especially those forming erect colonies several centimetre-to-decimetre in size, such as *Adeonella calveti*, *Myriapora truncata*, *Pentapora fascialis*, *Reteporella* spp., *Smittina cervicornis* and *Turbicellepora avicularis*, that can be recognised based on colony colour and morphology, especially branch shape and size, and branching pattern. Only a few further taxa, such as large encrusters forming both membraniporiform and celleporeform colonies, are usually only hardly and tentatively recognisable at genus level (e.g. *Schizomavella*), with a few possible exceptions including *Celleporina caminata* (e.g. Casoli et al. 2020; Çinar et al. 2020; Pinna et al. 2021; Astruch et al. 2025). However, even if these species can be detected through photo/video surveys or scuba

diving assessments, only sufficiently large colonies located on the exposed outer surfaces can be reliably distinguished. Nevertheless, almost all species grow in small colonies, the majority thriving within cavities and therefore remaining completely unapparent or hidden inside the bioconstruction. Colonies are usually undetectable even when attached to the outer surfaces because of the variably dense canopy, largely consisting of sciaphilous fleshy algae and sessile invertebrates (e.g. anthozoans and sponges), which prevents the observation of the underlying substrate. Moreover, colonies growing on the canopy itself often remain not detectable, as they commonly occupy the lower canopy layer. Clear evidence that bryozoan diversity may be underestimated when only non-destructive techniques are used comes from studies on the same selected coralligenous build-up. Bracchi et al. (2022) analysed the build-up through photogrammetry, both with the canopy in place and after its removal, whereas Rosso et al. (2023) and Donato et al. (2024) examined the canopy and the underlying build-up under a stereomicroscope and selected colony fragments under scanning electric microscopy. This direct microscopic examination revealed a much richer bryozoan component than that detected through photogrammetry alone.

Actually, a large portion of bryozoan colonies (and biodiversity) can be overlooked if not specifically addressed when analysing coralligenous build-ups, due to their peculiar small-scale complexity and microhabitat diversification.

Bryozoans are known to play a relevant role in the coralligenous build-ups being among the most common and important animal constituents (e.g. Ballesteros 2006). Following Ferrigno et al. (2024), with 31 occurrences, bryozoans represent the third most reported group from coralligenous communities in a set of 339 papers published in the time interval 1965–2022. Pérès and Picard (1964) had already remarked on the importance of bryozoans in this habitat, and Hong (1980) highlighted that they represent the main animal group contributing to the edification of the bioconcretion and the filling of empty spaces. However, quantitative information on their actual contribution is absent. The only available estimate is provided by True (1970), who found that, in the Marseille area, bryozoans accounted for merely 0.6–5% of the total biomass (estimated at 500–1000 g/m² dry weight), but contributed a remarkable 5–33% of the carbonate production, totalling 1300–6250 g/m².

Data on biodiversity are less so scant, but mostly restricted to western Mediterranean localities, and especially to its northwestern part (Hong 1980, 1982, 1983; Laubier 1966; Harmelin 1976, 2017; Ballesteros et al. 1993) with a few more recent information on the Adriatic Sea (Novosel et al. 2004; RAC/SPA – UNEP/MAP 2014) and partly on the northeastern Ionian Sea (Mercurio et al. 2024; Corriero et al. 2025). Some data are also available for southwestern Ionian Sea (e.g. Rosso and Sanfilippo 2009; Rosso et al. 2023;

Donato et al. 2024), whereas main gaps exist for the Aegean and the Levantine Sea (e.g. Çinar et al. 2020).

In this context, the present paper aims to (1) describe the bryozoan community associated with coralligenous build-ups off Marzamemi (Sicily, Italy), in order to improve the understanding of coralligenous bryozoan diversity in the area, and (2) compare this bryozoan diversity with that of other coralligenous communities, in order to detect possible spatial/ecological variability within the Mediterranean Sea.

Materials and methods

The studied build-ups originate from an area off Marzamemi (southeastern Sicily, western Ionian Sea) situated between 33.5 and 37.2 m depth (Fig. 1, Table 1) below the local distribution of the *Posidonia oceanica* meadow, which was preliminarily surveyed through the FISIR_04543 project, CRESCIBLUREEF—Grown in the Blue: New Technologies for Knowledge and Conservation of Mediterranean Reefs (see Varzi et al. 2023).

The landscape is characterised by loosely to closely spaced discrete columnar coralligenous bioconstructions emerging from a biogenic coarse-grained seafloor of living maerl rhodoliths and locally grading into the hybrid bank coralligenous morphotype (Fig. 2). All build-ups already analysed from the area showed coralline algae as the main organism bioconstructors followed by serpulids and bryozoans, a remarkable primary and secondary porosity offering surfaces for bryozoan colonisation, and the occurrence of micrite infills (Di Geronimo et al. 2002; Bracchi et al. 2022; Cipriani et al. 2024; Bazzicalupo et al. 2025).

Sampling activities were carried out during the second field survey of the project, in early August 2021. Two entire coralligenous build-ups were collected and additional eight scraped samples, obtained manually by scuba diving, by detaching a surface layer of the bioconstruction as uniformly as possible.

Table 1 List of the investigated build-ups off Marzamemi (SE Sicily, western Ionian Sea). Location, depth (m), coralligenous build-up (C) morphotype are indicated

Build-ups	Location	Depth (m)	C morphotype
A	36°43.454' N; 15°09.657' E	37.2	Discrete build-ups
B	36°43.394' N; 15°09.469' E	36.2	Hybrid bank
C*	36°43.394' N; 15°09.469' E	36.2	Discrete build-ups
D	36°43.394' N; 15°09.469' E	36.2	Hybrid bank
E*	36°43.454' N; 15°09.657' E	36.7	Hybrid bank
F	36°43.394' N; 15°09.469' E	33.5	Hybrid bank

Asterisks (*) indicate build-ups that were entirely collected; all others were scraped

The two build-ups were obtained from areas with distinct coralligenous morphotypes: one from the hybrid banks (build-up C, sometimes reported as sample 7c; e.g. Bracchi et al. 2022, 2025) and one from the discrete build-ups (build-up E, sometimes reported as sample 21c; e.g. Bracchi et al. 2022, 2025). The scraped samples were collected from four build-ups—one from the area with discrete build-ups (build-up A) and three from the area with hybrid banks (build-ups B, D, and F)—by scraping two 400 cm² surfaces, one from the upper and one from the lower part of each build-up. Bryozoans were detected, often separated and identified under Zeiss Discovery 8 stereomicroscopes with different magnification configurations at the Paleontology Laboratory of the Department of Biological, Geological and Environmental Sciences (DSBGA). Selected colonies were examined untreated and/or cleaned from their organic tissues, but uncoated under a Tescan Vega 2 LMU, low vacuum scanning electron microscopy (SEM) at the Microscopical Laboratory of the same Department. Images were generated using back-scattered electrons. For the present study, only bryozoan colonies that were still attached to their substratum—either to the skeletons and skeletonised organisms forming the bioconstruction, or to organisms of the canopy—and

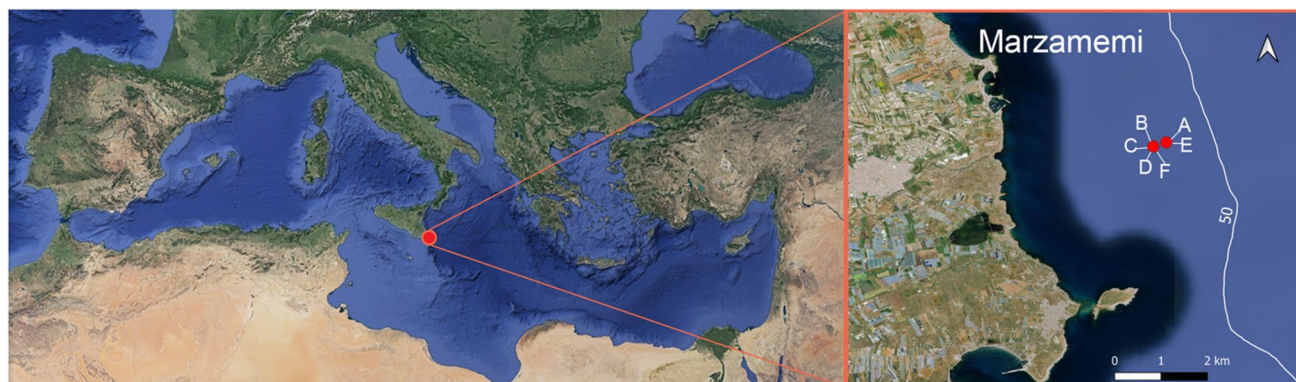


Fig. 1 Location of the investigated area off Marzamemi, SE Sicily, western Ionian Sea within the Mediterranean on the left, and its enlargement on the right

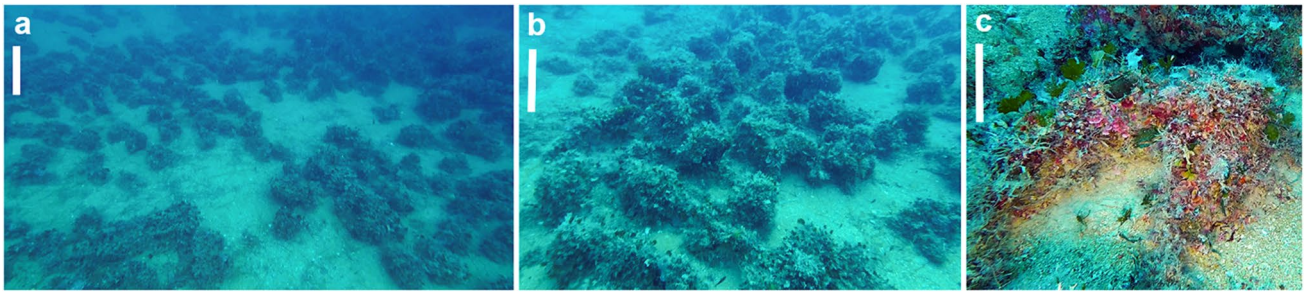


Fig. 2 The seascape at the sampling site at ca 36 m depth. **a** general aspect showing differently clustered build-ups; **b** cluster of closely spaced build-ups; **c** close-up of a build-up with a dense canopy mostly consisting of fleshy algae. Scale bars, 1 m (**a**, **b**); 10 cm (**c**)

were alive at the time of sampling, i.e. contained soft tissues in at least some zooids, were considered. Colonies were scored only if they included the ancestrula and/or the periancestrular area. Detached/broken fragments were considered when including alive modules and scored one only when no further colony of the same species was present in the sample. All species are listed (Supplementary Table 1) and synthetic information per build-up is provided in Table 2. To provide a synthetic indication of bryozoan diversity, the Shannon–Wiener index was calculated for each examined build-up.

The material is housed in the Palaeontological Museum (PMC) of the DSBGA, University of Catania, in the CBR Rosso bryozoan collection. Catalogue numbers are reported for several of these species illustrated with SEM photos. All species names provided in the tables (Supplementary Table 1, Table 3) are reported in the text without authority, that is, reported only for a few additional/synonym species not included there.

Analysis of bryozoan diversity in the Mediterranean is based on main monographs reporting bryozoan species

associated with coralligenous habitats, as well as on previous papers dealing with overall coralligenous biodiversity and listing bryozoan species (Table 2 and references therein). Constructing a comprehensive and reliable list of all bryozoan species reported for this habitat was challenging especially taking into consideration the relevant changes in taxonomy and species concept fostered by technological advances, including the use of SEM observations during the last six decades (see for instance comments in Harmelin and Rosso 2023; Rosso et al. 2025). Therefore, taxonomy was largely updated using indications about synonymies already reported in the checklists for Italian and Mediterranean bryozoans (Rosso et al. 2010; Rosso and Di Martino 2016, 2023), and/or in some particular papers published in the last years (see Results). The bryozoan web page (<https://bryozoa.net/>, accessed several times during August 2025) and the WoRMS–World Register of Marine Species (WoRMS Editorial Board 2025, <https://www.marinespecies.org/>, accessed in the same period) were also checked.

Table 2 List of bryozoan orders from off Marzamemi (SE Sicily, western Ionian Sea) with indication of the total number of species and colonies found in each of the six examined build-ups (A–F), reported as absolute numbers and percentages. The total number of species and colonies is also provided

Build-up	Number							Percentages					
	A	B	C	D	E	F	Total	A	B	C	D	E	F
Species													
Cyclostomatids	8	18	14	12	15	16	24	15.4	25.4	25.5	22.6	17.6	22.9
Ctenostomatids	3	3	2	1	5	2	6	5.8	4.2	3.6	1.9	5.9	2.9
Cheilostomatids	41	50	39	40	65	52	97	78.8	70.4	70.9	75.5	76.5	74.3
Total	52	71	55	53	85	70	127						
Colonies													
Cyclostomatids	41	106	116	86	330	172	851	13.8	22.3	35.3	32.0	17.5	28.6
Ctenostomatids	8	6	6	1	70	12	103	2.7	1.3	1.8	0.4	3.7	2.0
Cheilostomatids	248	363	207	182	1490	417	2907	83.5	76.4	62.9	67.7	78.8	69.4
Total	297	475	329	269	1890	601	3861						

Table 3 List of bryozoan species reported from the coralligenous in different localities of the Mediterranean Sea. B+: Ballesteros et al. (1993); C+: Corriero et al. (2025); G: Gautier (1962); H-1: Harmelin (1976); H-2: Harmelin (2017); Ho: Hong (1980, 1982); L: Laubier (1966); N+: Novosel et al. (2004) + RAC/SPA – UNEP/MAP (2014); R+: Rosso et al.: this paper, also including data in: Rosso & Sanfilippo (2009), Rosso et al. (2023) and Donato et al. (2024); Z: Zabala (1986). Authorities for some species are abbreviated as follows: Chimenz Gusso and Soule 2003; Chimenz Gusso & Soule, 2003; Haugen et al. 2020; Haugen, Novosel, Wisshak & Berning, 2020; López de la Cuadra and García-Gómez 1991; López de la Cuadra & García-

Gómez, 1991; Madurell et al. 2013; Madurell, Zabala, Dominguez-Carrió & Gili, 2013; Reverter-Gil and Fernández-Pulpeiro 1997; Reverter-Gil & Fernandez-Pulpeiro, 1997; Reverter-Gil et al. 2012; Reverter-Gil, Souto & Fernández-Pulpeiro, 2012; Reverter-Gil et al. 2016; Reverter-Gil, Souto, Novosel & Tilbrook, 2016; Souto et al. 2010; Souto, Fernández-Pulpeiro & Reverter-Gil, 2010; Souto et al. 2019; Souto, Nascimento, Reverter-Gil & Vieira, 2019. Note that some papers (Gautier 1962 and Corriero et al. 2025) only include cheilostomes, while ctenostomes are missing in Harmelin (1976, 2017) and in Corriero et al. (2025). Note also that different papers include different depth ranges in shallower or deeper settings

Sea	Western Mediterranean							Adriatic	Ionian	
Papers	Z	G	L	B+	Ha-1	Ho	Ha-2	N+	C+	R+
SpeciesDepth range (m)	< 60	?	24–30	40–95	14–75	10–34	16–40	10–40	25–35	33–60
<i>Annectocyma major</i> (Johnston, 1847)	*			*	*	*				*
<i>Annectocyma tubulosa</i> (Busk, 1875)	*			*	*	*				*
<i>Cardioecia' watersi</i> (O'Donoghue & De Watteville, 1939)	*				*	*				*
<i>Crisia cuneata</i> Maplestone, 1905					*	*				
<i>Crisia fistulosa</i> Heller, 1867	*			*	*	*	*			*
<i>Crisia occidentalis</i> Trask, 1857										*
<i>Crisia oranensis</i> Waters, 1916						*				
<i>Crisia pyrula</i> Harmelin, 1990					*	*	*			*
<i>Crisia ramosa</i> Harmer, 1891	*				*	*				*
<i>Crisia recurva</i> Heller, 1867							*			
<i>Crisia sigmoidea</i> Waters, 1916	*			*	*	*				*
<i>Diplosolen obelius</i> (Johnston, 1838)	*		*	*	*	*	*	*		*
<i>Disporella hispida</i> (Fleming, 1828)			*	*				*		*
<i>Disporella</i> sp. A										*
<i>Disporella neapolitana</i> (Waters, 1918)					*		*			
<i>Entalophoroecia deflexa</i> (Couch, 1842)	*			*	*	*				
<i>Entalophoroecia gracilis</i> Harmelin, 1976	*			*	*					
<i>Entalophoroecia robusta</i> Harmelin, 1976	*			*	*	*				
<i>Eurystrotos compacta</i> (Norman, 1866)					*	*	*			
<i>Eurystrotos occulta</i> (Harmelin, 1976)					*			*		*
<i>Filicrisia geniculata</i> (Milne-Edwards, 1838)					*	*	*			*
<i>Fron dipora verrucosa</i> (Lamouroux, 1821)	*		*	*		*		*		*
<i>Harmelinopora indistincta</i> (Canu & Bassler, 1929)	*			*	*	*				*
<i>Hornera frondiculata</i> Lamarck, 1816	*			*	*					
<i>Idmidronea triforis</i> (Heller, 1867)	*			*	*	*	*	*		*
<i>Idmidronea coerulea</i> Harmelin, 1976	*									
<i>Liripora amphorae</i> (Harmelin, 1976)					*					
<i>Liripora violacea</i> (Harmelin, 1976)					*					
<i>Mecynoecia delicatula</i> (Busk, 1875)	*				*	*	*			*
<i>'Microecia' occulta</i> Harmelin, 1976						*				*
<i>Patinella</i> cf. <i>mediterranea</i> (de Blainville, 1834)										*
<i>Patinella radiata</i> (Audouin & Savigny, 1826)			*			*	*	*		*
<i>Plagioecia dorsalis</i> (Waters, 1879)	*				*					
<i>Plagioecia inoedificata</i> (Jullien, 1882)					*	*				
<i>Plagioecia patina</i> (Lamarck, 1816)	*				*	*				*
<i>Plagioecia platydiscus</i> Harmelin, 1976										*
<i>Plagioecia sarniensis</i> (Norman, 1864)				*	*	*				*
<i>Platonea stoechas</i> Harmelin, 1976			*	*	*					*
? <i>Stomatopora</i> sp. A										*
<i>Tervia irregularis</i> (Meneghini, 1844)					*					

