

Infralittoral coralligenous reefs: structure and spatial variability of macroalgal assemblages

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Summary: Coralligenous reefs are calcareous structures edified mostly by coralline algae that characterize the circalittoral zone of the Mediterranean Sea. However, in some cases coralline algae can constitute peculiar infralittoral biogenic reefs which have been studied less than the circalittoral ones. This study aims to contribute to the knowledge of infralittoral coralligenous reefs by describing their macroalgal assemblages on a large rocky platform off the Tuscany coasts, northwestern Mediterranean Sea. To this end, a multifactorial sampling design was used to describe the structure of the assemblages and to evaluate the variability of the system at multiple spatial scales. A total of 71 macroalgal taxa were found on the coralline algae. Macroalgal assemblages were well structured, with high biodiversity values. The dominant taxa included both photophilous and sciaphilous species, guaranteeing peculiar characteristics in these assemblages, above all if compared with the typical infralittoral and circalittoral macroalgal communities of the same geographic area. The assemblages showed greater variability at a small and intermediate spatial scale than at a large scale. Although infralittoral coralligenous outcrops constitute a peculiar system, they are still poorly understood and should not only be the object of specific studies but also be included in monitoring programmes.

Keywords: biodiversity; coralligenous reef; infralittoral; macroalgae; Mediterranean Sea; spatial variability.

Arrecifes coralígenos infralitorales: estructura y variabilidad espacial de las comunidades de macroalgas

Resumen: Los arrecifes coralígenos son estructuras calcáreas edificadas principalmente por algas coralinas que caracterizan la zona circalitoral del Mar Mediterráneo. Sin embargo, en algunos casos las algas coralinas pueden constituir peculiares arrecifes biogénicos infralitorales menos investigados que los circalitorales. El estudio tiene como objetivo contribuir al conocimiento de los arrecifes coralígenos infralitorales describiendo sus comunidades de macroalgas en una gran plataforma rocosa frente a las costas de Toscana, al noroeste del mar Mediterráneo. Un diseño de muestreo multifactorial fue utilizado para describir la estructura de comunidades algales y evaluar la variabilidad del sistema en múltiples escalas espaciales. Se encontró un total de 71 taxones de macroalgas sobre las algas coralinas. Las comunidades de macroalgas estaban bien estructuradas con altos valores de biodiversidad. Los taxones dominantes incluyeron tanto especies fotófilas como esciáfilas, lo que garantizó características peculiares a estas comunidades si se comparan con las típicas comunidades de macroalgas infralitorales y circalitorales de la misma área geográfica. Las comunidades mostraron una variabilidad a pequeña e intermedia escala mayor que a gran escala espacial. Si bien los afloramientos coralígenos infralitorales constituyen un sistema peculiar, aún son poco conocidos y deberían ser objeto no solo de estudios específicos sino también incluidos en programas de monitoreo ambiental.

Palabras clave: arrecifes coralígenos; biodiversidad; infralitoral; macroalgas; mar Mediterráneo; variabilidad espaciales.

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INTRODUCTION

Several marine benthic organisms are able to edify calcified permanent structures called bio-constructions, which, in turn, constitute a secondary substrate, increasing the volume, complexity and heterogeneity of their habitat (Fox 2005). Marine bio-constructions are present worldwide, reaching their greatest development in tropical seas where coral reefs, edified by hermatypic scleractinians, are the key habitat (Bianchi 2002).

In the Mediterranean Sea, coral reefs are almost absent, and coralligenous reefs are the main biogenic habitat for distribution, biodiversity, productivity and role played in the CO₂ cycle (Ballesteros 2006). Coralligenous reefs are calcareous structures edified mostly by coralline algae which develop from 20-25 m to about 150 m depth, characterizing the circalittoral zone below the deeper limit of seagrass beds (Ballesteros 2006). Circalittoral coralligenous reefs are included in the European Directives (E.C. 2008) and have been investigated much more than their shallow counterparts in terms of structure and spatial variability of the assemblages (Ponti et al. 2011, Casas-Guell et al. 2015, Doxa et al. 2016).

