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Mollusk diversity of coralligenous build-ups in the southwestern Ionian Sea

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Abstract

The coralligenous algal reefs are priority ecosystems of the Circalittoral zone of the Mediterranean Sea shelves. Characterized by decimeter- to meter-high build-ups, these reefs create a complex environment hosting high biodiversity. Despite their common occurrence, the roles of mollusks within coralligenous structures have been overlooked until recently. To address this gap, the CRESCIBLUREEF project investigated samples of coralligenous build-ups collected from diverse settings at similar depths (33.5-37.2 m) along the SE Sicilian shelf (Italy). In the studied samples, we identified 158 mollusk species –mostly autochthonous– including some previously undocumented for this habitat. Our study underscores the importance of using appropriate sampling techniques in studying mollusk biodiversity and the pivotal role algal reefs play in supporting a diverse array of mollusk species, spanning not only those associated with hard substrates but also epiphytic, cryptic, and infaunal species. Despite the samples being sourced at similar depths, multivariate statistical analysis based on mollusk abundance indicated a distinction between coralligenous morphologies in the living assemblage. Overall, our findings contribute to improving the knowledge on mollusks associated with coralligenous reefs and emphasize the valuable role of mollusks as sensitive indicators of environmental conditions, confirming their vital importance in conservation science and benthic ecology.

Keywords: Algal reef; benthic biodiversity; biocoenosis; thanatocoenosis; conservation science; Mediterranean Sea.

Introduction

The project “CRESCIBLUREEF Grown in the blue: new technologies for knowledge and conservation of Mediterranean reefs” aimed to explore the components, growth-rate, and accretion style of the Mediterranean algal reefs (i.e., coralligenous reefs). Coralligenous reefs are among the most monumental bioconstructions of the Mediterranean Sea (Ballesteros, 2006), and are mainly built by crustose coralline algae (Laubier, 1966; Hong, 1980; 1982; Di Geronimo *et al.*, 2002; Ballesteros, 2006; Bracchi *et al.*, 2022; Basso *et al.*, 2022). Minor contributions are made by other habitat-forming, skeletonized invertebrates such as bryozoans and serpulids, as well as sponges and autochthonous-micrite (Laubier, 1966; Ballesteros, 2006; Bertolino *et al.*, 2019; Cipriani *et al.*, 2023, 2024; Rosso *et al.*, 2023; Sanfilippo *et al.*, 2023, 2025). The building of these reefs results in a complex and very heterogeneous substrate, forming both discrete structures and tabular banks (Bracchi *et al.*, 2017). The reefs provide microhabitats and niches at different scales, and along a light gradient from exposed surfaces to very dark cavities and crevices, supporting several kinds of communities (Hong, 1980; Ballesteros, 2006; Basso *et al.*, 2022; Donato *et al.*, 2024).

Several studies have explored the biodiversity and functional role of coralligenous reefs in the marine ecosystem, yielding lists of their associated invertebrates (Laubier, 1966; Hong, 1980; Ballesteros, 2006; Kipson *et al.*, 2011). Moreover, the Action Plan for the Conservation of the Coralligenous and other Calcareous Bio-Concretions in the Mediterranean Sea (UNEP-MAP-RAC/SPA, 2008; 2016) clearly indicated the need for coralligenous faunal and algal species lists, together with robust metadata to build a database with GIS incorporated into it. Data exist, for example, for Porifera (Bertolino *et al.*, 2013), although not in the form of a database with spatial information, while data are still scattered throughout the specialist literature for other major animal phyla such as Chordata, Arthropoda, Annelida, and Bryozoa, as well as Mollusca.

Mollusks are one of the most-studied phyla in the Mediterranean Sea, where they number more than 2000 species, which corresponds to 13% of the total benthic biodiversity (Coll *et al.*, 2010). The CorMol database (Poursanidis & Koutsoubas, 2015) contains information about coralligenous-reef-associated mollusk biodiversity based on bibliographical sources published in both scientific journals and the gray literature. This database includes 511 species of mollusks, which mostly comprise Gastropoda (357), followed by Bivalvia (137), Polyplacophora (14), Cephalopoda (2), and Scaphopoda (1). Literature on coralligenous malacofauna emphasizes its diversity and complexity compared to that of nearby soft-bottom assemblages (Laubier, 1966; Hong, 1980; Huelin & Ros, 1984; Martin *et al.*, 1990; Delongueville & Scaillet, 2005; Ballesteros, 2006; Romdhane *et al.*, 2007; Casellato & Stefanon, 2008; Albano & Sabelli, 2011; Urra *et al.*, 2012; Bedini *et al.*, 2014; Poursanidis & Koutsoubas, 2015; Donnarumma *et al.*, 2018; Casoli *et al.*, 2019; Sini *et al.*, 2019; Albano *et al.*, 2022), but data are still sparse and limited. There are several reasons why mollusks that associate with coralligenous reefs are scarcely studied. For instance, while coralligenous reefs are the climax biocoenoses of the circalittoral zone of the Mediterranean Sea (Pérès & Picard, 1964), they also occur as enclaves in the infralittoral zone. The original definition of Pérès and Picard (1964) indicated several facies, but seafloor exploration in recent decades has expanded the list (Cánovas Molina *et al.*, 2016; Bracchi *et al.*, 2017; Corriero *et al.*, 2019), broadening the original concept of coralligenous reefs and stimulating a reflection on its definition. This has prompted several –albeit still few– site-specific studies of coralligenous malacofauna, which had previously not been studied in the context of its geomorphological and bathymetric variability. Moreover, there are technical limits to obtaining appropriate samples to study, to evaluate coralligenous biodiversity with. This is due to the depth at which coralligenous build-ups occur (often well beyond recreational scuba diver limits), and to the unavailability of suitable devices and/or the use of inadequate ones such as photoquadrats (Romdhane *et al.*, 2007; Sini *et al.*, 2019) or dredges (Urra *et al.*, 2012; Albano *et al.*, 2022).