Table 3 (continued)

Sea	Western Mediterranean							Adriatic		Ionian
	Z	G	L	B+	Ha-1	Ho	Ha-2	N+	C+	R+
Papers	< 60	?	24–30	40–95	14–75	10–34	16–40	10–40	25–35	33–60
<i>Tubulipora aperta</i> Harmer, 1898					*	*				*
<i>Tubulipora hemiphragmata</i> Harmelin, 1976			*		*	*	*			*
<i>Tubulipora liliacea</i> (Pallas, 1766)	*			*	*	*		*		*
<i>Tubulipora plumosa</i> Harmer, 1898	*			*	*	*				*
<i>Tubulipora ziczac</i> Harmelin, 1976					*					
Cyclostomes	20	—	6	17	33	27	11	7	0	29
<i>Alcyonidium gelatinosum</i> (Linnaeus, 1761)										*
<i>Amathia delicatula</i> Souto et al. 2010										*
<i>Amathia lendigera</i> (Linnaeus, 1758)				*						
<i>Amathia pruvoti</i> (Calvet, 1911)	*		*							
<i>Bantariella verticillata</i> (Heller, 1867)	*					*				
<i>Bowerbankia gracilis</i> Leidy, 1855				*						
<i>Mimosella gracilis</i> Hincks, 1851			*							*
<i>Nolella dilatata</i> (Hincks, 1860)	*		*							*
<i>Nolella stipata</i> Gosse, 1855	*			*		*				
<i>Pherusella tubulosa</i> (Ellis & Solander, 1786)			*							*
<i>Walkeria tuberosa</i> (Heller, 1867)			*	*				*		*
Ctenostomes	4	—	5	4	0	2	0	1	0	6
<i>Adeonella pallasii</i> (Heller, 1867)								*		
<i>Adeonella calveti</i> Canu & Bassler, 1930	*	*	*		*		*		*	
<i>Aetea anguina</i> (Linnaeus, 1758)					*					
<i>Aetea longicollis</i> (Jullien, 1903)	*									
<i>Aetea sica</i> (Couch, 1844)			*	*	*	*	*	*		
<i>Aetea truncata</i> (Landsborough, 1852)	*		*	*	*			*		*
<i>Allantopora minuta</i> (Harmelin, 1973)					*					
<i>Amphiblestrum lyrulatum</i> (Calvet, 1907)	*									
<i>Aplousina capriensis</i> (Waters, 1898)										*
<i>Arthropoma cecilii</i> (Audouin & Savigny, 1826)		*	*	*		*				*
<i>Beania cylindrica</i> (Hincks, 1886)	*	*	*	*?						*
<i>Beania hirtissima</i> (Heller, 1867)	*	*	*		*	*		*		*
<i>Beania mediterranea</i> Souto, Nascimento, Reverter-Gil & Vieira, 2019	*	*	*	*	*	*	*	*	*	*
<i>Beania mirabilis</i> Johnston, 1840					*	*		*		*
<i>Bertorsonidra prenanti</i> (Gautier 1955)		*	*							
<i>Bryocryptella koelheri</i> (Calvet, 1896)		*								
<i>Bryocryptella tubulata</i> (Busk, 1861)			*							
<i>Buffonellaria</i> sp.				*				*		
<i>Bugula gautieri</i> Ryland, 1962					*				*	
<i>Bugula plumosa</i> (Pallas, 1766)								*		
<i>Bugulina calathus calathus</i> (Norman, 1868) *	*	*	*		*			*		
<i>Bugulina</i> cf. <i>flabellata</i> (Thompson in Gray, 1848)										*
<i>Bugulina flabellata</i> (Thompson in Gray, 1848)	*	*	*		*					
<i>Bugulina</i> cf. <i>fulva</i> (Ryland, 1960)	*					*		*		*
<i>Bugulina simplex</i> (Hincks, 1886)	*				*					
<i>Bugulina spicata</i> (Hincks, 1886)	*	*							*	
<i>Bugulina turbinata</i> (Alder, 1857)	*	*	*		*					
<i>Buskea dichotoma</i> (Hincks, 1862)	*	*		*	*					
<i>Buskea nitida</i> Heller, 1867	*	*			*					
<i>Caberea boryi</i> (Audouin & Savigny, 1826)	*	*	*	*	*	*	*	*	*	*
<i>Callopora dumerilii dumerilii</i> (Audouin & Savigny, 1826) *	*	*	*	*	*	*		*		*

Table 3 (continued)

Sea	Western Mediterranean							Adriatic	Ionian	
	Z	G	L	B+	Ha-1	Ho	Ha-2	N+	C+	R+
Papers	< 60	?	24-30	40-75	14-75	10-34	16-40	10-40	25-35	33-60
<i>Callopora dumerilii pouillei</i> (Alder, 1857)	*	*								
<i>Callopora lineata</i> (Linnaeus, 1767)	*	*						*		
<i>Calpensia nobilis</i> (Esper, 1796)	*	*							*	*
<i>Calypotheca rugosa</i> Hayward, 1974				*?		*				*
<i>Cellaria fistulosa</i> (Linnaeus, 1758)	*	*	*		*				*	
<i>Cellaria normani</i> (Hastings, 1947)	*				*	*				
<i>Cellaria salicornioides</i> Lamouroux, 1816	*	*		*	*				*	*
<i>Cellepora adriatica</i> Hayward & McKinney, 2002	*	*	*			*				
<i>Cellepora pumicosa</i> (Pallas, 1766)				*		*		*		*
<i>Celleporina caminata</i> (Waters, 1879)	*	*	*	*	*	*	*	*	*	*
<i>Celleporina hassallii</i> (Johnston, 1847)			*		*			*	*	*
<i>Celleporina lucida</i> (Hincks, 1880)	*			*	*	*		*		
<i>Celleporina siphuncula</i> Hayward & McKinney, 2002										*
<i>Celleporina tubulosa</i> (Hincks, 1880)	*							*		
<i>Celleporina</i> sp. A, aff. <i>C. canariensis</i>										*
<i>Celleporina</i> sp. B										*
<i>Celleporina</i> sp. C										*
<i>Chartella papyrea</i> (Pallas, 1766)	*	*								*
<i>Chartella tenella</i> (Hincks, 1887)	*		*							
<i>Chlidonia pyriformis</i> (Bertoloni, 1810)					*	*				
<i>Chorizopora brongniartii</i> (Audouin & Savigny, 1826)		*		*	*	*	*	*		*
<i>Collarina</i> sp.								*		
<i>Copidozoum planum</i> (Hincks, 1880)	*	*	*		*			*	*	*
<i>Copidozoum tenuirostre</i> (Hincks, 1880)	*	*			*					*
<i>Corbulella maderensis</i> (Waters, 1898)	*			*	*	*		*		*
<i>Coronellina fagei</i> (Gautier, 1962)		*			*	*				*
<i>Cradoscrupocellaria hirsuta</i> (Jullien & Calvet, 1903)										*
<i>Cradoscrupocellaria macrorhyncha</i> (Gautier, 1962)	*	*								*
<i>Cradoscrupocellaria</i> sp.		*		*?	*					
<i>Crassimarginatella matildae</i> Pica & Berning, 2022		*	*		*	*		*		*
<i>Crassimarginatella solidula</i> (Hincks, 1860)				*	*					*
<i>Cribellopora trichotoma</i> (Waters, 1919)	*	*		*						
<i>Cribrilaria hincksi</i> (Friedl, 1917)		*		*	*		*	*		*
<i>Cribrilaria innominata</i> (Couch, 1844)	*			*	*	*		*		
<i>Cribrilaria ps. pseudoradiata</i> (Harmelin & Aristegui, 1988)										*
<i>Cribrilaria radiata</i> (Moll, 1803)	*	*	*	*	*	*	*	*	*	*
<i>Cribrilaria venusta</i> Canu & Bassler, 1925		*			*	*				*
<i>Cryptosula pallasiana</i> (Moll, 1803)										*
<i>Dentiporella sardonica</i> (Waters, 1879)	*	*	*		*	*	*			*
<i>Ellisina gautieri</i> Fernández Pulpeiro & Reverter Gil, 1993	*	*			*					*
<i>Epistomia bursaria</i> (Linnaeus, 1758)		*	*			*				
<i>Escharella immersa</i> (Fleming, 1828)					*					
<i>Escharella octodentata</i> (Hincks, 1880)		*								
<i>Escharella rylandi</i> Geraci, 1974	*									
<i>Escharella variolosa</i> (Johnston, 1838)		*		*	*	*				
<i>Escharella ventricosa</i> (Hassall, 1842)	*	*								
<i>Escharina protecta</i> Zabala, Maluquer & Harmelin, 1993	*				*	*		*		*
<i>Escharina vulgaris</i> (Moll, 1803)	*	*		*	*	*	*	*		*
<i>Escharoides coccinea</i> (Abildgaard, 1806)	*	*	*	*	*	*	*	*		*

Table 3 (continued)

Sea	Western Mediterranean							Adriatic	Ionian	
	Z	G	L	B+	Ha-1	Ho	Ha-2	N+	C+	R+
Papers	< 60	?	24–30	40–95	14–75	10–34	16–40	10–40	25–35	33–60
<i>Escharoides mamillata</i> (Wood, 1844)										*
<i>Fenestrulina</i> sp.	*	*	*		*	*		*		
<i>Figularia figularis</i> (Johnston, 1847)	*	*	*	*	*	*				*
<i>Glabrilaria orient. orientalis</i> (Harmelin & Aristegui, 1988)										*
<i>Glabrilaria pedunculata</i> (Gautier, 1956)		*			*			*		*
<i>Gregarinidra gregaria</i> (Heller, 1867)	*		*	*		*		*		*
<i>Hagiosynodos latus</i> (Busk, 1856)				*		*		*		
<i>Haplopoma bimucronatum bimucronatum</i> (Moll, 1803)	*	*								
<i>Haplopoma impressum</i> (Audouin & Savigny, 1826)	*	*			*		*	*		*
<i>Hemicyclopora neatonensis</i> Harmelin & Rosso, 2023										*
<i>Herentia hyndmanni</i> (Johnston, 1847)					*					*
<i>Herentia majae</i> Berning, Tilbrook & Rosso, 2008								*		
<i>Hincksina</i> sp.	*	*		*	*	*				
<i>Hippaliosina depressa</i> (Busk, 1854)									*	
<i>Hippellozoon mediterraneum</i> (Waters, 1895)	*	*								*
<i>Hippomenella mucronelliformis</i> (Waters, 1899)	*			*		*				*
<i>Hippopleurifera pulchra</i> (Manzoni, 1870)	*	*			*	*				*
<i>Hippopodina ambita</i> (Hayward, 1974)										*
<i>Hippoporina lineolifera</i> (Hincks, 1886)		*								
<i>Hippoporina pertusa</i> (Esper, 1796)	*	*								*
<i>Hippothoa divaricata</i> Lamouroux, 1821		*								
<i>Hippothoa flagellum</i> Manzoni, 1870				*	*					*
<i>Lagenipora lepralioides</i> (Norman, 1868)								*		
<i>Margaretta cereoides</i> (Ellis & Solander, 1786)	*	*		*	*				*	*
<i>Membraniporella nitida</i> (Johnston, 1838)	*	*		*			*			
<i>Metropieriella mesogeia</i> Berning, Achilleos & Wisshak, 2019	*	*			*	*	*	*		*
<i>Micropora coriacea</i> (Johnston, 1791)	*	*		*						*
<i>Microporella appendiculata</i> (Heller, 1867)	*	*	*	*?				*?	*	
<i>Microporella bicollaris</i> Di Martino & Rosso, 2021										*
<i>Microporella modesta</i> Di Martino, Taylor & Gordon, 2020	*	*	*		*		*			*
<i>Microporella verrucosa</i> (Peach, 1868)	*				*	*				
<i>Microporella</i> sp.				*		*		*		
<i>Mollia circumcincta</i> (Heller, 1867)	*	*						*		*
<i>Mollia multijuncta</i> (Waters, 1879)						*				
<i>Mollia patellaria</i> (Moll, 1803)		*	*	*	*	*	*	*	*	*
<i>Myriapora truncata</i> (Pallas, 1766)	*	*	*	*	*	*	*	*	*	*
<i>Omalosecosa ramulosa</i> (Linnaeus, 1767)	*	*	*		*	*				
<i>Onychocella marioni</i> (Jullien, 1881)	*	*	*		*	*				*
<i>Palmiskenea gautieri</i> Madurell et al., 2013										*
<i>Parasmittina raigii</i> (Audouin & Savigny, 1826)		*						*?		*
<i>Parasmittina rouvillei</i> (Calvet, 1902)	*	*			*		*		*	
<i>Parasmittina parsevalii</i> (Audouin & Savigny, 1826)						*				
<i>Parellisina curvirostris</i> (Hincks, 1862)	*	*		*						*
<i>Pentapora fascialis</i> (Pallas, 1766)	*	*	*	*	*	*	*	*	*	
<i>Pentapora ottomuellieriana</i> (Moll, 1803)			*			*				
<i>Phoceana columnaris</i> Jullien, 1903		*								
<i>Plesiocleidochasma mediterraneum</i> Chimenz Gusso & Soule, 2003										*
<i>Porella concinna concinna</i> (Busk, 1854)	*	*	*		*					*

Table 3 (continued)

Sea	Western Mediterranean							Adriatic	Ionian	
	Z	G	L	B+	Ha-1	Ho	Ha-2	N+	C+	R+
Papers	< 60	?	24–30	40–95	14–75	10–34	16–40	10–40	25–35	33–60
<i>Porella concinna tubulata</i> Calvet, 1927		*	*							
<i>Porella minuta</i> (Norman, 1868)		*			*	*				
<i>Prenantia cheilostoma</i> (Manzoni, 1869)				*	*		*	*		*
<i>Prenantia inerma</i> (Calvet, 1906)					*	*				*
<i>Puellina gattyae</i> (Landsborough, 1852)	*	*			*	*	*	*		*
<i>Puellina setosa</i> (Waters, 1899)					*	*				*
<i>Reptadeonella violacea</i> (Johnston, 1847)	*	*				*		*	*	*
<i>Reptadeonella zabalai</i> Haugen et al., 2020										*
<i>Reteporella aporosa</i> (Waters, 1894)		*								*
<i>Reteporella complanata</i> (Waters, 1894)	*	*								
<i>Reteporella couchii biaviculata</i> (Waters, 1894)		*								
<i>Reteporella couchii couchii</i> (Hincks, 1878)	*	*	*	*	*				*	*
<i>Reteporella elegans</i> Harmelin, 1976										*
<i>Reteporella feuerborni</i> (Hass, 1848)				*						
<i>Reteporella grimaldii</i> (Jullien, 1903)	*	*		*	*	*	*	*		*
<i>Reteporella mediterranea</i> (Smitt, 1867)	*	*	*		*	*				*
<i>Reteporella soudbournensis</i> (Gautier, 1962)		*								*
<i>Rhynchozoon bispinosum</i> (Johnston, 1847)	*	*		*						
<i>Rhynchozoon digitatum</i> (Waters, 1879)	*	*			*	*				
<i>Rhynchozoon neapolitanum</i> Gautier, 1962		*		*		*				*
<i>Rhynchozoon pseudodigitatum</i> Zabala & Maluquer, 1988				*						*
<i>Rhynchozoon quadrispinatum</i> Zabala & Maluquer, 1988				*						
<i>Rosselliana rossellii</i> (Audouin & Savigny, 1826)		*	*							
<i>Savignyella lafontii</i> (Audouin & Savigny, 1826)	*	*	*		*	*	*	*	*	
<i>Schizobrachiella sanguinea</i> (Norman, 1868)	*			*	*	*		*		
<i>Schizomavella</i> (S.) <i>asymetrica</i> (Calvet, 1927)					*		*		*	
<i>Schizomavella</i> (S.) <i>cornuta</i> (Heller, 1867)	*	*	*	*	*	*	*	*	*	*
<i>Schizomavella</i> (S.) cf. <i>halimedeae</i> (Gautier 1955)						*	*	*		*
<i>Schizomavella</i> (S.) <i>hastata</i> (Hincks, 1862)	*	*		*	*					*
<i>Schizomavella</i> (S.) <i>hirsuta</i> (Calvet, 1927)	*	*								
<i>Schizomavella</i> (S.) <i>linearis</i> (Hassall, 1841)	*	*	*	*	*	*	*			*
<i>Schizomavella</i> (S.) <i>mamillata</i> (Hincks, 1880)	*	*		*	*	*	*	*	*	
<i>Schizomavella</i> (S.) <i>rudis</i> (Manzoni, 1870)				*						*
<i>Schizomavella</i> (S.) <i>subsolana</i> Hayward & McKinney, 2002										*
<i>Schizomavella</i> (S.) <i>tubulata</i> Reverter-Gil et al., 2016										*
<i>Schizomavella</i> (Calvetomavella) <i>biancae</i> Pica & Berning, 2022	*	*	*	*	*	*			*	*
<i>Schizomavella</i> sp. A										*
<i>Schizoporella dunkeri</i> (Reuss, 1848)	*	*		*	*			*	*	
<i>Schizoporella magnifica</i> (Hincks, 1886)	*	*			*	*		*		
<i>Schizoporella mutabilis</i> Calvet, 1927	*	*								
<i>Schizoporella unicornis</i> (Johnston, 1844)		*	*							
<i>Schizoretepora serratimargo</i> (Hincks, 1886)				*				*	*	
<i>Schizoretepora solanderia</i> (Risso, 1826)		*		*						*
<i>Schizotheca fissa</i> (Busk, 1856)	*	*		*	*	*				*
<i>Scruparia ambigua</i> (d'Orbigny, 1841)					*					
<i>Scrupocaberea maderensis</i> (Busk, 1860)	*			*	*	*			*	
<i>Scrupocellaria aegeensis</i> Harmelin, 1969				*						*
<i>Scrupocellaria delilii</i> (Audouin & Savigny, 1826)	*			*				*		*
<i>Scrupocellaria incurvata</i> Waters, 1896										*