The Mediterranean infralittoral bottoms where coralline algae build calcareous structures, alternating with seagrass beds, have often been included in what are called “pre-coralligenous reefs” (Pérès and Picard 1964, Gili and Ros 1985) or infralittoral coralligenous reefs (enclaves of the circalittoral zone) (Montefalcone et al. 2021, SPA/RAC-UN ENVIRONMENT/MAP 2021). The latter are considered by some authors an impoverished facies of the coralligenous biocoenosis (Bressan and Babbini 2003) because they are shallower, light is more intense, and hence the calcareous rhodophyceans are not capable to develop major bio-construction and high-diversity assemblages. Other authors consider infralittoral coralligenous assemblages transitional assemblages between the photophilous communities and the deeper coralligenous biocoenosis (Bellan-Santini et al. 1994), characterized by lower bio-construction, lower quantity of sciaphilous soft algae and a lower number of invertebrate species than typical coralligenous habitats (Bellan-Santini et al. 2002). However, in some cases coralline algae can constitute conspicuous structures several decimetres wide even on shallow bottoms, where they form peculiar infralittoral biogenic reefs with characteristics similar to circalittoral coralligenous formations (SPA/RAC-UN ENVIRONMENT/MAP 2019, 2021). These infralittoral coralligenous reefs are considered to have an ecological role comparable to that of circalittoral coralligenous reefs (SPA/RAC-UN ENVIRONMENT/MAP 2021), but they have received much less attention than other Mediterranean habitats. The macroalgal composition of assemblages developing on infralittoral biogenic reefs has been studied since the 1970s (Boudouresque 1973, 1984, Giaccone et al. 1994), but the biodiversity patterns, spatial variability and sensitivity to disturbance of infralittoral coralligenous reefs assemblages have been little investigated.

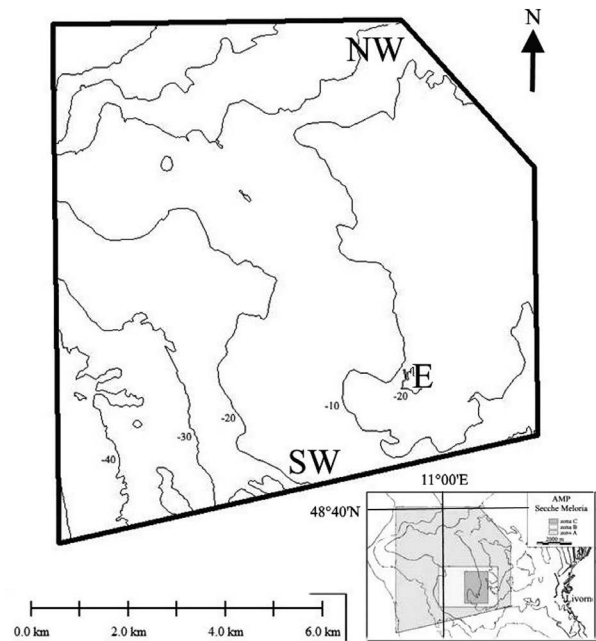


Fig. 1. – Map of Meloria Shoals with the three different study sites.

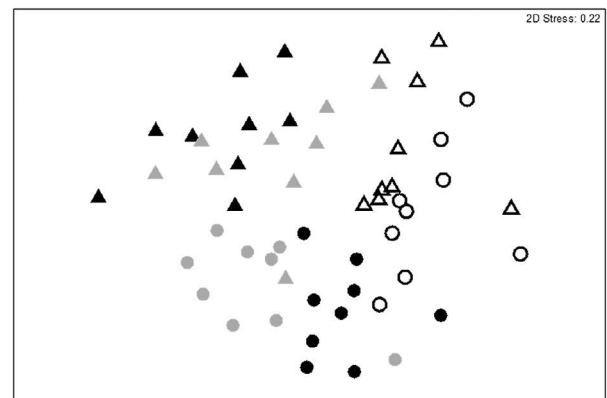


Fig. 2. – MDS ordination of infralittoral coralligenous macroalgal assemblages. Black, southwest; grey, northwest; white, east; symbols indicate the two areas sampled in each site.

This study aims to contribute to knowledge of the infralittoral coralligenous reefs by describing the associated macroalgal assemblages on a large rocky platform off the Tuscany coasts. In this area infralittoral biogenic outcrops are very common and are the main assemblages between 10 and 20 m depth after seagrass beds. A multifactorial sampling design was used to describe the structure of the assemblages and to evaluate the variability of the system at multiple spatial scales. Moreover, the assemblages were compared with both circalittoral coralligenous reefs and infralittoral rocky bottoms of the same geographic zone, using available datasets.