To improve the knowledge on coralligenous algal reefs, the CRESCIBLUREEF project devoted specific activities to the description and quantification of their associated biodiversity. Within this framework, it was possible to collect appropriate samples of coralligenous build-ups from different environmental settings in an area located in front of the Marzamemi coast (Sicily, Southern Italy) at *ca.* 35 m depth. In the studied area, the algal reefs exhibit both discrete columns, separated distinct build-ups and hybrid banks, and merged adjacent build-ups to form a structure that resembles a small platform (Bracchi *et al.*, 2017).

The compositional fidelity of mollusk species and genera to biotic and edaphic factors has been widely studied, also suggesting that molluscan dead assemblages accurately record a wide range of ecological patterns (Kidwell, 2001; 2002; 2007; 2013; Kidwell *et al.*, 1991; Dietl *et al.*, 2016). The aim of this paper is to contribute to our knowledge of the coralligenous environment by describing its mollusk biodiversity and enhancing our quantitative understanding of both living (biocoenosis) and dead (thanatocoenosis) mollusk assemblages. Additionally, we assessed the efficacy of utilizing the mollusk assemblages as tools for discerning different coralligenous morphotypes and environmental features.

Materials and Methods

Within the framework of campaign CBR2 of the CRESCIBLUREEF project (August 2021), scuba divers collected samples from an offshore Marzamemi (SW Ionian Sea, Sicily). In this location, coralligenous reefs occur within the depth interval of approximately 30 m to 90 m (Fig. 1, Table 1, Varzi *et al.*, 2023), with the samples being collected between 33.5 and 37.2 m (Table 1). Two entire build-ups (samples CBR2_3_7c and CBR2_4_21c, Fig. 1a-c) were collected from areas where the coralligenous structure formed hybrid banks and discrete columns, respectively (Fig. 1a-c, Table 1). These two samples are respectively referred to as 7c and 21c throughout the text. We sampled four further build-ups (build-up A, sampled from discrete columns, and build-ups B, D, and F, sampled from hybrid banks; Fig. 1a-c, Table 1) during dive activities through both the air-sucking of vagile fauna and the scraping of surface material. For sucking, we used an airlift sampler, consisting of a 100-cm-long PVC tube with a diameter of 6 cm, fitted 10 cm above the mouth with a scuba cylinder supplying air. At the other end of the tube, we fixed a removable bag. For scraping, we collected manually detached surface portions of the previously air-sucking-sampled build-ups.

All living and dead specimens (>1 mm, following Basso & Corselli, 2002) were picked up at immediately after collection. We identified mollusks under a binocular microscope using the relevant literature (e.g., Tebble, 1966; Parenzan, 1970; 1974; D'Angelo & Gargiullo, 1991; Poppe & Goto, 1991, 1993; Giannuzzi-Savelli *et al.*, 2001; Repetto *et al.*, 2005; Scuderi & Terlizzi, 2012; Caro, 2025) and quantified their occurrence in living/dead assemblages following the rationale of Basso & Corselli (2007). The final data matrix is provided in Supplementary 1. The criteria for retaining and counting shell remains in dead assemblages followed Di Geronimo & Robba (1976). We coded the status (i.e., the size/age distribution of individuals of each species) populations with only juveniles (J), only adults (A), or both (J+A), and provided a code to indicate the best preservation state (from 1 to 5) observed for each species in each sample, following Basso & Corselli (2007). Species that occurred in both biocoenosis and thanatocoenosis were coded as 5, but the numbers of living/dead specimens were recorded (Supplementary 1). We extracted data on substrate preference, life habit, motility, and feeding guilds from the literature