Table 3 (continued)

Sea	Western Mediterranean							Adriatic		Ionian
	Z	G	L	B+	Ha-1	Ho	Ha-2	N+	C+	R+
Papers										
SpeciesDepth range (m)	< 60	?	24–30	40–75	14–75	10–34	16–40	10–40	25–35	33–60
<i>Scrupocellaria scruposa</i> Busk, 1851		*	*	*	*			*	*	*
<i>Scrupocellaria scruposa</i> (Linnaeus, 1758)	*	*	*		*			*		*
<i>Scutocyclopora dentata</i> (López Cuadra & Garcia-G., 1991)										*
<i>Securiflustra securifrons</i> (Pallas, 1766)	*									
<i>Smittina cervicornis</i> (Pallas, 1766)	*	*	*	*	*			*	*	
<i>Smittina colleti</i> (Jullien, 1903)		*								
<i>Smittina landsborovii</i> (Johnston, 1847)		*								
<i>Smittoidea marmorea</i> (Hincks, 1877)	*				*			*		
<i>Smittoidea ophidiana</i> (Waters, 1879)	*	*			*					
<i>Smittoidea reticulata</i> (MacGillivray, 1842)	*	*	*	*	*	*		*		*
<i>Stephanollona armata</i> (Hincks, 1861)	*	*	*	*		*				*
<i>Stephanotheca arrogata</i> (Waters, 1879)	*									
<i>Stephanotheca leontiniensis</i> (Waters, 1878)	*	*								
<i>Stephanotheca monoecensis</i> (Calvet, 1927)	*	*			*					
<i>Synnotum egyptiacum</i> (Audouin & Savigny, 1826)	*	*			*	*		*		*
<i>Terwasipora complanata</i> (Norman, 1864)										*
<i>Therenia rosei</i> Berning, Tilbrook & Rosso, 2008	*									*
<i>Turbicellepora coronopus</i> (Wood, 1844)	*	*			*	*				*
<i>Turbicellepora coronopusoida</i> (Calvet, 1931)		*		*	*	*				*
<i>Turbicellepora incrassata</i> (Lamrck, 1816)	*	*	*	*	*	*	*			
<i>Turbicellepora torquata</i> Hayward, 1978										*
<i>Turbicellepora tubigera</i> (Busk, 1859)	*									
<i>Umbonula ovicellata</i> Hastings, 1944							*			*
<i>Watersipora subtorquata</i> (d'Orbigny, 1852)				*						*
Cheilostomes	105	112	52	69	95	71	30	63	31	110
Bryozoan species	129	112	63	90	128	100	41	71	31	145

Results

Bryozoan diversity of the Marzamemi coralligenous build-ups

A total of 127 bryozoan species (Fig. 3, Tables 2 and 3, Supplementary Table 1), some of which figured (Figs. 4, 5, 6, 7, 8, 9, 10, and 11), were detected thriving in and/or on the examined build-ups, including 24 cyclostomes, 6 ctenostomes, and 97 cheilostomes accounting for 18.9%, 4.7%, and 76.4%, respectively. However, species richness is remarkably lower when looking at single build-ups with a range between 52 (build-up A) and 85 (build-up E) species. Cheilostomes always dominate (70.4–78.8%) being represented by 39–41 species in the less diversified build-ups (C, D and A) up to 65 species in the build-up E with intermediate numbers (50 and 52 species) in the B and F build-ups, respectively (Fig. 3; Table 2). Cyclostomes follow with 8–18 species (and

percentages ranging from 15.4 to 25.5), whereas ctenostomes are decidedly subordinate with only 1–5 species per build-up and ranges of 1.9–5.9%.

A core group of 20 species (15.7% of the total assemblage) was shared by all build-ups. These include five cyclostomes, i.e. *Crisia fistulosa*, *C. ramosa*, *Diplosolen obelius*, *Disporella hispida*, and *Mecynoecia delicatula*, the only ctenostome *Amathia delicatula*, and 14 cheilostomes, i.e. *Aetea truncata*, *Celleporina caminata*, *C. siphuncula*, *Chorizopora brongniartii*, *Copidozoon planum*, *Escharina vulgaris*, *Margaretta cereoides*, *Metroperiella mesogeia*, *Microporella bicollaris*, *M. modesta*, *Plesiocleidochasma mediterraneum*, *Prenantia cheilostoma*, *Puellina gattyae*, and *Scrupocellaria delilii*. Many other species occurred in 3–5 build-ups (46 species = 36.2%) but a relevant number were restricted to only 2 build-ups (23 species, accounting for 18.1%) or even a single one (38 species, accounting for 29.9%). This last group almost entirely consists of

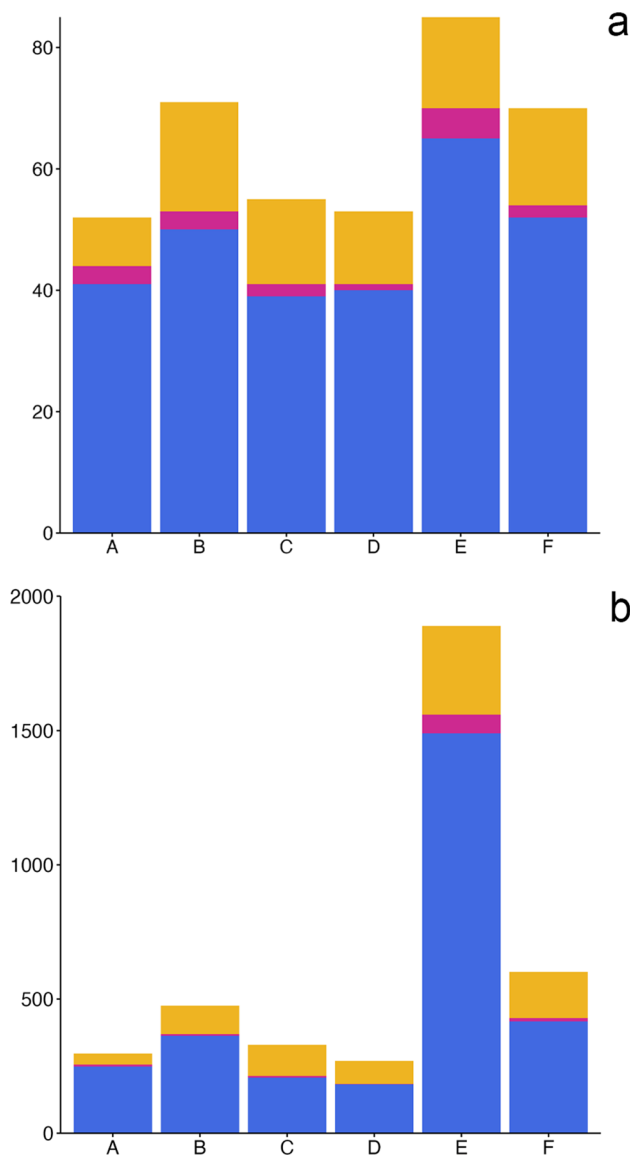


Fig. 3 Histograms showing bryozoan diversity in the six examined build-ups, indicated with the letters A–F. **a** Number of species; **b** number of colonies. Cyclostomes (orange); ctenostomes (purple); cheilostomes (blue)

cheilostomes, with 34 species. However, when looking at the number of colonies, although limited in number, the most frequent species account for a large part of the assemblage (56.7%). In contrast, the colony abundance of almost half the species (61) occurring only sporadically, with frequency values of 1 or 2, represents only a subordinate part of the assemblage (overall 7.7%). Although with differences between build-ups, the cheilostomes *C. caminata* and *S. delilii* are the species with the highest abundances, followed by the cyclostomes *M. delicatula* and *C. ramosa* as well as by the cheilostomes *A. truncata*, *C. planum*, and *M. cereoides*, all exceeding 100 colonies out of the almost 3900

found. Values of the Shannon–Wiener index range from 3.33 to 3.35 for build-ups D and A, respectively, and increase to 3.59–3.61 for build-ups E and B, respectively, with intermediate values of 3.45 for C and 3.52 for F.

All bryozoans found were almost unapparent when looking at collected samples. Indeed, except for a few species, such as *M. cereoides*, *M. truncata*, and *Reteporella* spp., which can grow in large colonies, easily recognisable to the naked eye and sometimes even from underwater videos and imaging, colonies are small-sized, usually not exceeding a few to several square millimetres. Except for *M. cereoides* on build-up E (see also Rosso et al. 2023), even large-sized species often occurred with small colonies, rarely a couple of cm in height and/or in diameter. From a morphological point of view, species with encrusting growths largely prevail with 84 species. These mainly consist of “membraniporiform” colonies, i.e. unilaminar, variably outlined patches, and spots (71 species), and to a much lesser extent of celoporiforms (13 species), i.e. thick colonies formed by irregularly superimposed or piled-up autozooids producing knobby to hemispheric or globular morphologies usually on 2- and 3D substrata, respectively. Whereas a plethora of species belonging to several genera constitute the former group, the latter mostly consists of species of the families Celleporidae (*Celleporina* and *Turbicellepora*), Phidoloporidae (*Rhynchozoon*), and Bitectiporidae (*Schizomavella*). Species with erect colonies are less numerous. They are especially represented by flexible species (26), usually dichotomously branched bushes consisting of articulated, variably long internodes. Many of them are biserial (species of the cyclostome genera *Crisia* and *Filicrisia* and some cheilostomes such as *Caberea*, *Cradoscrupocellaria*, *Scrupocellaria*) but a few are pauciserial (*Cellaria*, *Margaretta*). Few species, such as most ctenostomes and the cheilostome genera *Beania*, *Bugulina*, and *Synnotum*, have very slightly mineralised, variably arranged zooids. Erect rigid species (14) are either reteporiform, i.e. possess a reticulate colony, such as species of the genera *Reteporella* and *Hippellozoon*, or vincularian, with small poorly branched, tree-shaped colonies. These latter include some cyclostomes (e.g. *Idmidronea*, and some colonies of *Annectocyma* and *Platonea* and also colonies of *M. delicatula* typically growing as a single or two-to-three, basally branched, short diverging rods) and the cheilostomes *M. truncata* and *Schizoretepora solanderia*.

Except for 10 species and 18 colonies, almost all species and colonies were found still attached to their own substratum in the collected samples. Out of these 117 species, 38 were exclusively found encrusting on the carbonate frame, whereas 20 occurred on fleshy algae and other elements of the canopy, including the erect articulated bryozoan *M. cereoides* (see details in Rosso et al. 2023 for the build-up E). Most of them usually showed low-frequency values and colony numbers, except for a

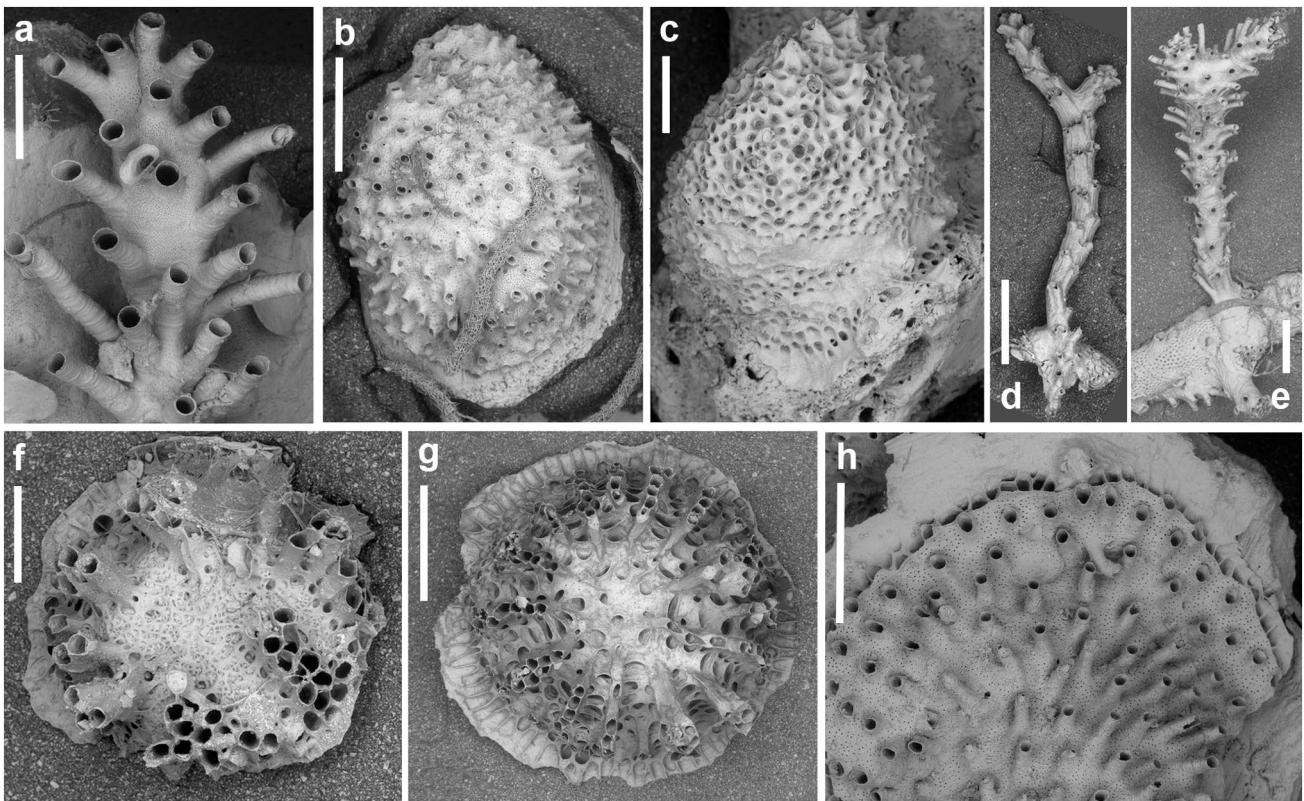


Fig. 4 Selected cyclostome species (1) from the coralligenous off Marzamemi (SE Sicily, Ionian Sea). **a** *Annectocyma major*, PMC Rosso-Collection I. H. B.161.a; **b** *Diplosolen obelius*, PMC. R.I.H. B-12.b; **c** *Disporella* sp. A, PMC Rosso-Collection I. H. B.164.a; **d** *Idmidronea triforis*, PMC Rosso-Collection I. H. B.165.a; **e** *Mecy-*

noecia delicatula, PMC Rosso-Collection I. H. B.50.b; **f** *Patinella mediterranea*, PMC Rosso-Collection I. H. B.166.a; **g** *Patinella radiata*, PMC Rosso-Collection I. H. B.55.b; **h** *Plagioecia sarniensis*, PMC Rosso-Collection I. H. B.49.b. Scale bars, 1 mm (**a, b, d, e, g, h**); 500 μ m (**c, f**)

few ones, including the ctenostome *A. delicatula* and, to a lesser extent, the ctenostome *Walkeria tuberosa*, and the cheilostomes *Haplopoma* cf. *impressum* and *Puellina setosa* among those found in the canopy, and a group of nine cheilostome species (*Calyptotheca rugosa*, *Cribrilaria radiata*, *Coronellina fagei*, *Prenantia inerma*, *Schizotheca fissa*, *Ellisina gautieri*, *Hippopleurifera pulchra*, *Parellisina curvirostris*, and *S. solanderia*) for those restricted to the frame. However, an almost similar number of species (59) have been found on both the mineralised framework and elements of the canopy, usually with a higher number of colonies in the latter. Only a few species show a significantly higher number of colonies in the frame, i.e. the cyclostome *D. obelius*, and the cheilostomes *Beania hirtissima*, *Escharina vulgaris*, *Mollia patellaria*, and *Onychocella marioni* as well as *M. truncata* that was found in the canopy with a single small colony. Further two cheilostomes (*Cribrilaria venusta* and *M. mesogeia*) both occurred with a double number of colonies in the frame rather than in the canopy. It could also be remarked that unmineralised or slightly mineralised species, including ctenostomes and a few cheilostomes, essentially grew

in the canopy. Besides being flexible, species in the canopy often occurred with relatively small colonies and were mostly localised on the more robust and persistent substrata. These included the few mineralised elements, such as *M. cereoides* and slightly skeletonised algae, such as peyssonneliaceans, as well as thick thalli of *Osmundaria volubilis* (Linnaeus) R.A. Norris, and particularly the stems of *Flabellia petiolata* Turra (Nizzamudin), as also reported for the build-up E in Rosso et al. (2023). In the frame, colonies directly encrust coralline algae or other skeletonised organisms including other bryozoans or the tubes of serpulids and rare vermetids. Bryozoans occur either on the outer surface of the build-ups, sometimes with colonies being several cm wide (e.g. the few ones belonging to *H. pulchra*) or within small and large cavities, usually with small colonies.