MATERIALS AND METHODS

The study was performed in the Meloria Shoals, a rocky platform about 90 km² wide off the Tuscany

Table 1. – List of taxa and their abundance expressed as mean percent cover at each study site. NW, northwest; SW, southwest; E, east.

TAXA	NW	SW	E
Ochrophyta			
<i>Aglaozonia parvula</i> spor. di <i>Cutleria multifida</i> (Turner) Greville	0.00	0.04	0.02
<i>Dictyota</i> spp.	5.63	9.05	10.16
<i>Halopteris filicina</i> (Grateloup) Kützing	0.16	0.36	2.78
<i>Nereia filiformis</i> (J. Agardh) Zanardini	0.72	0.00	0.10
<i>Padina pavonica</i> (Linnaeus) Thivy	6.27	8.81	20.64
<i>Sargassum vulgare</i> C. Agardh	0.00	0.00	0.44
<i>Sphacelaria cirrosa</i> (P.H. Roth) C. Agardh	6.87	9.53	3.89
<i>Sphacelaria plumula</i> Zanardini	0.00	0.00	0.01
<i>Stilophora tenella</i> (Esper) P.C. Silva	0.01	0.00	0.07
<i>Zanardinia typus</i> (Nardo) G. Furnari	9.86	0.14	4.38
Chlorophyta			
<i>Caulerpa cylindracea</i> Sonder	4.07	2.17	11.61
<i>Cladophora echinus</i> (Biaioletto) Kützing	0.33	0.02	0.00
<i>Cladophora prolifera</i> (Roth) Kützing	0.04	0.44	0.16
<i>Codium bursa</i> (Oliv) C. Agardh	0.31	1.28	0.07
<i>Derbesia tenuissima</i> (Moris & De Notaris) P.Crouan & H.Crouan	0.00	0.56	0.28
<i>Flabellia petiolata</i> (Turra) Nizamuddin	8.93	7.44	4.38
<i>Halimeda tuna</i> (J. Ellis et Solander) J.V. Lamouroux	0.95	1.55	0.67
<i>Pseudochlorodesmis furcellata</i> (Zanardini) Børgesen	0.24	0.08	0.46
<i>Valonia macrophysa</i> Kützing	0.00	0.01	0.02
Rhodophyta			
<i>Acrodiscus vidovichii</i> (Meneghini) Zanardini	1.37	2.62	0.61
<i>Acrosorium ciliolatum</i> (Havey) Kylin	0.00	0.00	0.13
<i>Acrothamnion preissii</i> (Sonder) Wollaston	0.00	0.01	0.08
<i>Amphiroa rubra</i> (Philippi) Woelkerling	0.39	1.24	1.54
<i>Antithamnion cruciatum</i> (C. Agardh) Nägeli	0.18	0.04	0.01
<i>Antithamnion piliferum</i> Cormaci & G.Furnari	0.06	0.00	0.00
<i>Apoglossum gregarium</i> (E. Y. Dawson) M. J. Wynne	0.02	0.00	0.00
<i>Apoglossum ruscifolium</i> (Turner) J. Agardh	0.01	0.00	0.00
<i>Botryocladia botryoides</i> (Wulfen) Feldmann	0.39	0.27	0.01
<i>Ceramium circinatum</i> (Kützing) J. Agardh	0.00	0.00	0.01
<i>Ceramium codii</i> (H. Richards) Feldmann-Mazoyer	0.13	0.09	0.13
<i>Ceramium diaphanum</i> (Lighfoot) Roth	0.16	0.10	0.05
<i>Champia intricata</i> (Clemente) Cremades	0.00	0.04	0.13
<i>Contarinia squamariae</i> (Meneghini) Denizot	0.14	0.45	0.71
<i>Dasya rigidula</i> (Kützing) Ardissonne	0.07	0.01	0.55
<i>Ellisolandia elongata</i> (J.Ellis & Solander) K.R.Hind	0.00	0.56	0.16
<i>Eupogodon planus</i> (C. Agardh) Kützing	0.27	0.25	0.05
<i>Feldmannophycus rayssiae</i> (Feldmann et Feldmann-Mazoyer)	0.18	0.42	0.19
<i>Gayliella flaccida</i> (Harvey ex Kützing) T.O.Cho et L.J.McIvor	0.00	0.01	0.17
<i>Gelidium bipectinatum</i> G. Furnari	1.52	0.99	0.14