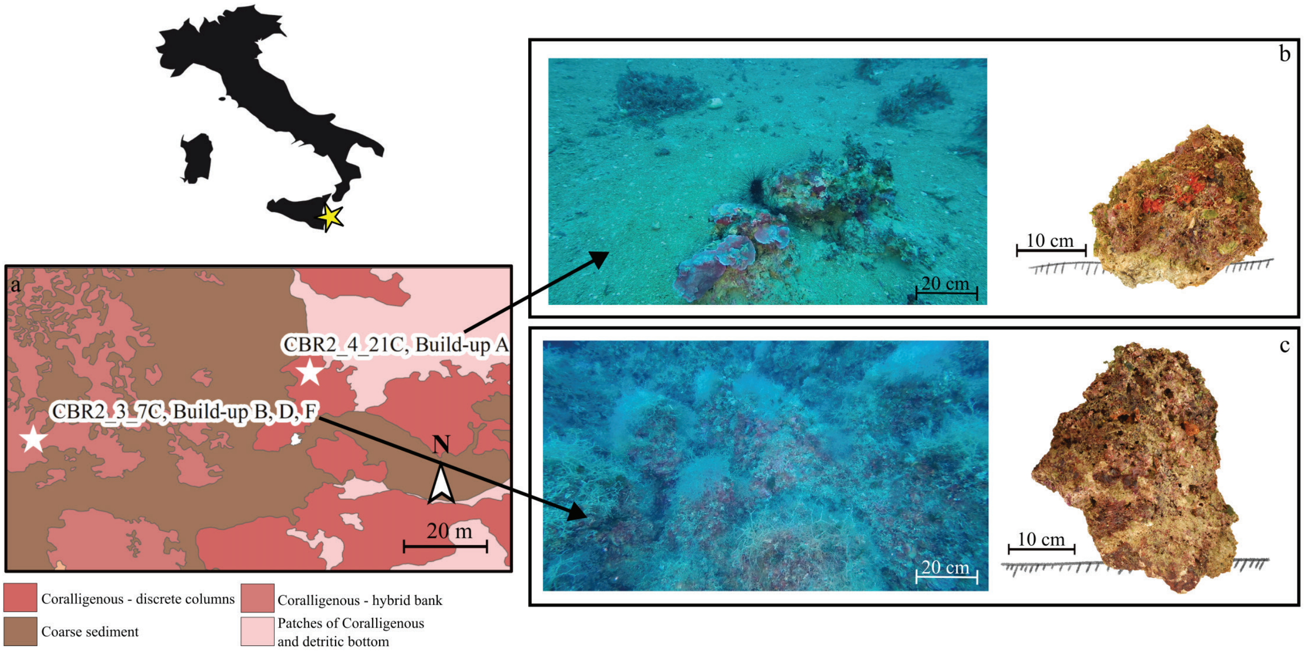

Fig. 1: Geographical setting of the studied samples, with the indication of the study area. a) Sampling sites plotted on the habitat map of Varzi et al., (2023). b) Example of Coralligenous as discrete columns and the sample CBR2_4_21c. c) Example of Coralligenous as hybrid bank and the sample CBR2_3_7c.

Table 1. List of the collected samples, with location, depth (m) and C morphotype. Results of the univariate statistics: mollusk species richness (S) and specimen abundance (N) for the whole samples (tot), and for species that occur in biocoenosis (*bioc*) and thanatocoenosis (*than*).

Sample	Location	Depth (m)	C morphotype	S tot	N tot	S *bioc*	N *bioc*	S *than*	N *than*
Build-up A	36.72423° N, 15.16095° E	37.2	Discrete build-ups	72	581	28	165	68	416
21c	36.72423° N, 15.16095° E	36.7	Discrete build-ups	82	559	35	327	67	232
Build-up B	36.72323° N, 15.15781° E	36.2	Hybrid bank	64	343	19	118	59	225
Build-up D	36.72322° N, 15.15780° E	36.2	Hybrid bank	79	539	25	209	75	330
Build-up F	36.72323° N, 15.15781° E	33.5	Hybrid bank	69	409	20	217	60	192
7c	36.72322° N, 15.15780° E	36.2	Hybrid bank	93	295	24	59	86	236

and available databases. For life habit, we used epifaunal for species living on and above the substrate, infaunal for species that live inside the substrate, and, among infaunal, we specified endolithic for species with nestling or boring life-habit. Motility was expressed as either vagile, sedentary (for infaunal species that do not move and/or for species with scarce movement), or sessile (for species that live encrusted on, or fixed with a strong byssus to the substrate) (Supplementary 1). We identified five categories for feeding guilds: predators (P), ectoparasites (E), grazers (G, both micro and macro), deposit feeders (DF), and suspension feeders (SF). Biocoenosis fidelity was extracted from the literature (Pérès & Picard, 1964; Pérès, 1982; Basso & Corselli, 2002; MNHN & OFB, 2024) and recorded as "excl" for species with exclusive fidelity and "pref" for those with preferential fidelity. The biocoenoses cited in this paper, with their corresponding acronyms in brackets, are summarized in Table 2. Finally, for some species, no level of fidelity could be found in the literature; nevertheless, they may currently occur in some biocoenoses and not in others, thus showing a generic affinity with them.

Statistical treatment of the results, using PRIMER-E7 (Primer-e/Quest Research Limited, Albany, New Zealand), defined similarity and dissimilarity among samples and live/dead assemblages (i.e., biocoenosis and thanatocoenosis, respectively). Univariate statistics calculated the species richness (number of species), as well as the specimen abundance for each species (Table 2). We used cluster analysis based on Bray–Curtis similarity for the hierarchical classification of mollusk abundance data. The SIMPER routine (Clarke & Warwick, 2001) was used to define which species were the greatest contributors to the similarity/dissimilarity between/within clusters in biocoenosis and thanatocoenosis.

Table 2. List of the biocoenoses sensu Pérès & Picard (1964) used in the text. Definitions and acronyms are from Pérès & Picard (1964) and MNHN & OFB (2024).

Infralittoral zone	Infralittoral algae (ex Photophylous algae)	**IA (ex AP)**
	Posidonia meadows	**HP**
	Muddy sands in sheltered waters	**SVMC**
	Well-sorted fine sands	**SFBC**
Circalittoral zone	Coralligenous	**C**
	Coastal detritic	**DC**
Bathyal zone	Deep-sea mud	**VP**
Unrelated to zonation	Coarse sand and fine gravel under the influence of bottom currents	**SGCF**
	Heterogeneous assemblages	**PE**

Results

We identified 158 species, including 60 bivalves, 96 gastropods, and 2 polyplacophorans (Supplementary 1). The number of species per sampled site ranged between 64 (build-up B) and 93 (7c), while the number of specimens from 295 (7c) to 581 (build-up A) (Table 2). Sixty-six species out of 158 occurred in at least one sample in a living assemblage, ranging from 19 living species in build-up B to 35 in 21c (Table 2, Supplementary 1). Among them, 12 species were found exclusively in biocoenosis, whereas 54 also included specimens found in thanatocoenosis (Supplementary 1). There were 146 species occurring in thanatocoenosis, among which 92 were exclusively dead (Supplementary 1). The number of species in thanatocoenosis per sample ranged between 59 (build-up B) and 86 (7c), and was represented by between 192 (build-up F) and 416 (build-up A) specimens (Table 2, Supplementary 1).