Bryozoan diversity of the Mediterranean coralligenous habitat

To compile a comprehensive updated list (Table 3) illustrating the bryozoan diversity of the coralligenous habitat in the

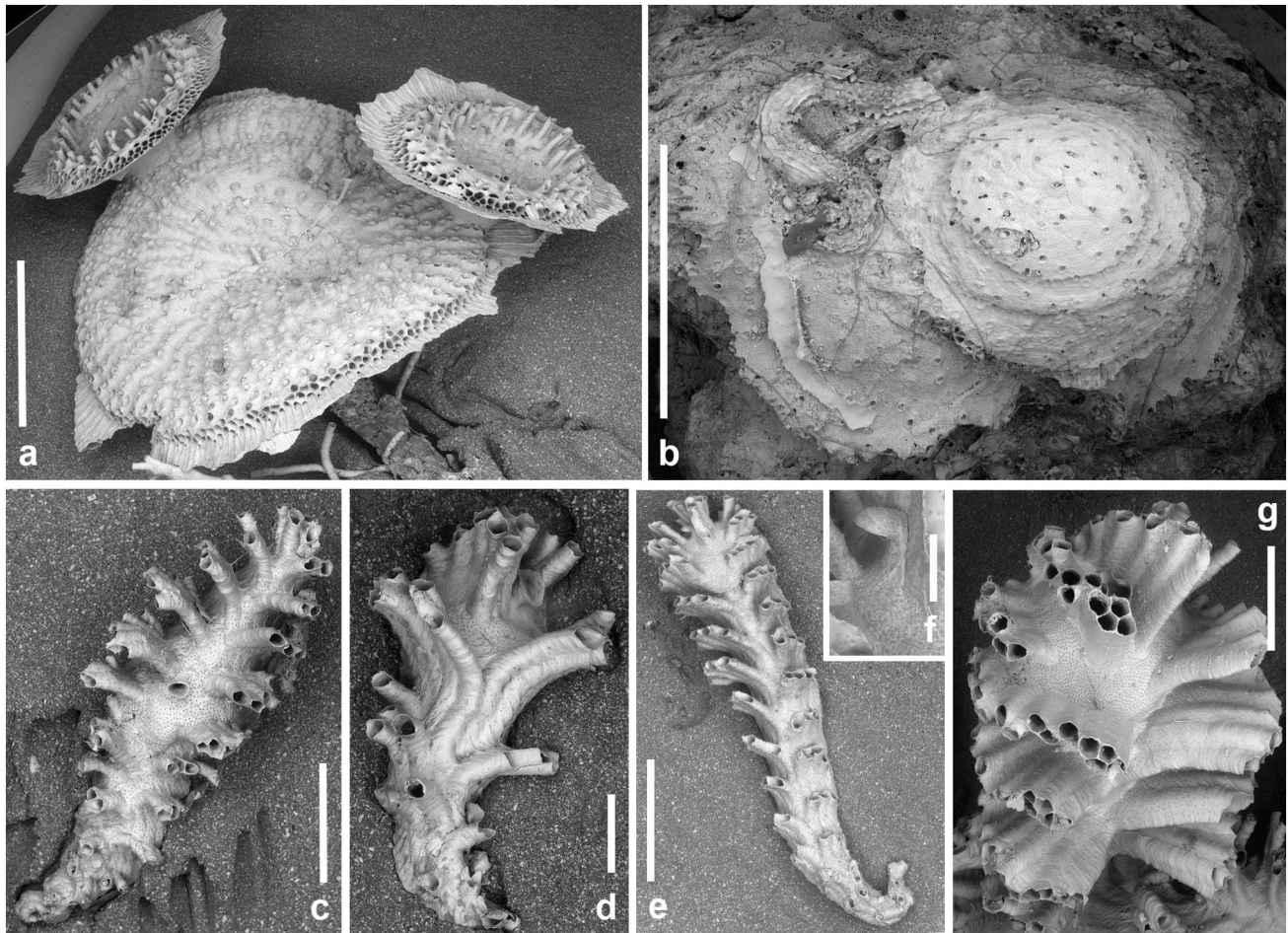


Fig. 5 Selected cyclostome species (2) from the Coralligenous off Marzamemi (SE Sicily, Ionian Sea). **a** *Plagioecia patina*, PMC Rosso-Collection I. H. B.102.a; **b** *Plagioecia platydiscus*, PMC Rosso-Collection I. H. B.167.a; **c** *Platonea stoechas*, PMC Rosso-

Collection I. H. B.168.a; **d** *Tubulipora aperta*, PMC Rosso-Collection I. H. B.169.a; **e**, **f** *Tubulipora liliacea*, PMC Rosso-Collection I. H. B.170.a; **g** *Tubulipora plumosa*, PMC Rosso-Collection I. H. B.171.a. Scale bars, 5 mm (**a**, **b**); 1 mm (**c**, **e**, **g**); 500 µm (**d**); 200 µm (**f**)

Mediterranean Sea, we selected nine key publications. These included the general bryozoan papers by Gautier (1962), Harmelin (1976) and Zabala (1986), which mainly focused on the western Mediterranean and the Sicily Strait, the Provence and the Catalonia regions, respectively. Additional data were extracted from inventories for particular areas, such as Balasteros et al. (1993) for Cabrera Island (Balearic Archipelago), and Novosel et al. (2004) and the RAC/SPA-UNEP/MAP (2014) also compiled by Novosel for the Croatian coast (northeastern Adriatic Sea). We also examined the studies specifically addressing coralligenous biodiversity published by Laubier (1966) and Hong (1980, 1982), as well as Corriero et al. (2025) and Mercurio et al. (2024). The first two focused on northwestern Mediterranean (Les Albères and Marseille areas, respectively), while the last two addressed the same Apulian bioconstructions (southern Adriatic and northern Ionian seas). A few additional papers were examined, specifically dealing with coralligenous bryozoans from selected

facies around Port Cros and Bagaud Isles, Provence region (Harmelin 2017) and from the Marzamemi area, southeastern Sicily, Ionian Sea (Rosso and Sanfilippo 2009; Rosso et al. 2023 and Donato et al. 2024). Data from the last three papers from the very same area studied here were reported together in column R+ of Table 3 and the R+ donut chart of Fig. 12. In contrast, papers dealing with animal-dominated mesophotic habitats and the so-called animal forests were not taken into consideration.

In compiling the list for Mediterranean coralligenous communities, we omitted some species. The most relevant examples include *Buffonellaria divergens* (Smitt, 1873), *Crassimarginatella crassimarginata* (Hinks, 1880), *Fenestulina malusii* (Audouin & Savigny, 1826), *Hinckesia flustroides* (Hincks, 1877), *Microporella ciliata* (Pallas, 1766), *Schizomavella auriculata* (Hassal, 1862), *Schizomavella discoidea* (Busk, 1859), *Scrupocellaria reptans* (Linnaeus, 1758), *Turbicellepora avicularis* (Hincks, 1860),

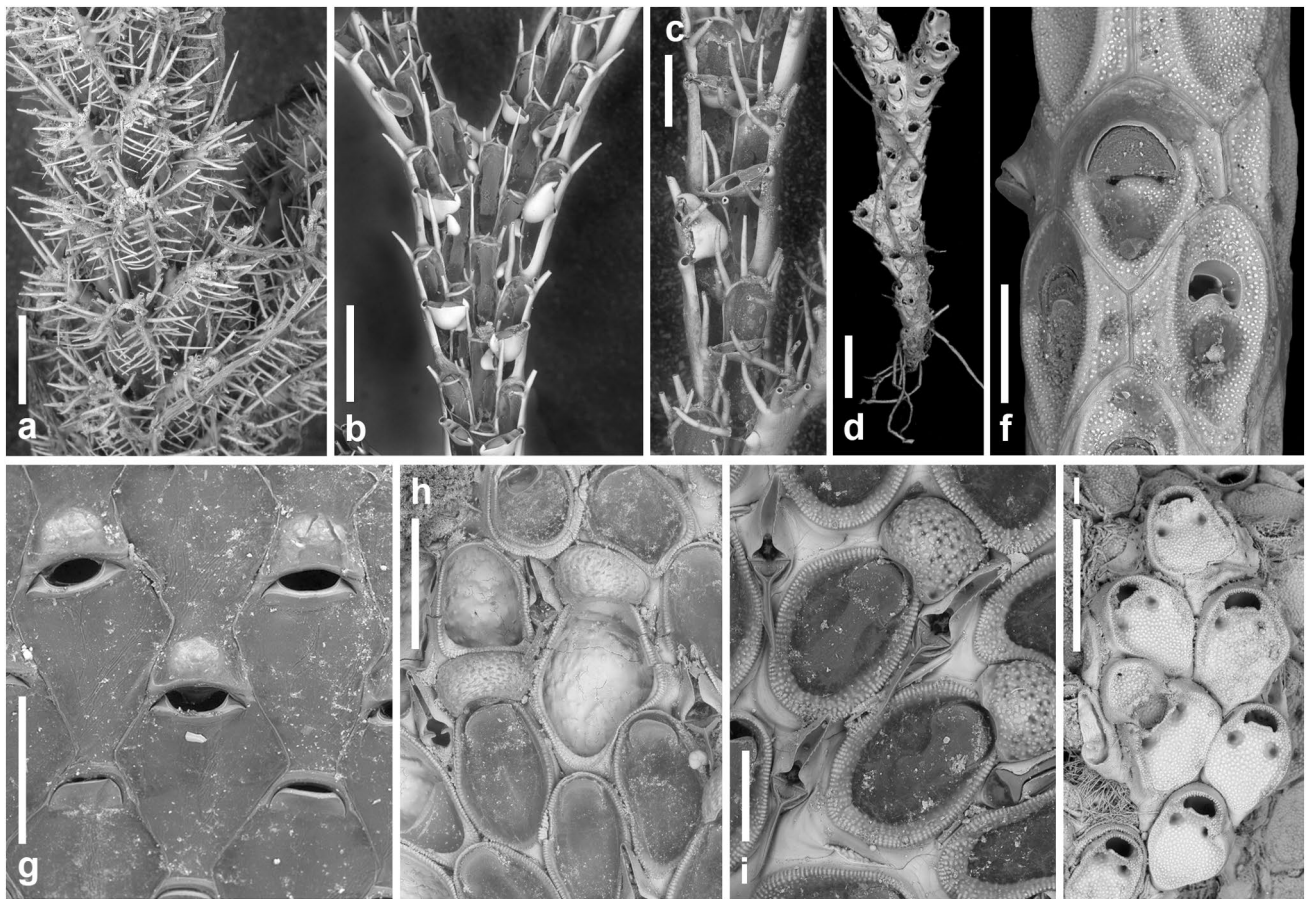


Fig. 6 Selected anascan-grade cheilostome species (1) from the Coralligenous off Marzamemi (SE Sicily, Ionian Sea). **a** *Beania cylindrica*, PMC Rosso-Collection I. H. B.101.a; **b** *Bugulina* cf. *flabellata*, PMC Rosso-Collection I. H. B.65.b; **c** *Bugulina* cf. *fulva*, PMC Rosso-Collection I. H. B.103.a.; **d** *Caberea boryi*, PMC Rosso-Collection I. H. B.66.b.; **e** *Cellaria salicornioides*, PMC Rosso-Col-

lection I. H. B.172.a; **f** *Chartella papyrea*, PMC Rosso-Collection I. H. B.173.a; **g** *Copidozoum planum*, PMC Rosso-Collection I. H. B.174.a; **h** *Copidozoum tenuirostre*, PMC Rosso-Collection I. H. B.62.b; **i** *Coronellina fagei*, PMC Rosso-Collection I. H. B.175.a. Scale bars, 500 μ m (**a**, **b**, **f**, **g**, **i**); 200 μ m (**c**–**e**, **h**)

all commonly reported, and a few ones, i.e. *Carbasea carbasea* (Ellis & Solander, 1786), *Collarina balzaci* (Audouin, 1826), and *Hemicyclopora neatonensis* (Busk, 1861), that were only occasionally reported. In doing this, we considered that some of these species were synonymised with other species, and hence we replaced them in the list with their currently accepted synonyms. This is the case for *S. auriculata*, here reported as *S. cornuta* (see Rosso et al. 2010, 2023; Rosso and Di Martino 2016,) and for *T. avicularis*, here reported with the corresponding senior synonym *T. incrassata* (see Rosso et al. 2020). For other species, an extra-Mediterranean distribution has been recognised and their previous records from the Mediterranean Sea are now considered to result from misidentifications or to correspond to different recently described species. This applies to records of *C. carbasea* possibly corresponding to *Chartella papyrea*, *H. multispinata*, represented in the studied area by *H. neatonensis*, and *C. crassimarginata* and *S. discoidea*

possibly fully corresponding to *C. matildae* and *S. biancae*, respectively.

In contrast, and regardless they are still considered occurring or not in the Mediterranean, some nominal species have been split into two or more taxonomic entities potentially thriving in different areas and/or habitats, many described as new, but usually based on restricted examples of examined material, either physical or illustrated (photographed). In these cases, it is impossible to ascertain which new species (among the two or more new ones occurring in the Mediterranean) is hidden under “old” species names without examination of original material. Consequently, we reported *Buffonellaria* sp. instead of *B. divergens* (see Berning and Kukliński 2008), *Collarina* sp. instead of *C. balzaci* (see Harmelin et al. 2019), *Fenestulina* sp. instead of *F. malusii* (see Rosso et al. 2025), *Hincksina* sp. instead of *H. flustroides* (see Berning et al. 2021), *Microporella* sp. instead of *M. ciliata* (see Di Martino and Rosso 2021), *Cradoscrupocellaria* sp. instead of

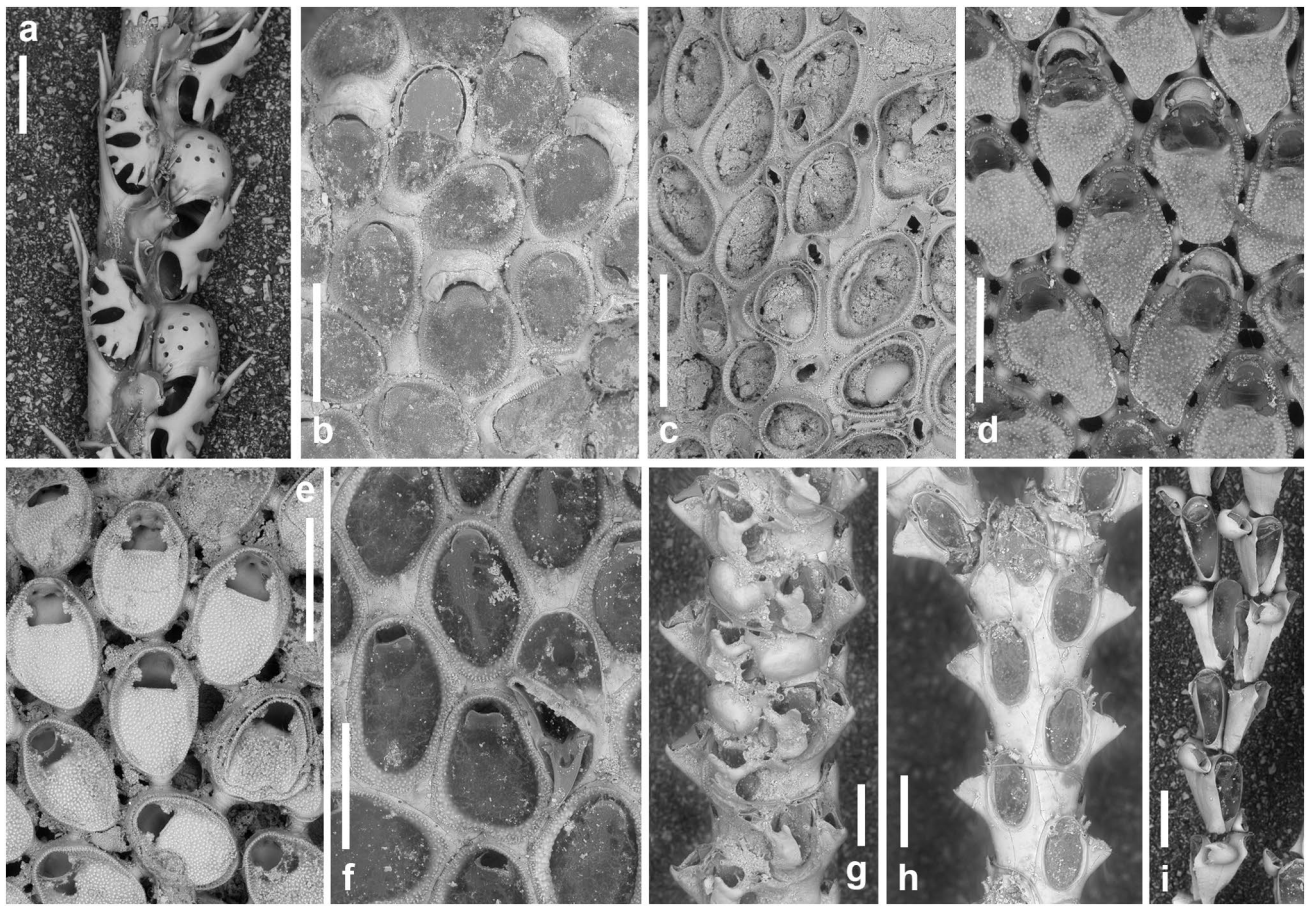


Fig. 7 Selected anascan-grade cheilostome species (2) from the coral-ligenous off Marzamemi (SE Sicily, Ionian Sea). **a** *Cradoscrupocellaria macrorhyncha*, PMC Rosso-Collection I. H. B.67.b; **b** *Cras-simarginatella solidula*, PMC Rosso-Collection I. H. B.176.a; **c** *Ellisina gautieri*, PMC Rosso-Collection I. H. B.177.a; **d** *Mollia circumcincta*, PMC Rosso-Collection I. H. B.178.a; **e** *Mollia patellaria*,