TAXA	NW	SW	E
<i>Griffithsia schousboei</i> Montagne	0.00	0.00	0.01
<i>Halopithys incurva</i> (Hudson) Batters	0.13	0.06	0.00
<i>Halydyction mirabile</i> Zanardini	0.01	0.00	0.00
<i>Herposiphonia secunda</i> (C. Agardh) Ambronn	0.01	0.01	0.45
<i>Heterosiphonia crispella</i> (C. Agardh) M.J. Wynne	0.00	0.00	1.30
<i>Hypoglossum hypoglossoides</i> (Stackhouse) Collins et Harvey	0.00	0.01	0.00
<i>Jania virgata</i> (Zanardini) Montagne	3.26	3.38	3.81
<i>Laurencia chondrioides</i> Børgesen	11.36	12.55	0.22
<i>Lomentaria chylocradiella</i> Funk	0.00	0.02	0.01
<i>Lophosiphonia cristata</i> Falkenberg	0.13	0.00	0.00
<i>Meredithia microphylla</i> (J. Agardh) J. Agardh	1.38	2.72	1.27
<i>Monosporus pedicellatus</i> (J.E. Smith) Solier	0.00	0.00	0.04
<i>Osmundaria volubilis</i> (Linnaeus) R.E. Norri	0.06	0.00	0.00
<i>Osmundea pelagosae</i> (Schiffner) F.W. Nam	0.15	0.00	0.02
<i>Peyssonnelia rubra</i> (Greville) J. Agardh	7.80	10.15	12.33
<i>Peyssonnelia squamaria</i> (S.G. Gmelin) Decaisne	4.80	5.30	6.30
<i>Peyssonnelia stoechas</i> Boudouresque et Denizot	2.04	0.12	0.69
<i>Plocamium cartilagineum</i> (Linnaeus) P.S.Dixon	0.02	0.00	0.01
<i>Polysiphonia perforans</i> Cormaci, G. Furnari, Pizzuto et Serio	0.02	0.02	0.02
<i>Predaea ollivierii</i> J. Feldmann	0.00	0.00	0.01
<i>Pterothamnion plumula</i> (J. Ellis) Nägeli	0.00	0.00	0.01
<i>Ptilothamnion pluma</i> (Dillwyn) Thuret	0.00	0.00	0.02
<i>Rhodophyllis divaricata</i> (Stackhouse) Papenfuss	0.00	0.01	0.00
<i>Rhodymenia ardissoni</i> J. Feldmann	0.17	0.00	0.00
<i>Rodriguezella strafforelloii</i> F. Schmitz	0.00	0.02	0.04
<i>Seirospora</i> sp.	0.00	0.00	0.02
<i>Spermothamnion flabellatum</i> Bornet	0.00	0.00	0.02
<i>Sphaerococcus coronopifolius</i> Stackhouse	0.11	0.06	5.34
<i>Tricleocarpa fragilis</i> (Linnaeus) Huisman	2.28	3.04	1.18
<i>Vertebrata furcellata</i> (C. Agardh) Kuntze	0.06	0.04	0.00
<i>Vertebrata subulifera</i> (C. Agardh) Kuntze	0.00	0.10	0.06
<i>Womersleyella setacea</i> (Hollenberg) R.E. Norris	13.57	17.35	7.40
<i>Wrangelia penicillata</i> (C. Agardh) C. Agardh	0.00	0.00	0.32

Table 2. – PERMANOVA results of infralittoral coralligenous macroalgal assemblages. NW, northwest; SW, southwest; E, east.

Source	Multivariate analysis				Number of species		
	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(MC)
Site = S	2	9117.3	1.70	0.135	982.9	18.07	0.018
Area(S) = A(S)	3	5346.8	3.26	0.001	54.3	1.18	0.342
Plot(A(S))	12	1636.8	1.76	0.001	45.7	1.23	0.305
Residual	36	927.7			37.0		
Pairwise test (S)					E>NW=SW		