In terms of life habit, the sampled mollusks included 104 epifaunal (82 vagile, 20 sessile, and 2 sedentary), 30 infaunal, and 11 endolithic species, as well as 13 taxa to which a lifestyle could not be attributed because the specimens were not defined at the species level (Supplementary 1). Suspension feeders (57 species) were dominant, followed by grazers (38), predators (31), ectoparasites (8), scavengers (9), and 16 unknown and/or unattributable feeding types for the specimens that were not identified at the species level (Supplementary 1).

Biocoenosis

Among the 66 living species of the biocoenoses, we identified 31 bivalves, 34 gastropods, and 1 polyplacophorans (Supplementary 1). Forty-five species were collected with both juvenile and adult specimens, six with only adults, and 16 with only juveniles (Supplementary1). Twelve species occurred exclusively in biocoenosis, whereas the other 54 were also sampled as dead specimens. Interestingly, among the 12 species occurring exclusively in biocoenosis, only a few specimens and only juveniles were sampled for most of them, with the sole exception of *Acar clathrata* (Supplementary 1). Suspension feeders were abundant (30), as were grazers (16), whereas predators (7), detritus feeders (4), and ectoparasites (3) were less abundant (Supplementary 1). We recorded 42 epifaunal species, among which 28 were vagile, 13 sessile, and 1 sedentary; we also identified 11 infaunal and 9 endolithic species (Supplementary 1). Among the sessile epifauna, species that encrust coralligenous build-ups were recorded (*Thylacodes arenarius*, *Vermetus granulatus*, and *V. triquetrus*).

There were only three species associated with Coralligenous (C) biocoenosis (*Bolma rugosa*, *Pteria hirundo*, and *Lithophaga lithophaga*), but none of them were exclusive nor preferential to this biocoenosis (Supplementary 1). Other significant species were *Glans trapezia* (excl HP, J+A) and *Modiolula phaseolina* (excl DC, J+A), together with two preferential DC (*Kellia suborbicularis* and *Papillicardium papillosum*, both J+A) and one preferential IA (*Arca noae*, J) species (Table 3, Supplementary 1).

Multivariate statistical analysis based on mollusk abundance in biocoenosis identified two clusters with a similarity of 50% (Fig. 2). Cluster B1 included the 21c and A sample sites, both corresponding to discrete columns, whereas cluster B2 included samples collected from hybrid banks (Fig. 2). The SIMPER routine identified *Gregariella semigranata*, *Striarca lactea*, and *Bittium latreillii* as the most statistically significant species for both similarity within clusters and dissimilarity between clusters (Table 4, Supplementary 2). Specifically, *G. semigranata* and *B. latreillii* were more abundant in cluster B1 than B2, whereas *S. lactea* showed the opposite trend, with higher abundance in cluster B2. In addition, *Caecum auriculatum* was more abundant in cluster B2 than B1 (Supplementary 2). *Coripia corbis* occurred exclusively in cluster B, while *Neolepton sulcatum*, *Asperarca magdalenae*, and *Dacrydium hyalinum* occurred exclusively in cluster B2 (Table 4, Supplementary 2).

Thanatocoenosis

We recorded 146 species in thanatocoenosis (Table 2), of which 92 were found exclusively in this state. The preservation of 78 species out of the total corresponded to 3 or 4 (Supplementary 1). These species were represented by populations of variable age (J, A, or both). Species

Table 3. Synthesis of the species in biocoenosis and thanatocoenosis with respect to the Preservation and Status. Number refers to species. Indication of the contribution of species with ecological fidelity *sensu* Pérès & Picard (1964) is reported.

	Preservation	**Status**		
		J	**A**	**J+A**
Biocoenosis	5	1 pref IA		1 excl DC; 2 pref DC; 1 excl HP
Thanatocoenosis	4	1 pref DC	1 pref SGCF	1 excl DC; 1 excl VP; 1 excl SGCF
	3			1 excl HP; 1 excl DC; 1 acc DC
	2	1 pref PE; 1 excl SVMC	1 excl SFBC	

occurring as J+A with preservation of 3 or 4 included two excl DC species (*Limatula gwyni* and *Turritella turbona*), one excl VP (*Limatula subauriculata*), one excl SCGF (*Venus casina*), and one excl HP (*Venus verrucosa*) species. Only adult and juvenile specimens, respectively, were recorded for *Laevicardium crassum* (pref SGCF) and *Gibbula magus* (pref DC) (Table 3, Supplementary 1). Among the species in thanatocoenosis, more epifaunal species (96, among which 77 were vagile, 17 sessile, and 2 sedentary) than infaunal (30) and endolithic (11) species were recorded, and a total of 13 suspension-feeders, 9 grazers, 9 predators, 2 detritus-feeders, and 2 ectoparasites occurred (Supplementary 1). Table 3 also presents the results related to preservation states 1 and 2. Notably, species associated with infralittoral biocoenoses such as SFBC and SVMC were recorded, but only with juvenile or adult specimens, respectively (Table 3, Supplementary 1). In addition, *Varicorbula gibba* (preferential PE) occurred (Table 3).

Multivariate statistical analysis identified a complex structure, with two evident clusters at a level of 59% of Bray–Curtis similarity and two isolated samples (Fig. 3). The first cluster (T1) included build-ups B and 7c; the second cluster (T2) included build-ups A and D. The other two samples, build-ups 21c and F, remained separated (Fig. 3). The clustering did not clearly correspond to the morphology of the build-ups, although build-ups D, B, and 7c remained close. The SIMPER routine identified a list of species responsible for the similarity/dissimilarity among samples (Supplementary 2). Table 5 presents the pair comparisons between clusters/samples based on the exclusive occurrence of species. Clusters T1 and T2 showed few differences, whereas the list of pairs in other cluster comparisons was longer. Interestingly, *Vermetus granulatus*, *Flexopecten flexuosus*, *Musculus costulatus*, and *Caecum trachea* were unique to sample 21 c, and *Calyptraea chinensis* was unique to sample F.