PMC Rosso-Collection I. H. B.179.a; **f** *Parellisina curvirostris*, PMC Rosso-Collection I. H. B.180.a; **g** *Scrupocellaria delilii*, PMC Rosso-Collection I. H. B.107.a; **h** *Scrupocellaria scruposa*, PMC Rosso-Collection I. H. B.106.a; **i** *Synnotum aegiptiacum*, PMC Rosso-Collection I. H. B.181.a. Scale bars, 200 µm (a, g–i); 500 µm (b–f)

S. reptans (see Vieira et al. 2013). We also considered *Celleporina caminata* instead of *C. mangnevellana* (Lamouroux, 1816) and *C. hassalli* instead of *C. caliciformis* (Lamouroux, 1816) notwithstanding the synonymy proposed by d'Hondt (2000) which has not yet achieved unanimous acceptance and still awaits formal confirmation supported by SEM images of type specimens. Finally, for all species usually reported under the authority of Audouin, 1826, we adopted instead the authority Audouin & Savigny, 1826, following insights of Harmelin et al. (2011) and Di Martino and Rosso (2021) on *Microporella*, and Rosso et al. (2025) on *Fenestulina* to recognise Savigny's merit in drawing all species that Audouin later simply named, often even without information about their origin (see Rosso et al. 2025).

The resulting list counts 257 species (Table 3) including 45 cyclostomes, 11 ctenostomes, and a large dominance of cheilostomes species (201). However, only a small number of species are frequent, i.e. occur in many areas. In particular,

only five species (*B. mediterranea*, *C. boryi*, *C. caminata*, *C. radiata*, and *M. truncata*), accounting for 1.9%, are present in all the 10 considered areas and further four, i.e. *E. coccinea*, *M. patellaria*, *P. fascialis*, and *S. (S.) cornuta* (1.6%), occur in 9 of them. This means that only nine out of the overall reported 257 species (representing 3.5% of the whole diversity) are very frequent. In contrast, 72 species (28%) occur in only one area. In general, most species, i.e. 203 species, accounting for 79% of the total diversity, show frequency values ranging 1–5, whereas the remaining 54 (21%) were found in 6–10 areas.

The total number of species per area is highly variable from 31 to 145. However, cyclostomes and also ctenostomes are not always examined, as it is the case for Gautier (1962) only focusing on cheilostomes, or Corriero et al. (2025) citing the occurrence of cyclostomes but not distinguishing individual species. In contrast, Harmelin (1976) focused on cyclostomes but also listed all found cheilostomes. In papers dealing with all orders, cheilostomes are always dominant

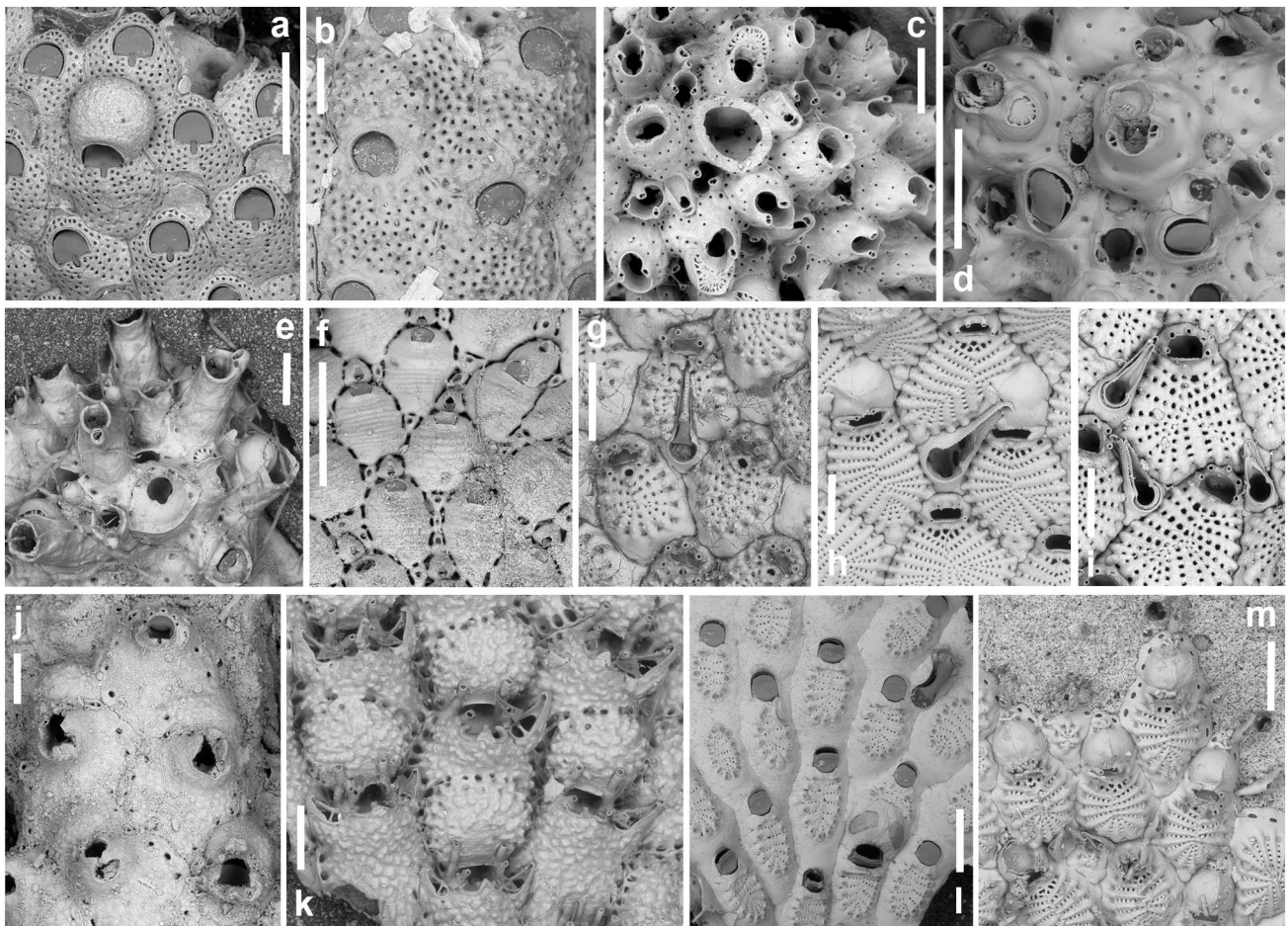


Fig. 8 Selected ascophoran-grade cheilostome species (1) from the coralligenous off Marzamemi (SE Sicily, Ionian Sea). **a** *Arthropoma ceciliai*, PMC Rosso-Collection I. H. B.100.a; **b** *Calypotheca rugosa*, PMC Rosso-Collection I. H. B.114.a; **c** *Celleporina caminata*, PMC Rosso-Collection I. H. B.98.a; **d** *Celleporina* sp. A cf. *C. canariensis*, PMC Rosso-Collection I. H. B.182.a; **e** *Celleporina siphuncula*, PMC Rosso-Collection I. H. B.183.a; **f** *Chorizopora brongniartii*, PMC Rosso-Collection I. H. B.99.a; **g** *Cribrilaria hincksi*, PMC

Rosso-Collection I. H. B.70.b; **h** *Cribrilaria radiata*, PMC Rosso-Collection I. H. B.184.a; **i** *Cribrilaria venusta*, PMC Rosso-Collection I. H. B.185.a; **j** *Escharina protecta*, PMC Rosso-Collection I. H. B.186.a; **k** *Escharoides mamillata*, PMC Rosso-Collection I. H. B.109.a; **l** *Figularia figularis*, PMC Rosso-Collection I. H. B.71.d; **m** *Glabrilaria pedunculata*, PMC Rosso-Collection I. H. B.81.b. Scale bars, 500 μ m (**a**, **c**, **d**, **f**, **l**); 200 μ m (**b**, **e**, **g**–**k**, **m**)

ranging from at least more than 71% up to almost 89% (Fig. 12). Cyclostomes are subordinate representing from almost 10 to almost 27%, whereas ctenostomes are always negligible representing usually less than 4.5% except for almost 8% in a single area.

Discussion

Bryozoan diversity of the Marzamemi coralligenous build-ups

Bryozoans from the coralligenous build-ups off Marzamemi examined here substantially increase the bryozoan

biodiversity previously reported for the same area. Previous knowledge was based on Di Geronimo et al. (2001) who detected only a dozen species from a build-up collected at about 32 m depth, in the same area of this study. Rosso and Sanfilippo (2009) later found 64 species with a prevalence of cheilostomes (47 species) over cyclostomes (17 species) and no ctenostomes examining coralligenous fragments from fishermen's nets coming from 35 to 55 m depth range. Whereas 44 species are shared between present build-ups and deep algal fragments studied by Rosso and Sanfilippo (2009), some species represent new records raising diversity for the Marzamemi Coralligenous to 145 species (see Table 3 and Bryozoan diversity of the Mediterranean Coralligenous).

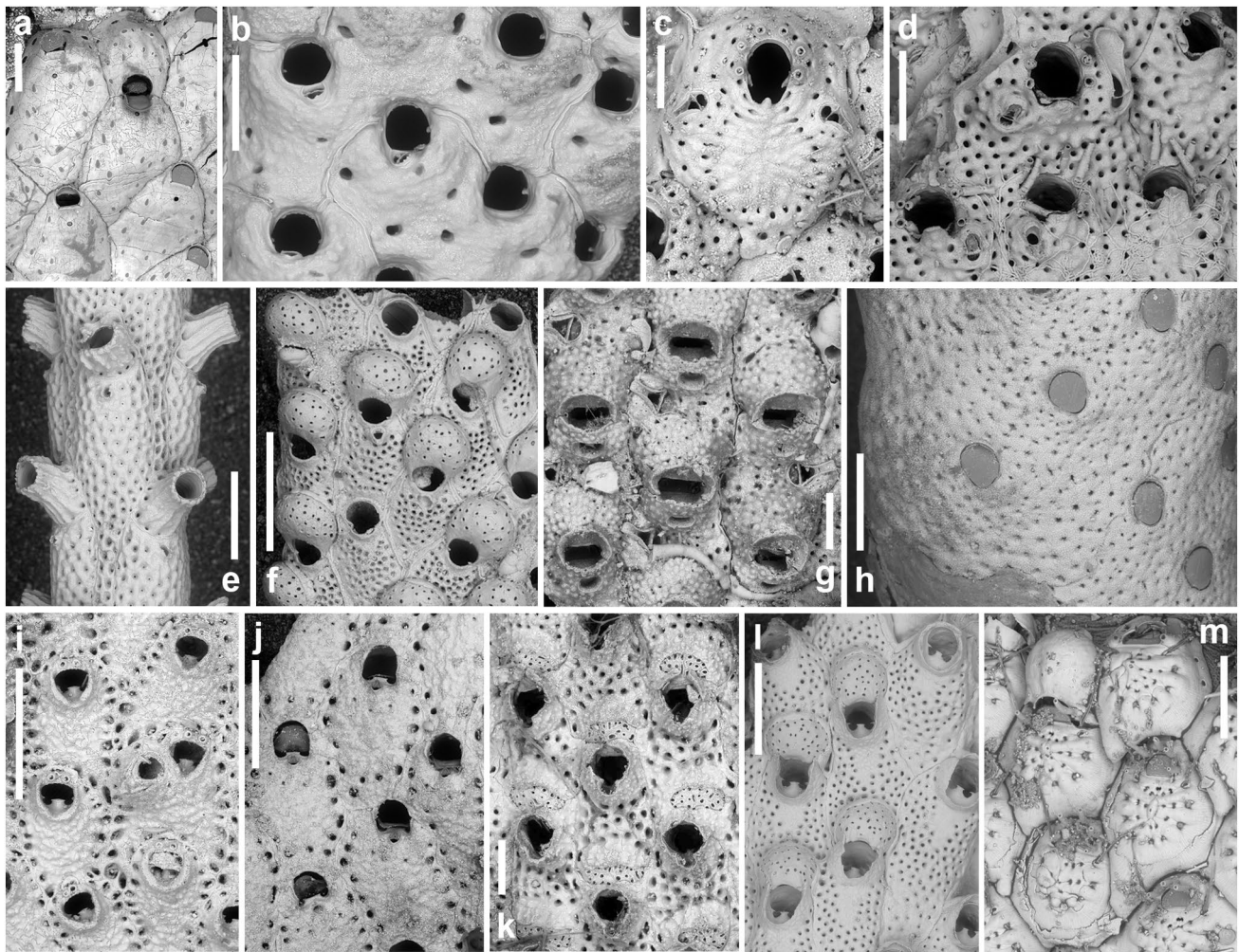


Fig. 9 Selected ascophoran-grade cheilostome species (2) from the Coralligenous off Marzamemi (SE Sicily, Ionian Sea). **a** *Haplopoma impressum*, PMC Rosso-Collection I. H. B.110.a; **b** *Hippellozoon mediterraneum*, PMC Rosso-Collection I. H. B.187.a; **c** *Hippomenella mucronelliformis*, PM PMC Rosso-Collection I. H. B.188.a; **d** *Hippopleurifera pulchra*, PMC Rosso-Collection I. H. B.189.a; **e** *Margaretta cereoides*, PMC Rosso-Collection I. H. B.190.a; **f** *Metroperiella mesogeia*, PMC Rosso-Collection I. H. B.95.a; **g** *Micropo-*

rella bicollaris, PMC Rosso-Collection I. H. B.96.a; **h** *Myriapora truncata*, PMC Rosso-Collection I. H. B.191.a; **i** *Parasmittina raigii*, PMC Rosso-Collection I. H. B.192.a; **j** *Porella concinna*, PMC Rosso-Collection I. H. B.193.a; **k** *Prenantia cheilostoma*, PMC Rosso-Collection I. H. B.194.a; **l** *Prenantia inerma*, PMC Rosso-Collection I. H. B.195.a; **m** *Puellina gattyae*, PMC Rosso-Collection I. H. B.105.a. Scale bars, 200 μ m (**a–c**, **g**, **k**, **m**); 500 μ m (**d–f**, **h**, **j**, **l**)

Values of Shannon–Wiener indexes calculated for individual build-ups sampled for the current study are always higher than 3 and up to 3.61, and point to a high biodiversity, indicating the occurrence of an elevated number of species with an even distribution in each sample. This data, so far unavailable in literature, represent a first indication for future comparisons.