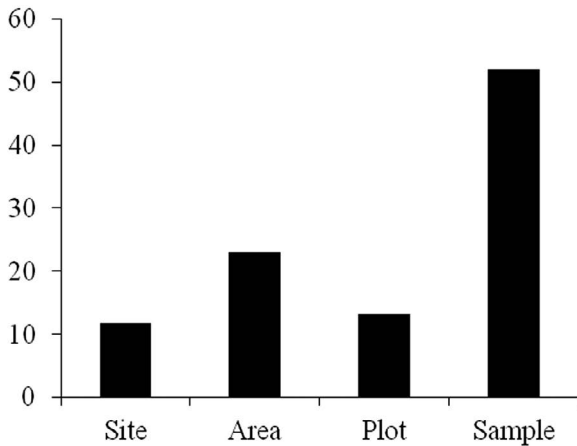


Fig. 3. – Pseudo-components of variance of infralittoral coralligenous macroalgal assemblages at the spatial scales considered in the study.

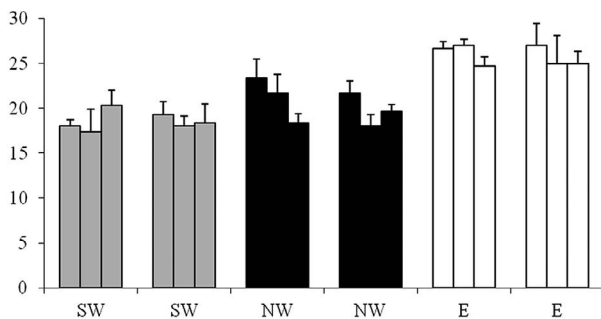


Fig. 4. – Alpha diversity of infralittoral coralligenous macroalgal assemblages. NW, northwest; SW, southwest; E, east.

coast surrounded by sandy bottoms (Fig. 1) that has been part of a marine protected area since 2010. Most of the platform extends between 10 and 20 m depth. Between about 6 and 30 m depth, the Shoal is colonized by *Posidonia oceanica* (L.) Delile, while its deepest rocky portion is characterized by typical coralligenous assemblages. Many scattered biogenic calcareous outcrops interrupt the seagrass bed between 10 and 20 m depth, covering a total surface of about 10 km². The bio-construction is well developed everywhere, with a thickness ranging from 10 cm to several decimetres.

The field activities were carried out in summer 2020. Three sites kilometres apart from each other were selected in three different portions of the Shoals: the northwestern, southwestern and eastern areas. At each site, two areas hundreds of metres apart were randomly chosen, and in each area three plots tens of metres apart were sampled. On each plot, three replicate samples were collected with a hammer and a chisel scraping all the macroalgae within a frame 400 cm² wide (Boudouresque 1971). In the laboratory, all the taxa were identified, and their abundance was expressed as percentage cover of the sample surface. The alpha diversity of the assemblages was estimated as the number of species per sample, while the beta diversity was evaluated at each considered spatial scale as the distance of samples from centroids calculated by PERMDISP analysis on a Bray-Curtis

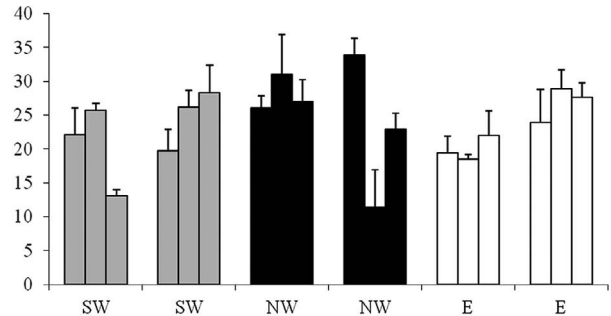


Fig. 5. – Beta diversity of infralittoral coralligenous macroalgal assemblages. NW, northwest; SW, southwest; E, east.

similarity matrix of untransformed data (Primer 6 + PERMANOVA; Anderson et al. 2006).

Spatial differences in the structure of assemblages (presence and abundance of species) were analysed by a permutational analysis of variance (Primer6 + PERMANOVA, Anderson 2001) based on a Bray-Curtis resemblance matrix after fourth-root transformation. A three-way model was used with Site (NW vs SW vs E) as a fixed factor, Area (two levels) as a random factor nested in Site and Plot (three levels) as a random factor nested in Area. The pairwise test was used to discriminate between levels of significant factors. The Montecarlo procedure was used when the number of permutations was low. The ordination plot was obtained by means of non-metric multidimensional scaling (n-MDS), which gives a clear graphical representation of the results. The number of taxa/groups per sample was analysed by PERMANOVA based on Euclidean distance with the same model applied in the multivariate analysis. One-way PERMANOVA and SIMPER tests were used to compare macroalgal assemblages of *Meloria* infralittoral outcrops with those of both circalittoral coralligenous reefs and infralittoral rocky bottoms of the same geographic zone, using available datasets (Piazzi et al. 2004, Piazzi and Balata 2011).