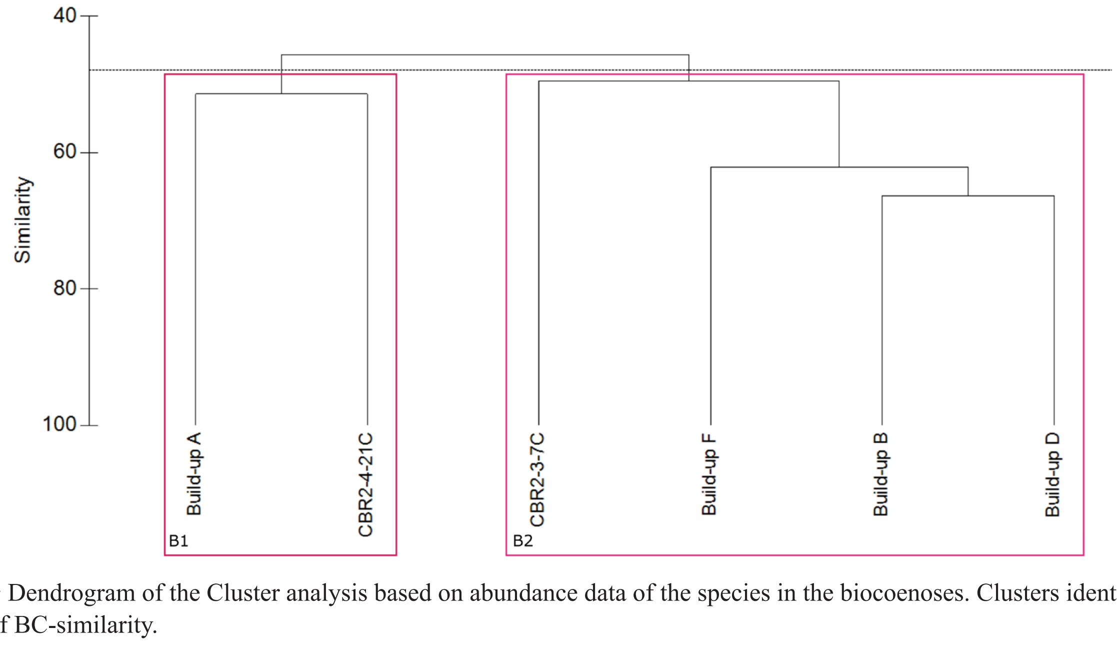

Fig. 2: Dendrogram of the Cluster analysis based on abundance data of the species in the biocoenoses. Clusters identified at 50% level of BC-similarity.

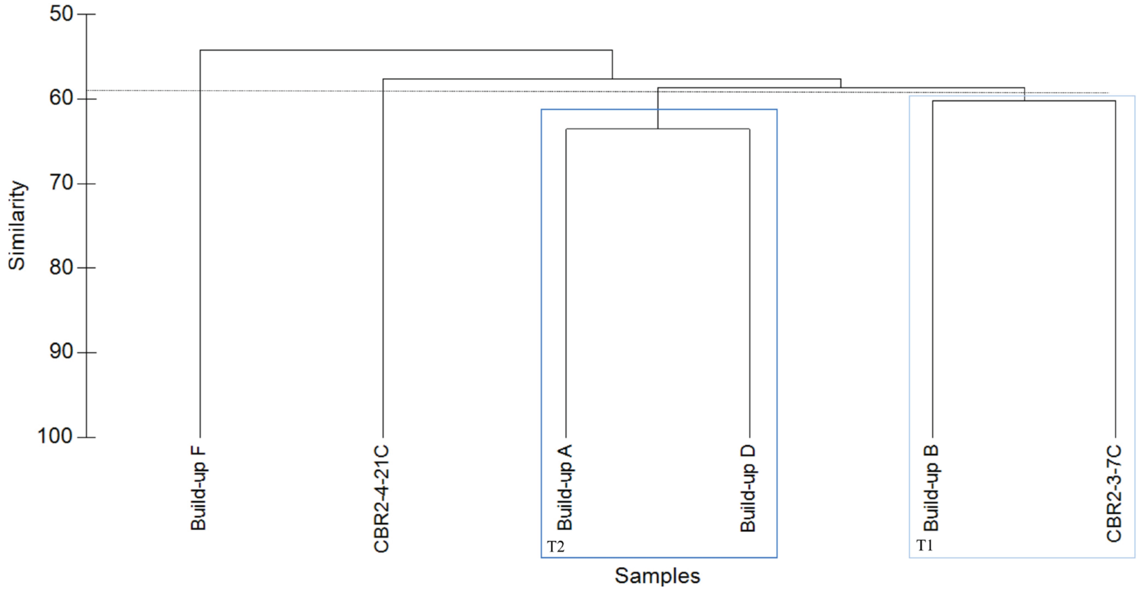

Fig. 3: Dendrogram of the Cluster analysis based on abundance data of species occurring in the thanatocoenoses. Clusters identified at 59% level of BC-similarity.

Table 4. Results of the SIMPER analysis, showing the species that are responsible for the similarity/dissimilarity between clusters B1 and B2 in biocoenosis (Cum%-50% cut-off).