The total number of species found (127) is likely to increase with further samples, because a pool of additional species represented by recently dead colonies was observed, suggesting that they may still occur alive on other build-ups. These species include one cyclostome, *Plagioecia inoedificata* (Jullien, 1882) and six

cheilostomes, i.e. *Cribellopora simplex* Gautier, 1957, *Distansescharella seguenzai* Cipolla, 1921, *Gregarinidra gregaria* (Heller, 1867), *Schizobrachiella sanguinea* (Norman, 1868), *Setosella rossanae* Rosso, Di Martino & Gerovasileiou, 2020, and *Trypostega venusta* (Norman, 1868). Most of them (*P. inoedificata*, *C. simplex*, *D. seguenzai*, *S. rossanae*, and *T. venusta*) are even additional to the above-mentioned 145 species representing the total diversity so far known for coralligenous communities in SE Sicily. All these dead species are possibly rare constituents in the community, whose colonies can be however preserved in the dead assemblage (or thanatocoenosis) owing to their mineralised skeletons. Like molluscs in the same

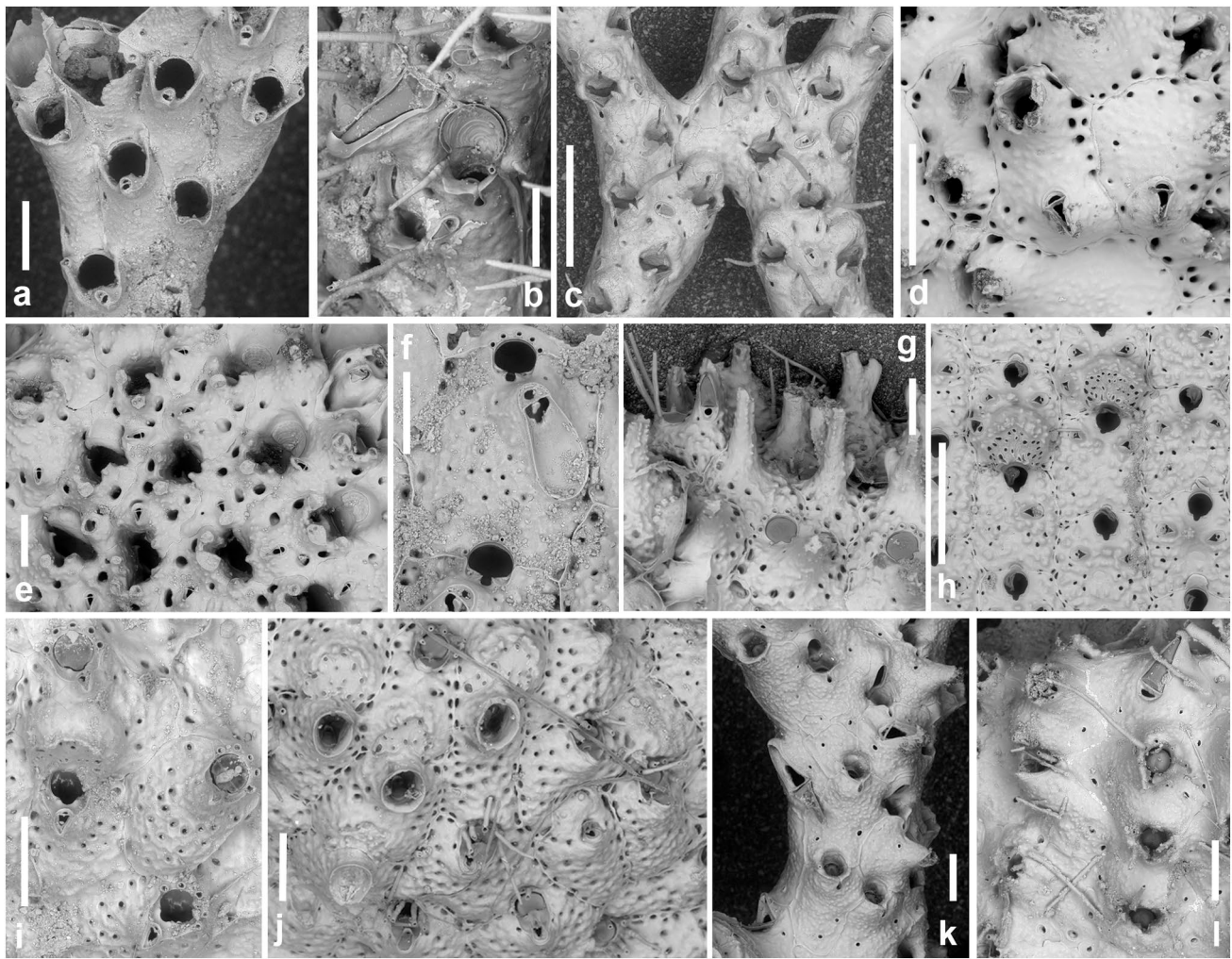


Fig. 10 Selected ascophoran-grade cheilostome species (3) from the coralligenous off Marzamemi (SE Sicily, Ionian Sea). **a** *Reteporella aporosa*, PMC Rosso-Collection I. H. B.196.a; **b** *Reteporella grimaldi*, PMC Rosso-Collection I. H. B.197.a; **c** *Reteporella sudbournensis*, PMC Rosso-Collection I. H. B.198.a; **d** *Rhynchozoon neapolitanum*, PMC Rosso-Collection I. H. B.199.a; **e** *Rhynchozoon pseudodigitatum*, PMC Rosso-Collection I. H. B.200.a; **f** *Schizomavella* (*S.*) cf. *halimedeae* (Gautier 1955), PMC Rosso-Collection I. H.

B.201.a; **g** *Schizomavella* (*S.*) *hastata*, PMC Rosso-Collection I. H. B.202.a; **h** *Schizomavella* (*S.*) *linearis*, PMC Rosso-Collection I. H. B.104.a; **i** *Schizomavella* (*S.*) *subsolana*, PMC Rosso-Collection I. H. B.203.a; **j** *Schizomavella* (*S.*) *tubulata*, PMC Rosso-Collection I. H. B.204.a; **k** *Schizoretepora solanderia*, PMC. Rosso-Collection R.I.H. B-14b; **l** *Schizotheca fissa*, PMC Rosso-Collection I. H. B.205.a. Scale bars, 200 µm (**a**, **b**, **e**–**g**, **i**–**l**); 500 µm (**c**, **d**, **h**)

coralligenous structures (Bracchi et al. 2025), and presumably more reliably than for soft-bottom assemblages (e.g. Rosso 1996 for bryozoans in the same area; Kidwell 2013 and Bracchi et al. 2025, for molluscs), these species provide complementary knowledge on the potential overall bryozoan variability within the Marzamemi coralligenous build-ups. Moreover, owing to their in situ preservation, they also offer insights into the recent history of these build-up communities.

Differences among build-ups (Supplementary Table 1), involving both the total number of species and colonies as well as the species composition showing only a limited number of species shared by all samples and many species restricted to

single or a few build-ups, support the idea of a high spatial variability of coralligenous communities at small scale (e.g. Balasteros 2006 for a review). Literature has widely and repeatedly highlighted the high complexity of this habitat, in which constructional (or frame-building) skeletonised organisms (also including some bryozoans) form a 3D structure that provides a wide range of microhabitats with varying environmental conditions which can be exploited by a variety of species exhibiting specific adaptations (e.g. Hong 1980; and Harmelin 1976 and Zabala 1986, specifically for bryozoans). A differentiation in species composition can be envisaged between the outer surfaces of the studied build-ups and the variably sized cavities of the bioconstruction resembling cave habitats and

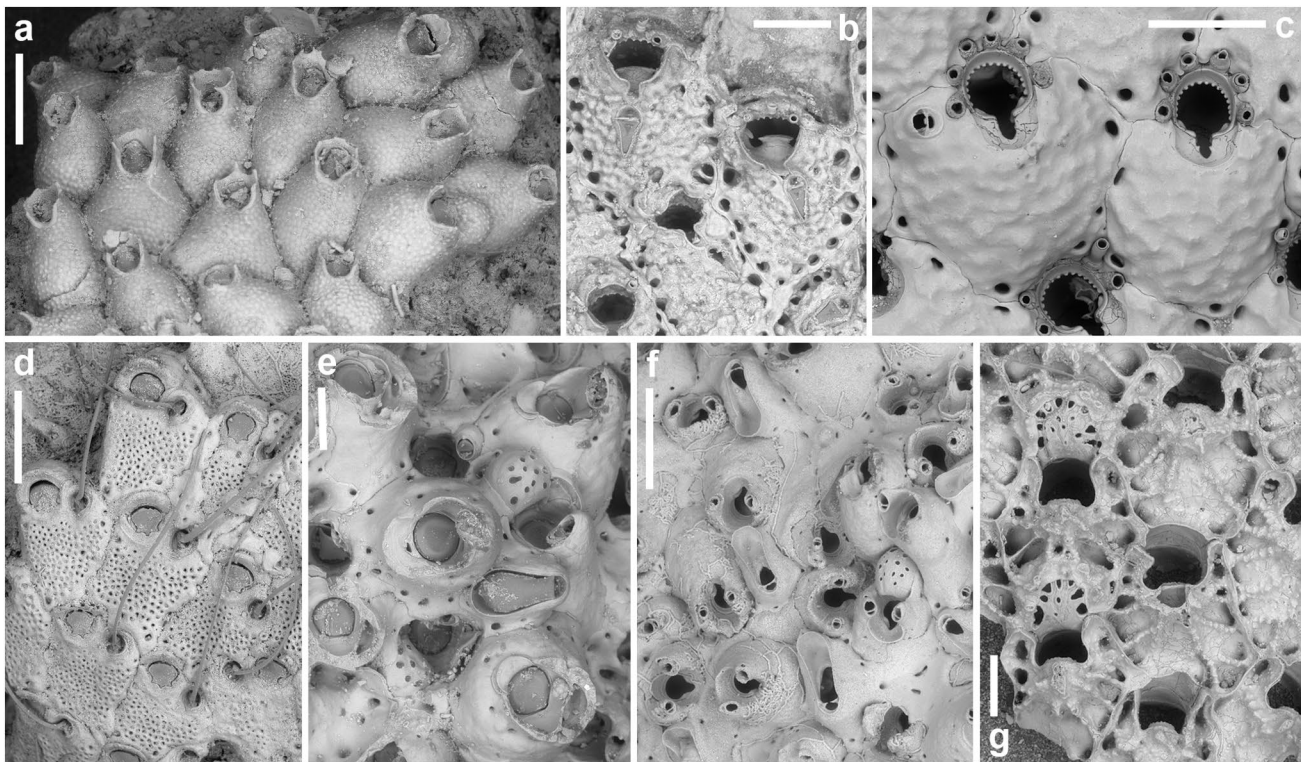


Fig. 11 Selected ascophoran-grade cheilostome species (4) from the coralligenous off Marzamemi (SE Sicily, Ionian Sea). **a** *Scutocytopora dentata*, PMC Rosso-Collection I. H. B.93.d; **b** *Smittoidea reticulata*, PMC Rosso-Collection I. H. B.206.a; **c** *Stephanollona armata*, PMC Rosso-Collection I. H. B.207.a; **d** *Therenia rosei*,

PMC Rosso-Collection I. H. B.4.c; **e** *Turbicellepora coronopus*, PMC Rosso-Collection I. H. B.208.a; **f** *Turbicellepora coronopusoida*, PMC Rosso-Collection I. H. B.209.a; **g** *Umbonula ovicellata*, PMC Rosso-Collection I. H. B.210.a. Scale bars, 500 µm (**a, d, f**); 200 µm (**b, c, e, g**)

particularly semi-dark caves, as indicated by Zabala (1986). Surfaces are usually wide and directly exposed to the surrounding marine environment in large cavities, where erect or large-sized, presumably fast-growing competitive encrusters (e.g. *H. pulchra*, even detectable in photogrammetric analyses: Bracchi et al. 2022) occur. In contrast, small and deep microcavities are characterised by a range of light and water flux attenuation possibly leading to a reduction in food availability and lower competition allowing colonisation by small-sized, less demanding species adapted to such conditions (such as *C. rugosa*, *E. protecta*, *G. pedunculata*, and *S. subsolana*), some only detectable under a microscope. Further variability derives from the development and composition of the canopy, which provides bryozoans with a wide range of substrata for colonisation — from ephemeral to persistent, filiform to laminar, flexible to hard, and smooth to rough surfaces. These substrata host a variety of species developing unmineralised or slightly mineralised colonies. Some are erect and flexible, attached by numerous rhizoids; others are small, erect, and poorly branched, with limited encrusting parts, and still others are unilaminar, consisting of loosely jointed autozooids that allow a certain degree of flexibility, as already highlighted by Rosso et al. (2023). Consequently, a high small- to large-scale

variability is also expected at the canopy level, as shown for *Cystoseira* s.l. communities by Piazzini et al. (2018). In our case, while the present study confirmed the known small-scale heterogeneity in species richness, colony abundance, and species composition, it did not investigate the underlying factors driving these patterns. Nevertheless, this variability is evident even within a restricted area and bathymetric range, where different coralligenous types — namely discrete build-ups and hybrid banks sensu Bracchi et al. (2017) — develop, as documented by Varzi et al. (2023). Further targeted investigation is required to clarify the role of environmental parameters and their interplay with primary and secondary porosity (sensu Cipriani et al. 2024), as well as with biotic interactions. In the absence of a possible depth gradient (and related temperatures) usually indicated as one of the main drivers of coralligenous biodiversity (e.g. Pinna et al. 2021), local hydrodynamic conditions could play a role. Slight differences in sediment smothering, presumably related to the onset of individual build-ups on more or less elevated seafloor areas, either connected or not to a submarine channel, were assumed by Bazzicalupo et al. (2025) as an additional driver of variation, as also suggested for bryozoan communities by Harmelin (1976) and Zabala (1986) and for bryozoans compared to algae by Balata et al. (2005).

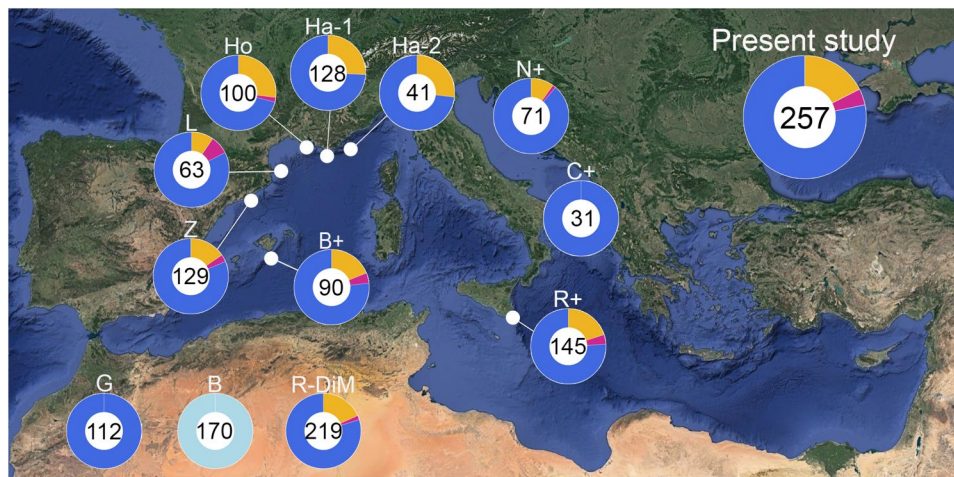


Fig. 12 Bryozoan biodiversity in the Mediterranean Coralligenous from main monographs on particular areas derived from: B+: Ballesteros et al. (1993); C+: Corriero et al. (2025); H-1: Harmelin (1976); H-2: Harmelin (2017); Ho: Hong (1980, 1982); L: Laubier (1966); N+: Novosel et al. (2004) + RAC/SPA - UNEP/MAP (2014); R+: Rosso et al.: present paper for the Marzamemi area, also including data in Rosso and Sanfilippo (2009), Rosso et al. (2023) and Donato

et al. (2024); Z: Zabala (1986), also including data in Zabala (1984) and comprehensive papers on the entire Mediterranean, including: B: Ballesteros (2006); G: Gautier (1962); R-DiM: Rosso and Di Martino (2023). Donuts' colors: cyclostomes (orange); ctenostomes (purple); cheilostomes (blue). Absence of ctenostomes in Ha-1 and Ha-2 and cyclostomes in C+ and G indicate that these groups were not reported in those papers. Pale blue in B refers to all three bryozoan orders

Sedimentation is also reported as a dissimilarity driver in “coralligenous platforms” by Piazzini et al. (2022, and references therein). Moreover, small-scale variations in sediment deposition could also be influenced by the morphology and spatial arrangement of elevated build-ups, which interact with local hydrodynamic fluxes similarly to cold-water-coral colonies in deep-sea settings (see Bartzke et al. 2025). Such environmental and structural variability is reflected in the composition and abundance patterns of the associated bryozoan fauna.

Frequent species are usually abundant pointing to their ability to proliferate in the coralligenous habitat whereas rare species are occasional, thus representing a negligible fraction in the assemblage. A comparable structure was reported by Gautier (1962, fig. 90) who showed that the four most abundant species he recorded (i.e., *T. incrassata*, as *Schismopora avicularis*, *S. cornuta*, as *S. auriculata*, *P. fascialis* as *Hippopleurifera fascialis* and *C. fistulosa*) represented half of the assemblages he examined, whereas 46 species accounted for the remaining half. Analogously, Hong (1982) remarked that 45% of bryozoan species were occasional in the build-ups he analysed, with frequency of 1–2 in his more than 50 samples, each consisting of scraped volumes of 400 cm² surfaces by 10 cm thickness.

However, these frequent species are not restricted to the coralligenous assemblage; in fact, most of them seem to be relatively flexible, typically showing a wide ecological distribution. In contrast, at least some of the infrequent and rare species occurring with few colonies are likely to be more typical representatives of the coralligenous communities. However, the identification of species indicative of the coralligenous habitat

is challenging due to its internal complexity (produced by constructional organisms) and the interplay of physico-chemical (especially edaphic) parameters and biotic drivers. These factors generate a plethora of facies, each comprising a multiplicity of microhabitats which can be exploited by a surprisingly large number of bryozoan species, each characterised by particular adaptations and often also by intraspecific plasticity (e.g. Harmelin 1976). Usually, only species lists (or lists of recurrent species) are provided, traditionally divided according to the “coralligenous type”, including (1) a precoralligenous aspect, characterised by dominant fleshy algae such as *Flabellia petiolata* and *Halimeda tuna* (J.Ellis & Solander) J.V.Lamouroux; (2) a coralligenous on sub-horizontal surfaces, typically with *Eunicella cavolini*; (3) one on shallow-water vertical walls, characterised by *Paramuricea* gorgonian species; (4) a coralligenous developed on cliffs, within microcavities and at cave entrances; and (5) a deep-water coralligenous (e.g. Harmelin 1976; Zabala 1984, 1986). However, distinction among these types is not clear-cut, and more comprehensive, detailed analyses are required to identify potential indicator species for each assemblage (if any), also including measurements of environmental parameters.