Average similarity	Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
B1 - 51.45%	*Gregariella semigranata*	11.4	16.24		31.56	31.56
	Bittium latreillii	5.99	5.65		10.97	42.54
	Striarca lactea	3.16	5.38		10.46	53.00
B2 - 56.56%	*Gregariella semigranata*	6.75	9.38	2.48	16.59	16.59
	Bittium latreillii	4.73	8.58	5.60	15.16	31.75
	Striarca lactea	3.45	6.07	3.00	10.72	42.48
	Asperarca magdalenae	2.64	5.74	6.94	10.15	52.63

Average dissimilarity	Species	Av.Abund B1	Av.Abund B2	Av.Sim	Sim/SD	Contrib%	Cum.%
B1/B2 - 54.29%	*Gregariella semigranata*	11.4	6.75	5.21	1.53	9.59	9.59
	Neolepton sulcatulum	0	2.93	2.84	4.39	5.23	14.82
	Bittium latreillii	5.99	4.73	2.61	1.55	4.81	19.64
	Asperarca magdalenae	0	2.64	2.61	6.20	4.80	24.44
	Caecum auriculatum	0.71	2.67	1.89	1.50	3.48	27.92
	Pusillina inconspicua	2.09	0.25	1.82	3.03	3.35	31.27
	Dacrydium hyalinum	0	1.60	1.54	1.28	2.84	34.11
	Williamia gussoni	1.62	0.25	1.27	1.87	2.35	36.45
	Haminoea hydatis	1.22	0.50	1.27	1.23	2.34	38.80
	Pusillina philippi	1.83	0.81	1.24	1.35	2.29	41.08
	Striarca lactea	3.16	3.45	1.01	1.88	1.86	42.94
	Coripia corbis	1.00	0	0.99	7.68	1.82	44.76
	Musculus costulatus	2.22	1.30	0.98	1.00	1.81	46.57
	Lima lima	1.21	0.25	0.94	1.78	1.73	48.29
	Rissoella inflata	0.87	0.75	0.91	1.15	1.67	49.97
	Limaria sp.	1.00	0	0.90	0.93	1.66	51.63

Table 5. Results of the SIMPER analysis for thanatocoenosis (Cum%-30% cut-off). Columns A and B indicate the pairs of clusters/samples that are compared in each row. Column C includes the list of species that are only in the clusters/samples of the column A. Column D includes the list of species that are only in the clusters/samples of the column B. In bold, species that occur exclusively in one clusters/samples of columns A or B respectively.

A	B	C	D
T1	**T2**	*Eulimella acicula, Limatula gwyni*	*Retusa mamillata, Skenea serpuloides, Haminoea hydatis, Thracia distorta*
	21c	*Bolma rugosa, Neolepton sulcatum, Rissoa violacea, Moerella pulchella*	***Vermetus granulatus**, Haminoea hydatis, Retusa mamillata, **Flexopecten flexuosus**, **Musculus costulatus**, **Caecum trachea**, Skenea corbuloides*
	F	*Coripia corbis, Eulimella acicula, Williamia gussoni, Rissoa violacea, Moerella pulchella, Alvania geryonia, Homalopoma sanguineum, Venus casina, Odostomia plicata, Partenina interstincta*	***Calyptraea chinensis**, Mangelia taeniata, Metaxia metaxa*
T2	**21c**	*Obtusella intersecta, Bolma rugosa, Petalopoma elisabettae, Granulina boucheti, Gibbula guttadauri*	***Vermetus granulatus**, **Flexopecten flexuosus**, Talochlamys multistriata, Pusia savignyi*
	F	*Parthenina interstincta, Williamia gussoni, Rissoella inflata, Retusa mammillata, Petalopoma elisabettae, Skenea serpuloides, Haminoea hydatis, Coripia corbis*	***Calyptraea chinensis***
21c	**F**	***Vermetus granulatus**, Haminoea hydatis, Coripia corbis, Retusa mammillata, **Flexopecten flexuosus**, **Musculus costulatus**, Talochlamys multistriata, **Caecum trachea***	*Murexus aradasii, **Calyptraea chinensis**, Limatula subauriculata, Neolepton sulcatulum, Cerithiopsis barleei*

Discussion

Previous studies

The scarcity of studies concerning the diversity of mollusks associated with coralligenous algal reefs can be primarily attributed to the inadequate understanding of mollusks' distribution and nature. This underscores the need for further investigation into their distribution and ecology to better understand the role of coralligenous mollusks within Mediterranean marine ecosystems. The pioneering French and Spanish studies on coralligenous reefs provided the earliest indications about the occurrence and significance of the mollusks associated with them; all references are from a small geographic area of the NW Mediterranean (Table 6). Ballesteros (2006), in his synthesis on the knowledge of the Mediterranean coralligenous assemblage, summarized these results and commented that mollusks contribute to biodiversity, having a role as bioconstructors, borers, and dwellers. After that, a few other studies were published, contributing to the knowledge on coralligenous mollusk biodiversity across the Mediterranean Sea (Table 6). The number of coralligenous-reef-associated mollusk species from literature-based data ranges from 4 to 508 (Table 6). Comparing the species lists extracted from individual published contributions with our results, we note that our new entries from Marzamemi are always greater than the number of shared species (Table 6). The shared species are more numerous in case studies of similar depth ranges (Table 6), whereas they decrease when shallower localities are sampled (Romdhane *et al.*, 2007; Urra *et al.*, 2012). This suggests that shallow coralligenous facies or enclaves can remarkably differ from deeper ones, also supporting different assemblages. Notably, only two papers describe mollusks associated with deep mesophotic rocky reefs (80 m depth, Corse, Delongueville & Scaillet, 2005; 92 m depth, northern Israel, Albano *et al.*, 2022); interestingly, we share 36 (36%) and 53 (40%) out of the 101 and 131 species that they listed, respectively.

Urra *et al.* (2012) emphasized that the richness of mollusk assemblages on hard (e.g., coralligenous) substrates exhibits higher diversity values compared to surrounding soft bottoms. This discrepancy in diversity is attributable to the structural complexity of coralligenous reefs, which provide both hard and soft substrates suitable for mollusks. Mercurio *et al.* (2024) listed mollusk species associated with mesophotic reefs occurring along

Table 6. Review of the literature on mollusks related to Coralligenous in the Mediterranean Sea, with the indication of: authors, depth (m), location, C morphotype when expressed or attributable, sampling methods, species abundance, and number of species shared with Marzamemi. The abbreviatio n.a. means not applicable.