Bryozoan diversity of the Mediterranean coralligenous habitat

The bryozoan diversity associated with Mediterranean coralligenous habitat is remarkable, comprising 257 species (Fig. 12, Table 3). The analysis of the coralligenous build-ups off Marzamemi adds 24 species (2 cyclostomes, 2 ctenostomes,

and 19 cheilostomes) to the 219 species reported by Rosso and Di Martino (2016). Among these, *C. occidentalis*, *A. capriensis*, *C. pallasiana*, *E. mamillata*, *H. ambita*, and *R. elegans* represent new records for the coralligenous habitat. In addition, five species (i.e., ?*Stomatopora* sp. A, *Celleporina* sp. A cf *C. canariensis*, *Celleporina* sp. B, *Celleporina* sp. C, and *Schizomavella* sp. A) are still undescribed and are likely new species to be described in future studies. Further records pertain to species recently erected from the Mediterranean or even the same or neighbouring areas. They include *A. delicatula*, *C. siphuncula*, *H. neatonensis*, *M. bicollaris*, *Schizomavella* (S.) *subsolana*, and *S. (S.) tubulata* (Reverter-Gil et al. 2016). All these species are therefore absent from the examined papers (see above and Table 3) because they are largely published in the last years. Additional taxa at subspecies rank also contribute to the observed diversity. Their apparent absence from previous lists is difficult to verify, as subspecies are not always explicitly recognised and may have been reported under the nominal species name (see asterisks in Table 3, marking nominal subspecies when an additional one, not previously mentioned, was recognised from the Marzamemi material). Finally, it is not possible to understand if our taxa *Disporella* sp. A and *Patinella* cf. *mediterranea* correspond to any of the taxa previously referred to as undetermined lichenoporiids or left in open nomenclature (e.g. Hong 1980, 1982).

Scantiness of species shared among papers (only nine species reported in 9–10 papers, accounting for merely 3.5% of the entire diversity of 257 species) even exceeds data obtained from the comparison of the Marzamemi build-ups, where 20 species were shared by all build-ups, accounting for ca 15%. This paucity of shared species, together with the concomitant increase in the number and percentage of rare species within the total observed biodiversity seemingly results from both geographical and ecological factors. However, no clear geographic distribution pattern emerges from our review and individual species can be even found alternatively in the western Mediterranean, the Ionian and/or the Adriatic Sea. The genus *Escharella*, by contrast, appears restricted to the western Mediterranean, where it is represented by as many as five species (Table 3). A similar pattern also occurs in photo-quadrat biodiversity assessments. When examining the total biodiversity of 313 species (including 20 bryozoans) associated with the coralligenous habitat from far apart Mediterranean regions in the Gulf of Lions, western Ionian Sea, and north-eastern Aegean Sea (clustered together for France, Greece and Turkey), Féral et al. (2016) found that species shared by the three areas were about 46% and that differences among groups existed with bryozoans more diversified in the French region. Geographical differences at the Mediterranean scale are expected not necessarily only in relation to geographic distance and the highest number of shared species was found by Féral et al. (2016) between France and Turkey. Rather, differences may relate to different

environmental parameters, particularly temperature ranges and water circulation patterns. Pinna et al. (2021) considered thermal conditions and hydrodynamics as the main possible drivers of spatial variability in structuring assemblages associated with coralligenous cliffs along the depth gradient 18–38 m in different sectors of western and eastern Sardinia. Similarly, even at a smaller scale within the Tyrrhenian Sea, Piazzini et al. (2023) found that latitudinal and continental-to-island gradients were the main factors influencing assemblages associated with coralligenous cliffs along the Tuscany coast. Besides focusing on different geographical areas (sometimes based on isolated samples from wide areas in the western Mediterranean, such as Gautier 1962), papers examined for the present overview also include different depth ranges from very shallow settings (c 10 m) in the Adriatic and Marseille areas (Novosel et al. 2004 and Hong 1980, 1982, respectively) to intermediate depths of c 60 m (SE Sicily, Ionian Sea: Rosso and Sanfilippo 2009) and down to 75 m (Harmelin 1976: Marseille region) and even 95 m (Ballesteros et al. 1993: Cabrera, Balearic Islands).

Accordingly, the marked variability observed among regions also reflects differences in the vertical distribution of species, which remain best known from shallow-water settings (e.g. Harmelin 1976; Ferdeghini et al. 2000; Balata et al. 2006; Piazzini et al. 2021). In line with this variability, different coralligenous facies are reported in the examined papers, although usually not explicitly indicated. Establishment of these facies in a given area is also influenced by depth and light penetration together with the geological and physiographic nature of substrata, and by local hydrodynamic and other environmental conditions. In this respect, whereas large-sized bryozoan colonies, exclusively consisting of *Reteporella* species, were only observed through ROV inspections at greater depths off Marzamemi, the absence of large-sized bryozoans (such as *S. cervicornis*, *P. fascialis*, *A. calveti* and *T. magnevilleana* = *T. avicularis*) which are generally considered as indicators of healthy coralligenous communities (e.g. Gatti et al. 2015), or their occurrence with very small, even cryptic colonies (such as *M. truncata*), could simply represent a distinctive feature of the studied coralligenous. As remarked by Pinna et al. (2021), the absence of an elevated bryozoan (and gorgonian) layer does not necessarily indicate the occurrence of environmental alterations but could also be typical of pristine conditions in particular areas, which we expected to be the case for the coralligenous habitat of Marzamemi. However, several species are sensitive to environmental parameters and Hong (1983) documented a remarkable species loss along a pollution gradient.

Furthermore, in each facies, the intrinsic 3D complexity produced by the growth of coralligenous bioconstructors (or frame-builders) jointed with the particular development of the canopy contribute to small-scale spatial heterogeneity and the diversification of microhabitats furtherly promoting biodiversity. Interestingly, several facies at different

depths are included in the list by Harmelin (1976) reported in Table 3 which documents as many as 128 species from the Marseille area, when including in the coralligenous also the so-called precoralligenous and coralligenous concretions.

The total of 257 bryozoan species so far reported for the coralligenous habitat largely outnumbers the 170 species indicated in Ballesteros (2006) and the 219 species (40 cyclostomes, four ctenostomes and 175 cheilostomes; Fig. 5) considered by Rosso and Di Martino (2016). The present total diversity accounts for almost 44% of the overall bryozoan diversity of 588 species currently known for the Mediterranean Sea (Rosso and Di Martino 2023) and even overcomes the 40% previously reported by Rosso and Di Martino (2016) based on a total number of 556 bryozoan species known at that time. However, this number is expected to increase further in the future taking into account that species presently known only from recently dead colonies could likely be found alive, and probably some of them such as *C. simplex* could seemingly already have been found although possibly confused with the better known, more widespread, congener *C. trichotoma*. Furthermore, the discovery of new species is plausible once biodiversity studies focused on coralligenous bioconstructions are extended to still understudied areas, such as some of eastern and southern sectors of the Mediterranean and especially the Aegean and Levantine seas where coralligenous communities are possibly less studied for their deeper location owing to elevated water transparency and more oligotrophic conditions (Pérès and Picard 1958; Ballesteros 2006).

The high detected figures of bryozoan diversity, however, can only be achieved through detailed, small-scale sampling and laboratory analyses of collected material. In situ visual surveys alone, even when supported by underwater photography or ROV imagery, remain insufficient to capture the full extent of bryozoan diversity, although often used to assess the status of coralligenous habitat and regional biodiversity variations (e.g. Casoli et al. 2020, 2024). Most species are minute, encrusting, or cryptic, and their identification relies on microscopic examination of zooidal and skeletal features (see Donato et al. 2024, and references therein) that are invisible in standard images. Consequently, photographic and video-based studies mainly record few (usually 4–5) large, erect, or morphologically distinctive taxa (e.g. *Reteporella* spp.), while overlooking the vast majority of smaller species that dominate coralligenous assemblages.

Integrating targeted sampling with in situ documentation therefore represents the only effective strategy to obtain a realistic picture of bryozoan diversity within coralligenous habitats across the Mediterranean.

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References

- Astruch P, Boudouresque C-F, Cabral M, Schohn T, Ballesteros E, Bellan-Santini D, Belloni B, Nike Bianchi C, Cassetti O, Chevaldonné P, Fourn M, Guidetti P, Hartmann V, Jacob É, Le Diréac L, Michez N, Montefalcone M, Morri C, Nérini D, Pérez T, Pibot A, Poggiale J-C, Reveret C, Valance F, Ruitton S, Sartoretto S, Blouet S, Ricquiers L, Thibaut T, Vacelet J, Verlaque M (2025) An ecosystem-based index for Mediterranean coralligenous reefs: a protocol to assess the quality of a complex key habitat. *Mar Poll Bull* 220:118375. <https://doi.org/10.1016/j.marpolbul.2025.118375>
- Balata D, Acunto S, Cinelli F (2006) Spatio-temporal variability and vertical distribution of a low rocky subtidal assemblage in the

- north-west Mediterranean. *Estuar Coast Shelf Sci* 67:553–561. <https://doi.org/10.1016/j.ecss.2005.12.009>
- Balata D, Piazzì L, Cecchi E, Cinelli F (2005) Variability of Mediterranean coralligenous assemblages subject to local variation in sediment deposition. *Mar Environ Res* 60:403–421
- Ballesteros E (2003) The coralligenous in the Mediterranean Sea: definition of the coralligenous assemblage in the Mediterranean, its main builders, its richness and key role in benthic ecology as well as its threats. Project for the Preparation of a Strategic Action Plan for the Conservation of the Biodiversity in the Mediterranean Region (SAP BIO) UNEP-MAP-RAC/SPA, Tunis.
- Ballesteros E (2006) Mediterranean coralligenous assemblages: a synthesis of present knowledge. *Oceanogr Mar Biol, Annu Rev* 44:123–195
- Ballesteros E, Zabala M, Uriz MJ, Garcia-Rubies A, Turon X (1993) El bentos: les comunitats. In: Alcover JA, Ballesteros E, Fornós JJ (eds) *Història Natural de l'Arxipèlag de Cabrera*, vol vol 2. CSIC-Ed Moll Mon Soc Hist Nat Balears, p pp 687–730
- Bartzke G, Hebbeln D, Huhn K (2025) Hydro- and sediment dynamics in a cold-water coral reef: insights from a 3D numerical model. *Front Mar Sci* 12:1654625. <https://doi.org/10.3389/fmars.2025.1654625>
- Bavestrello G, Cerrano C, Zanzi D, Cattaneo-Vietti R (1997) Damage by fishing activities to the Gorgonian coral *Paramuricea clavata* in the Ligurian Sea. *Aquat Conserv* 7:253–262
- Bazzicalupo P, Bracchi VA, Cipriani M, Guido A, Rosso A, Sanfilippo R, Maspero F, Galli A, de Ponti E, Basso D (2025) A thousand-year journey of lithification: CT-analysis and radiocarbon dating of algal reef from Central Mediterranean. *Mar Geol* 489:107637
- Berning B, Kukliński P (2008) North-east Atlantic and Mediterranean species of the genus *Buffonellaria* (Bryozoa, Cheilostomata): implications for biodiversity and biogeography. *Zool J Linn Soc* 152:537–566. <https://doi.org/10.1111/j.1096-3642.2007.00379.x>
- Berning B, Spencer Jones, ME, Vieira, LM (2021) Revision of the European species of the genus *Hincksina* Norman, 1903 (Bryozoa, Cheilostomatida, Flustridae). *Zootaxa*, 5081 (3):333–352. <https://doi.org/10.11646/zootaxa.5081.3.2>
- Betti F, Bavestrello G, Fravega L, Bo M, Coppari M, Enrichetti F, Capanera V, Venturini S, Cattaneo-Vietti R (2019) On the effects of recreational SCUBA diving on fragile benthic species: the Portofino MPA (NW Mediterranean Sea) case study. *Ocean Coast Manage* 182:104926. <https://doi.org/10.1016/j.ocecoaman.2019.104926>
- Bracchi VA, Basso D, Marchese F, Corselli C, Savini A (2017) Coralligenous morphotypes on subhorizontal substrate: a new categorization. *Cont Shelf Res* 144:10–20
- Bracchi VA, Bazzicalupo P, Fallati L, Varzi AG, Savini A, Negri MP, Rosso A, Sanfilippo R, Guido A, Bertolino M, Costa G, De Ponti E, Leonardi R, Muzzupappa M, Basso D (2022) The main builders of Mediterranean coralligenous: 2D and 3D quantitative approaches for its identification. *Front Earth Sci, Paleontology* 10:910522. <https://doi.org/10.3389/feart.2022.910522>
- Bracchi V, Negri MP, Bazzicalupo P, Bertolino M, Cipriani M, Donato G, Guido A, Rosso A, Sanfilippo R, Sciuto F, Basso D (2025) Mollusks diversity of coralligenous build-ups in the southwestern Ionian Sea. *Mediterr Mar Sci* 26(3):472–483. <https://doi.org/10.12681/mms.38878>
- Casoli E, Moro S, Falasca M, Montefalcone M, Rizzo L, Teixidó N, Piazzì L, Longo C, Mercurio M, Gennaro P, Penna M, Gambi MC, Mirasole A, Ballesteros E, Andreollo M, Ventura D, Mancini G, Belluscio A, Fraschetti S, Ardizzone G, Jona-Lasinio G (2024) Structure and diversity patterns of coralligenous cliffs across three ecoregions in the Central-Western Mediterranean Sea. *Divers Distrib* 30(9):e13833. <https://doi.org/10.1111/ddi.13833>
- Casoli E, Piazzì L, Nicoletti L, Jona-Lasinio G, Cecchi E, Mancini G, Belluscio A, Ardizzone G (2020) Ecology, distribution and demography of erect bryozoans in Mediterranean coralligenous reefs. *Estuar Coast Shelf Sci* 235:106573. <https://doi.org/10.1016/j.ecss.2019.106573>
- Chimenz Gusso C, Soule DF (2003) First recognized occurrence of the genus *Plesiocleidochasma* in the Mediterranean region (Bryozoa, Cheilostomatida) with *Plesiocleidochasma mediterraneum*, new species. *Boll Mus Civ Stor Nat Verona Bot Zool* 27:71–76.
- Çinar ME, Féral J-P, Arvanitidis C, David R, Taşkın E, Sini M, Dailianis T, Doğan A, Gerovasileiou V, Evcen A, Chenuil A, Dağlı E, Aysel V, Issaris Y, Bakir K, Nalmpanti M, Sartoretto S, Salomidi M, Sapouna A, Açık S, Dimitriadis S, Koutsoubas D, Katakán T, Öztürk B, Koçak F, Erdogan-Dereli D, Önen S, Özgen Ö, Türkçü N, Kirkim F, Önen M (2020) Coralligenous assemblages along their geographical distribution: testing of concepts and implications for management. *Aquat Conserv* 30:1578–1594. <https://doi.org/10.1002/aqc.3365>
- Cipriani M, Apollaro C, Basso D, Bazzicalupo P, Bertolino M, Bracchi AV, Bruno F, Costa G, Dominici R, Gallo A, Muzzupappa A, Rosso A, Sanfilippo R, Sciuto F, Vespasiano G, Guido A (2024) Origin and role of non-skeletal carbonate in coralligenous build-ups: new geobiological perspectives in the biomineralisation processes. *Biogeosciences* 21:49–72. <https://doi.org/10.5194/bg-21-49-2024>
- Corriero G, Giménez G, Albano PG, Giampaolletti J, Longo C, Mercurio M, Nonnis Marzano C, Pirri C, Gravina MF (2025) Disentangling the mesophotic zone: algal and invertebrate bioconstructions host distinct benthic assemblages in the Mediterranean Sea. *Biodivers Conserv* 34(5):1751–1769. <https://doi.org/10.1007/s10531-025-03041-w>
- Council of the European Communities (1992) Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. *OJEU* 206:50
- d'Hondt JL (2000) Discovery of some types of cheilostomatous Bryozoa described from 1812 to 1824 by J-V-F Lamouroux. In: Herrera Cubilla A, Jackson JBC (eds) *Proceedings of the 11th International Bryozoology Association Conference*, pp 211–218. Smithsonian Tropical Research Institute, Balboa
- Di Camillo C, Ponti M, Pulido Mantas T, Roveta C, 2023 Review of the indexes to assess the ecological quality of coralligenous reefs: towards a unified approach. *Front Mar Sci* 10. <https://doi.org/10.3389/fmars.2023.1252969>
- Di Geronimo I, Di Geronimo R, Improta S, Rosso A, Sanfilippo R (2001) Preliminary observation on a columnar coralline build-up from off SE Sicily. *Biol Mar Mediterr* 8:229–237
- Di Geronimo I, Di Geronimo R, Rosso A, Sanfilippo R (2002) Structural and taphonomic analysis of a columnar build-up from Sicily shelf. *Géobios Mem Spec* 24(35):86–95
- Di Martino E, Rosso A (2021) Seek and ye shall find: new species and new records of *Microporella* (Bryozoa: Cheilostomata) in the Mediterranean. *Zookeys* 1053:1–42. <https://doi.org/10.3897/zookeys.1053.65324>
- Donato G, Sanfilippo R, Basso D, Bazzicalupo P, Bertolino M, Bracchi VA, Cipriani M, D'Alpa F, Guido A, Negri PM, Sciuto F, Serio D, Rosso A (2024) Biodiversity associated with a Coralligenous build-up off Sicily (Ionian Sea). *Reg Stud Mar Sci* 80:103868. <https://doi.org/10.1016/j.rsma.2024.103868>
- Féral JP, Arvanitidis C, Chenuil A, Çinar ME, David R, Egea E, Sartoretto S (2016) CIGESMED: Coralligenous based Indicators to evaluate and monitor the “Good Environmental Status” of the Mediterranean coastal waters. Research Report. ANR, 107 pp. <https://hal.science/hal-01448881>
- Ferdegini F, Acunto S, Cocito S, Cinelli F (2000) Variability at different spatial scales of a coralligenous assemblage at Giannutri Island (Tuscan Archipelago, northwest Mediterranean). *Hydrobiologia* 440:27–36. <https://doi.org/10.1023/A:1004124423718>