Authors	Depth (m)	Location	C morphotype	Sampling method	n° spp.	Shared species
Laubier (1966)	20-40	France	Hybrid bank	Dredge	67	16
Hong (1980)	15-35	France	Unknown	Scraping	142	28
Huelin & Ros (1984)	0-50	Spain	Discrete columns/bank/caves	Scraping	255	59
Martin *et al.* (1990)	8-27	Spain	Discrete, enclave infralittoral	Scraping	131	42
Delongueville & Scaillet (2005)	80	France	Unknown	Manual sampling	101	36
Rohmdhane *et al.* (2007)	13	Tunisia	Enclave at the base of *Posidonia* meadow	Photoquadrat	27	5
Casellato & Stefanon (2008)	9-40	Italy, North Adriatic Sea	Discrete columns/hybrid bank	Unreported	197	51
Albano & Sabelli (2011)	30	Italy, Tyrrhenian Sea	Hybrid bank	Airlift pump	132	53
Urrà *et al.* (2012)	13-18	Spain	Unreported	Dredge	117	29
Bedini *et al.* (2014)	35	Italy, Tyrrhenian Sea	Horizontal/vertical rocky bottoms	Scraping	27	8
Poursanidis & Koutsoubas (2015)	n.a.	Mediterranean Sea	n.a.	n.a.	508	101
Donnarumma *et al.* (2018)	28-33	Italy, Tyrrhenian Sea, Ionian Sea	Unreported	Airlift pump	38	22
Casoli *et al.* (2019)	30	Italy, Tyrrhenian Sea	Hybrid bank/bank	Scraping	59	48
Sini *et al.* (2019)	18-35	Greece, North Aegean Sea	Unreported	Photoquadrat	4	0
Albano *et al.* (2022)	92	Israel	Hybrid bank	Rock dredge	131	53
Mercurio *et al.* (2024)	25-65	Italy, South Adriatic Sea	Horizontal bottom	Visual census, manual sampling	110	28

the Apulian coast and dominated by either crustose coralline algae (MAB) or invertebrates (MIB). Their results showed that MAB had a higher mollusk diversity than MIB, both collected between 25 and 65 m of depth. We shared only 28 species of the 110 they listed (Table 6).

We have also suggested that technical difficulties can hamper the collection of representative samples for quantitative studies on coralligenous biodiversity and on mollusks. When photoquadrats are used (Romdhane *et al.*, 2007; Sini *et al.*, 2019), mollusk species diversity is incompletely detected. Several mollusk species would not be identifiable or even visible in a photograph of the coralligenous surface due to their small size or because they are cryptic or infaunal species, or just covered by an algal canopy, as our results indicate (Supplementary 1). Consequently, photoquadrats are not an appropriate method with which to assess the mollusk diversity associated with coralligenous reefs. In contrast, when using airlift pumps (Albano & Sabelli, 2011; Donnarumma *et al.*, 2018) or scraping (Casoli *et al.*, 2019) alone or in combination (as in the present study), as well as manual sampling after washing, drying, and breaking up coralligenous specimens (Delongueville & Scaillet, 2005), small-sized and hidden species become evident and results are more robust, allowing for a more precise picture of mollusk biodiversity. By using standardized and appropriate sampling methods, we can ensure more reliable and coherent comparisons, thus enhancing our understanding of the biodiversity and ecological dynamics of coralligenous reefs. However, even comparable samples obtained with the same technique may show significant differences (Table 6). Indeed, the variability of mollusks from distinct locations, as presented in Table 6, underscores the diverse nature of algal reefs. Local variations in the coralligenous structure are common, leading to the development of varied combinations of microenvironments within the reefs.

As a result, mollusk assemblages can vary significantly from one location to another (Laubier, 1966; Casellato & Stefanon, 2008; Donnarumma *et al.*, 2018; Casoli *et al.*, 2019), especially where coralligenous formations develop at different depths (Albano *et al.*, 2022) and environmental conditions.

The mollusk biocoenosis of Marzamemi coralligenous reefs

Our results provide new data on the mollusk diversity associated with coralligenous reefs, suggesting that their complexity supports a much more varied assemblage than previously thought. From a quantitative point of view, the most abundant species sampled in Marzamemi was *Gregariella semigranata* (Supplementary 1), which had previously been reported to associate with coralligenous substrates (Sanfilippo *et al.*, 2023; and references therein). The same is true for *Bittium latreillii* and *Striarca lactea* (Supplementary 1), which show a statistical robustness in defining similarity and dissimilarity through samples in biocoenosis (Supplementary 2).

Coralligenous build-ups primarily act as a hard substrate for epifaunal mollusks with different feeding strategies (Supplementary 1). Besides that, in the coralligenous framework, the surfaces on and in which mollusks can live are of different natures, sizes, and orientation, in turn affected by variable combinations of controlling factors such as water energy and light conditions, thus creating suitable habitats for distinct species. Our study focused on coralligenous build-ups occurring around 35 m depth, at the limit between the infralittoral and circalittoral zones, and not far from the lower limit of *Posidonia oceanica* meadows (personal observation). Although direct measurements are lacking, the available light is still strong enough to support part of such a canopy (green algae on the top of the coralligenous build-ups, Fig. 1c-e, Donato *et al.*, 2024). Therefore, we suggest that the species in our list that associate with vegetated bottoms and meadows, and that we recorded with J+A status (Supplementary 1), are not all transported from surrounding habitats, but thrive within the algal canopy of such coralligenous build-ups. Among the epifaunal species, there were some encrusters, such as *Vermetus* spp. These species are interesting because they add volume to the build-ups and contribute to accreting the whole structure.