- Ferrigno F, Rendina F, Sandulli R, Russo GF (2024) Coralligenous assemblages: research status and trends of a key Mediterranean biodiversity hotspot through bibliometric analysis. *Ecol Quest* 35(1):19–36. <https://doi.org/10.12775/EQ.2024.001>
- Garrabou J, Gómez-Gras D, Medrano A, Cerrano C, Ponti M, Schlegel R, Bensoussan N, Turicchia E, Sini M, Gerovasileiou V, Teixido N, Mirasole A, Tamburello L, Cebrian E, Rilov G, Ledoux J-B, Souissi JB, Khamassi F, Ghanem R, Benabdi M, Grimes S, Ocaña O, Bazairi H, Hereu B, Linares C, Kersting DK, la Rovira G, Ortega J, Casals D, Pagès-Escollà M, Margarit N, Capdevila P, Verdura J, Ramos A, Izquierdo A, Barbera C, Rubio-Portillo E, Anton I, López-Sendino P, Díaz D, Vázquez-Luis M, Duarte C, Marbà N, Aspíllaga E, Espinosa F, Grech D, Guala I, Azzurro E, Farina S, Gambi MC, Chimienti G, Montefalcone M, Azzola A, Mantas TP, Fraschetti S, Ceccherelli G, Kipson S, Bakran-Petricioli T, Petricioli D, Jimenez C, Katsanevakis S, Kizilkaya IT, Kizilkaya Z, Sartoretto S, Elodie R, Ruitton S, Comeau S, Gattuso J-P, Harmelin J-G (2022) Marine heatwaves drive recurrent mass mortalities in the Mediterranean sea. *Glob Change Biol* 28:5708–5725. <https://doi.org/10.1111/gcb.16301>
- Gatti G, Bianchi CN, Morri C, Montefalcone M, Sartoretto S (2015) Coralligenous reefs state along anthropized coasts: application and validation of the COARSE index, based on a rapid visual assessment (RVA) approach. *Ecol Indic* 52:567–576
- Gautier YV (1955) Bryozoaires de Castiglione. *Bull Stn Aquic Pêche Castiglione*, ns, 7:227–271.
- Gautier YV (1962) Recherches Écologiques Sur Les Bryozoaires Chilostomes En Méditerranée Occidentale. *Rec Trav Stat Mar Endoume* 38:1–434
- Harmelin J-G (1976) Le sous-ordre des Tubuliporina (Bryozoaires Cyclostomes) en Méditerranée. *Écologie et systématique*. *Mem Inst Oceanogr Monaco* 10:1–326
- Harmelin J-G (2017) 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* 31:105–123
- Harmelin J-G, Rosso A (2023) 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. *Zoosystema* 45(10):373–407
- Harmelin J-G, Bishop JDD, Madurell T, Souto J, Spencer Jones ME, Zabala M (2019) Unexpected diversity of the genus *Collarina* Jullien, 1886 (Bryozoa, Cheilostomatida) in the NE Atlantic-Mediterranean region: new species and reappraisal of *C. balzaci* (Audouin, 1826) and *C. fayalensis* Harmelin, 1978. *Zoosystema* 41(21):385–418. <https://doi.org/10.5252/zoosystema2019v41a21>
- Harmelin J-G, Ostrovsky AN, Cáceres-Chamizo JP, Sanner J (2011) Bryodiversity in the tropics: taxonomy of *Microporella* species (Bryozoa, Cheilostomata) with peronate maternal zooids from Indian Ocean, Red Sea and southeast Mediterranean. *Zootaxa* 2798:1–30. <https://doi.org/10.11646/zootaxa.2798.1.1>
- Haugen MN, Novosel M, Wisshak M, Berning B (2020) The genus *Reptadeonella* (Bryozoa, Cheilostomatida) in European waters: there’s more in it than meets the eye. In: Wyse Jackson PN, Zágoršek K (eds) *Bryozoan Studies 2019*. Czech Geological Survey, Prague, pp 59–68.
- Hong JS (1980) Etude faunistique d’un fond de concrétionnement de type coralligène soumis à un gradient de pollution en Méditerranée nord-occidentale (Golfe de Fos). Université Aix-Marseille II, Thèse de Doctorat
- Hong JS (1982) Contribution à l’étude des peuplements d’un fond de concrétionnement Coralligène dans la région marseillaise en Méditerranée nord-occidentale. *Bull KORDI* 4:27–51
- Hong JS (1983) Impact of the pollution on the benthic community. *Bull Korean Fish Soc* 16(3):273–290
- Kidwell SM (2013) Time-averaging and fidelity of modern death assemblages: building a taphonomic foundation for conservation palaeobiology. *Palaeontology* 56(3):487–522
- Kipson S, Fourn M, Teixido N, Cebrian E, Casas E, Ballesteros E, Zabala M, Garrabou J (2011) Rapid biodiversity assessment and monitoring method for highly diverse benthic communities: a case study of Mediterranean coralligenous outcrops. *PLoS One* 6(11):e27103. <https://doi.org/10.1371/journal.pone.0027103>
- Kipson S, Yahyaoui A, Aissi M, Ouerghi A, Robert A, Tunesi L, Rende F, Agnesi S, Annunziatellis A, Angiolillo M, Giusti M, Badredine A, Mavrič B, Bernardeau Esteller JA, Díaz D, Massutí E, Taşkın E., Çinar ME, Garrabou J (2022) Coralligenous and other calcareous bio-concretions within the Integrated Monitoring and Assessment Programme of the Mediterranean Sea. 4th Mediterranean Symposium on the conservation of Coralligenous & other Calcareous Bio-Concretions, Genoa, Italy, 20–21 September 2022
- Laubier L (1966) Le Coralligène Des Albères-Monographie Biocénotique. *Ann Inst Oceanogr* 43:137–316
- López de la Cuadra CM, García-Gómez JC (1991) A new species of *Hemicyclopora* (Bryozoa: Cheilostomata) from the southern coast of Spain. In: Bigey FP, d’Hondt J-L (eds) *Bryozoaires actuels et fossiles: Bryozoa living and fossil*. *Bull Soc Sci Nat Ouest Fr, Mém HS* 1:213–218.
- Madurell T, Zabala M, Domínguez-Carrió C, Gili JM (2013) Bryozoan faunal composition and community structure from the continental shelf off Cap de Creus (Northwestern Mediterranean). *J Sea Res* 83:123–136. <https://doi.org/10.1016/j.seares.2013.04.013>
- Mercurio M, Giménez G, Bavestrello G, Cardone F, Corriero G, Giam-paoletti J, Gravina MF, Pierri C, Longo C, Giangrande A, Nonnis Marzano C (2024) A dataset of benthic species from mesophotic bioconstructions on the Apulian Coast (southeastern Italy, Mediterranean Sea). *Data* 9:45. <https://doi.org/10.3390/data9030045>
- Montefalcone M, Morri C, Bianchi CN, Bavestrello G, Piazzi L (2017) The two facets of species sensitivity: stress and disturbance on coralligenous assemblages in space and time. *Mar Pollut Bull* 117:1–2. <https://doi.org/10.1016/j.marpolbul.2017.01.072>
- Montefalcone M, Tunesi L, Ouerghi A (2021) A review of the classification systems for marine benthic habitats and the new updated Barcelona Convention classification for the Mediterranean. *Mar Environ Res*. <https://doi.org/10.1016/j.marenvres.2021.105387>
- Novosel M, Pozar-Domac A, Pasaric M (2004) Diversity and distribution of the bryozoa along underwater cliffs in the Adriatic Sea with special reference to thermal regime. *Mar Ecol* 25(2):155–170. <https://doi.org/10.1111/j.1439-0485.2004.00022.x>
- Pérès JM, Picard J (1958) Manuel de bionomie benthique de la Mer Méditerranée. *Recl Trav Stn Mar Endoume* 23(14):5–122.
- Pérès JM, Picard J (1964) Nouveau manuel de bionomie benthique de la Mer Méditerranée. *Recl Trav Stn Mar Endoume* 31(47):5–137.
- Piazzi L, Bonaviri C, Castelli A, Ceccherelli G, Costa G, Curini-Galletti M, Langeneck J, Manconi R, Montefalcone M, Pipitone C, Rosso A, Pinna S (2018) Biodiversity in canopy-forming algae: structure and spatial variability of the Mediterranean *Cystoseira* assemblages. *Estuar Coast Shelf Sci* 207:132–141
- Piazzi L, Cecchi E, Cinti MF, Marino G, Nicastro A, Pacciardi L, Pertusati M, Ria M, De Biasi AM (2023) Coralligenous cliffs: distribution and extent along the Tuscany coasts and spatial variability of the associated assemblages. *Mediterr Mar Sci* 24(2):314–322. <https://doi.org/10.12681/mms.32119>
- Piazzi L, Cinti MF, Guala I, Grech D, La Manna G, Pansini A, Pinna F, Stipčich P, Ceccherelli G (2021) Variations in coralligenous assemblages from local to biogeographic spatial

- scale. Marine Environ Res. <https://doi.org/10.1016/j.marenvres.2021.105375>
- Piazzi L, Ferrigno F, Guala I, Cinti MF, Conforti A, De Falco G, De Luca M, Grech D, La Manna G, Pascucci V, Pansini A, Pinna F, Pireddu L, Puccini A, Russo GF, Sandulli R, Santonastaso A, Simeone S, Stelletti M, Stipcich P, Ceccherelli G (2022) Inconsistency in community structure and ecological quality between platform and cliff coralligenous assemblages. *Ecol Indic* 136:108657
- Piazzi L, Gennaro P, Montefalcone M, Bianchi CN, Cecchi E, Morri C, Serena F (2019) STAR: an integrated and standardized procedure to evaluate the ecological status of coralligenous reefs. *Aquat Conserv* 29:189–201
- Pinna F, Piazzi L, Cinti MF, Pansini A, Stipcich P, Ceccherelli G (2021) Vertical variation of coralligenous cliff assemblages in marine biogeographic areas. *Estuar Coast Shelf Sci* 261:107554. <https://doi.org/10.1016/j.ecss.2021.107554>
- RAC/SPA - UNEP/MAP (2014) Testing of monitoring protocol for coralligenous community: 2014 Field Report by Kipson S. RAC/SPA - MedMPAnet Project, Tunis, 91 pp + annexes
- Reverter-Gil O, Fernández-Pulpeiro E (1997) Two new species of *Shizomavella* [sic] (Bryozoa, Cheilostomatida). *Cah Biol Mar* 38(1):1–6.
- Reverter-Gil O, Souto J, Fernández-Pulpeiro E (2012) A new genus of *Lanceoporidae* (Bryozoa, Cheilostomata). *Zootaxa* 3339(1):1–29. <https://doi.org/10.11646/zootaxa.3339.1.1>
- Reverter-Gil O, Souto J, Novosel M, Tilbrook KJ (2016) Adriatic species of *Schizomavella* (Bryozoa: Cheilostomata). *J Nat Hist* 50(5–6):281–321. <https://doi.org/10.1080/00222933.2015.1062153>
- Rosso A (1996) Popolamenti e tanatocenosi a Briozoi di fondi mobili circolatori del Golfo di Noto (Sicilia SE). *Nat sicil, ser. 4*, 20(3–4):189–225
- Rosso A, Chimenz Gusso C, Balduzzi A (2010) Bryozoa. In: Relini G. Checklist della flora e della fauna dei mari italiani (parte II). *Biol Mar Mediterr* 17(suppl.):589–615
- Rosso A, Di Martino E (2016) Bryozoan diversity in the Mediterranean Sea: an up-date. *Mediterr Mar Sci* 17(2):567–607. <https://doi.org/10.12681/mms.1706>
- Rosso A, Di Martino E (2023) Capturing the moment: a snapshot of Mediterranean bryozoan diversity in the early 2023. *Mediterr Mar Sci* 24(2):426–445. <https://doi.org/10.12681/mms.34329>
- Rosso A, Di Martino E, Gerasileiou V (2020) Revision of the genus *Setosella* (Bryozoa: Cheilostomata) with description of new species from deep-waters and submarine caves of the Mediterranean Sea. *Zootaxa* 4728(4):401–442. <https://doi.org/10.11646/zootaxa.4728.4.1>
- Rosso A, Di Martino E, Donato G, Figuerola B, Gerasileiou V, Siddiolo C, Sinagra A, Sanfilippo R, Sciuto F (2025) Unlocking Mediterranean bryozoan diversity: seven new species unveiled after fixing a neotype for *Fenestulina malusii* (Audouin & Savigny, 1826). *Zookeys* 1254:1–74
- Rosso A, Donato G, Sanfilippo R, Serio D, Sciuto F, D'Alpa F, Bracchi VA, Negri MP, Basso D (2023) The bryozoan *Margaretta cereoides* as a habitat-former in the Coralligenous of Marzamemi (SE Sicily, Mediterranean Sea). In the special issue: Koulouri P, Gerasileiou V and Dailianis T (eds). Marine Benthic Biodiversity of Eastern Mediterranean Ecosystems. *J Mar Sci Eng* 11:590. <https://doi.org/10.3390/jmse11030590>
- Rosso A, Harmelin JG, Sanfilippo R, Sciuto F (2020) *Turbicellepora incrassata* and *Corallium rubrum*: unexpected relationships in a coralligenous habitat from NW Sardinia, Mediterranean Sea. In: Wyse Jackson PN, Zágorský K (eds) *Bryozoan Studies* 2019. Czech Geological Society, Prague, pp 125–137
- Rosso A, Sanfilippo R (2009) The contribution of Bryozoans and Serpuloideans to coralligenous concretions from SE Sicily. In: Pergent-Martini C, Brichet M (eds) *UNEP/MAP-RAC/SPA, proceedings of the first symposium on the coralligenous and other calcareous bioconcretions of the Mediterranean Sea*, Tabarka, Tunisia, 15–16 January 2009. RAC/SPA Publication, Tunis, Tunisia, pp 123–128
- Souto J, Fernández-Pulpeiro E, Reverter-Gil O (2010) The genus *Amathia* Lamouroux (Bryozoa: Ctenostomata) in Iberian waters. *Cah Biol Mar* 51(2):181–195.
- Souto J, Nascimento KB, Reverter-Gil O, Vieira LM (2019) Dismantling the *Beania magellanica* (Busk, 1852) species complex (Bryozoa, Cheilostomata): two new species from European waters. *Mar Biodivers* 49:1505–1518. <https://doi.org/10.1007/s12526-018-0925-2>
- True MA (1970) Étude quantitative de quatre peuplements sciaphiles sur substrat rocheux dans la région marseillaise. *Bull Inst Océanogr Monaco* 69(1401):1–48.
- UNEP-MAP-RAC/SPA (2008) Action plan for the conservation of the coralligenous and other calcareous bioconcretions in the Mediterranean Sea. Ed. RAC/SPA, Tunis, 21 pp.
- UNEP-MAP-RAC/SPA (2016) Action plan for the conservation of the coralligenous and other calcareous bioconcretions in the Mediterranean Sea. Ed. RAC/SPA, Tunis, 28 pp. + Annex
- Varzi AG, Fallati L, Savini A, Bracchi VA, Bazzicalupo P, Rosso A, Sanfilippo R, Bertolino M, Muzzupappa M, Basso D (2023) Geomorphological mapping of Coralligenous reefs offshore south-eastern Sicily (Ionian Sea). *J maps* 19(10):1–13. <https://doi.org/10.1080/17445647.2022.2161963>
- WoRMS (2025) Editorial Board. World Register of Marine Species. Accessed on August 2025. Available from <http://www.marinespecies.org>
- Zabala M (1984) Briozous de les illes Medes. In: Els sistemes naturals de les Illes Medes J. Ros, I. Olivella & J.M. Gili Eds. *Arxius Secció Ciències* 73:537–562. IEC, Barcelona
- Zabala M (1986) Fauna dels Briozous dels Països Catalans, vol vol 84. IEC Arxius de la Secció de Ciències, Barcelona, pp 1–836

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