Coralligenous build-ups also have crevices and cavities that host pockets of fine sediment, where microhabitats and niches develop, and where mud-loving epifaunal and infaunal species can thrive (Casoli *et al.*, 2019). In the analyzed samples, we identified 10 out of 11 infaunal species with J+A specimens, and we consider them to be autochthonous (Supplementary 1).

Coralligenous build-ups also provide a biogenic carbonate substrate suitable for nestling and endolithic species, as demonstrated by the nine endolithic species we found occurring in biocoenosis, including *G. semigranata* and *Lithophaga lithophaga*, with the former being the most abundant species in our collection (see Sanfilippo *et al.*, 2025).

The complexity illustrated above supports a mollusk assemblage where all feeding guilds are well represented, as previously underlined by Casoli *et al.* (2019). We can therefore assume that coralligenous build-ups, as substrate, create a wealth of opportunities for both space and food resources, which then translates into such a diversified assemblage.

The cluster analysis based on biocoenosis separated samples into two clusters (B1 and B2 in Fig. 2), which interestingly identifies samples associated with different coralligenous morphotypes in Marzamemi (Fig. 1ce, Supplementary 2). A total of 19 species are shared between the two clusters, whereas 30 occur only in B1 and 18 only in B2.

Species exclusive of B1 mostly require detritic, coarse substrate, are epifaunal, and suspension feeders and grazers. Species exclusive of B1 are mostly epifaunal species associated with coralligenous/hard substrate. This suggests that the mollusks are strictly dependent from the local differences in Coralligenous morphology, although they were at similar depths. It is also important to note that the studied samples show an algal canopy (Fig. 1), and they are not far from the limit of Posidonia meadows (personal observation), this supporting our interpretation that several species, although related to infralittoral biocoenoses, should be considered autochthonous for the Coralligenous in Marzamemi.

The mollusk thanatocoenosis of Marzamemi coralligenous reefs

The thanatocoenosis included a large number of species and specimens, and confirmed what the living specimens indicated: that is, the great biodiversity that can be associated with coralligenous substrate. The thanatocoenosis shared 54 species with the biocoenosis, while 92 were present only in the thanatocoenosis. Among the shared species, many were recorded population of both juvenile and adult specimens; this supports the hypothesis of their autochthony, being present with both living and dead specimens with different sizes. It is no coincidence that this portion of the thanatocoenosis includes both epifaunal and infaunal species, with all feeding guilds recorded. The species exclusively in thanatocoenosis include those that are typically associated with small hard substrates, coarse substrates, and species associated with the DC biocoenosis; we can interpret this as typical of a coralligenous environment. Among these species, however, there were juvenile species associated with infralittoral biocoenoses (SVMC, SFBC) that could instead be considered allochthonous. The thanatocoenosis can remain faithful to the environment, but may suffer from processes such as mixing, transport, time averaging and condensation. The results of the cluster analysis of the thanatocoenosis in Marzamemi (Fig. 3) identified two clusters, while two samples remained isolated. Therefore thanatocoenosis is less informative than biocoenosis with respect to Coralligenous morphology in Marzamemi. Additionally, the SIMPER routine for thanatocoenosis highlighted differences in species composition among clusters and samples, revealing some degree of exclusivity (Supplementary 2), but none of these differences clearly define the factors driving separation in clustering.

Conclusion

This quantitative study based on living and dead mollusk assemblages helps elucidate the biodiversity associated with coralligenous habitats from the Marzamemi area (Sicily, Italy). Coralligenous reefs represent a suite of different substrates and microhabitats that host to varied mollusk assemblages. They function as a catalyst for species with diverse ecological requirements, providing a heterogeneous habitat, or a complex of different microhabitats for organisms with varying edaphic needs. Appropriate sampling is required to provide a complete list of mollusk biodiversity, including infaunal and cryptic species whereas the preservation and status of the species must be carefully assessed to establish their autochthony. Moreover, the mollusk living assemblage serves as a robust, sensitive, and reliable indicator of coralligenous morphology and faithfully mirrors the relatively shallow environmental conditions and the local differences between coralligenous morphotypes. This suggests that mollusks offer valuable insights into the current ecology of these habitats, allowing researchers to understand their dynamics, over at least recent times. Continued investigation of mollusk assemblages within these habitats thus holds promise for advancing our understanding of Mediterranean marine ecosystems and their evolution over time.

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Supplementary Data

The following supplementary information is available online for the article:

Supplementary 1: Data matrix with the list of identified species, status, preservation, occurrence, lifestyle, motility, feeding guild, substrate requirements, and biocoenosis fidelity. The species name (column 1) is in bold if it occurs in the biocoenosis, whereas not in bold if it occurs only in the thanatocoenosis. Status includes J for only juvenile specimens, A for only adult specimens and J+A when both occur. Preservation ranges from 1 (bad preservation, broken, abraded) to 5 (species that occur with living individuals). Occurrence includes B for biocoenosis, B+T for biocoenosis and thanatocoenosis, and T for thanatocoenosis. Feeding guilds include G for grazers, SF for suspension feeder, DF for detritus feeder, P for predators, and E for ectoparasites. For biocoenosis codes, please refer to Table 1 of the text. For the abundance in each sample, red is used for living specimens, black for dead specimens. Columns "Cluster B1" and "Cluster B2" indicate the species that occur in each cluster. Subsequent columns indicate our new findings (NEW) with respect to the lists reported in previous papers.

Supplementary 2: Results of the SIMPER routine for species that occur in biocoenosis and thanatocoenosis.