RESULTS

The main outcrop builders were the Rhodophyta *Mesophyllum alternans* (Foslie) Cabiocch and M.L. Mendoza and *Lithophyllum stictiforme* (Areschoug) Hauck. A total of 71 macroalgal taxa were found as epiphytes on the coralline algae, 9 Chlorophyta, 9 Ochrophyta, and 53 Rhodophyta (Table 1, with nomenclature authority). The erect layer of the assemblage was dominated by *Laurencia chondrioides*, *Tricleocarpa fragilis*, *Flabellia petiolata*, *Padina pavonica* and *Dictyota* spp. In the turf, the most abundant taxa were *Jania virgata*, *Sphacelaria cirrosa* and the introduced Rhodophyta *Womersleyella setacea*. The prostate layer was constituted by *Zanardinia ty-* and *Peyssonnelia* spp.

PERMANOVA detected a significant variability between areas and plots, while the sites did not significantly differ from each other (Table 2, Fig. 2). The pseudo-components of variance confirmed this pat-

Table 3. – SIMPER test comparing macroalgal assemblages of infralittoral coralligenous reefs with those of circalittoral coralligenous reefs and shallower rocky bottoms in the same geographic zone.

Taxa	Av.Abund	Av.Abund	Contrib%
	Infralittoral coralligenous reefs	Circalittoral coralligenous reefs	dissim. = 73.1
<i>Peyssonnelia rubra</i>	10.03	26.73	13.60
<i>Padina pavonica</i>	11.91	0	9.80
<i>Dictyota</i> spp.	8.28	0	6.77
<i>Meredithia microphylla</i>	1.79	9.61	6.50
<i>Laurencia chondrioides</i>	8.04	0.5	6.27
<i>Sphacelaria cirrosa</i>	6.76	0.03	5.47
<i>Flabellia petiolata</i>	6.92	0.63	5.14
<i>Zanardinia typus</i>	4.80	0.08	3.93
<i>Osmundaea pelagosae</i>	0.06	4.82	3.87
<i>Jania virgata</i>	3.49	0	2.86
<i>Sphaerococcus coronopifolius</i>	1.84	0	1.53
<i>Halopteris filicina</i>	1.10	2.8	1.48
<i>Amphiroa rubra</i>	1.06	0	0.86
<i>Halimeda tuna</i>	1.06	0	0.86
<i>Rodriguezella strafforelloii</i>	0.01	0.93	0.74
	Infralittoral coralligenous reefs	Shallow rocky bottoms	dissim. = 56.3
<i>Dictyopteris polypodioides</i>	0	12.01	10.8
<i>Peyssonnelia rubra</i>	10.03	2.10	7.3
<i>Zanardinia typus</i>	4.80	0	4.5
<i>Tricleocarpa fragilis</i>	2.17	0	3.3
<i>Acrodiscus vidovichii</i>	1.53	0	3.1
<i>Sphaerococcus coronopifolius</i>	1.84	0	2.3
<i>Halopteris scoparia</i>	0	0.85	2.1
<i>Meredithia microphylla</i>	1.79	0.36	1.9
<i>Ellisolandia elongata</i>	0.24	2.61	1.8

tern, showing the highest values among samples and the lowest among sites (Fig. 3). On the other hand, the number of species per sample was higher at the eastern site (25.9 ± 1.5) than at the others (18.6 ± 1.6 at the southwestern site, 20.4 ± 1.4 at the northwestern site), whereas no significant differences were found between areas and plots (Table 2, Fig. 4). The beta diversity did not significantly vary at the three spatial scales ($F_{1,2} = 3.01$, $P = 0.082$ for Site, $F_{1,5} = 0.77$, $P = 0.627$ for Area, $F_{1,17} = 3.12$, $P = 0.217$ for Plot, Fig. 5).

The comparison with circalittoral coralligenous reefs and infralittoral rocky bottoms highlighted significant differences from both habitats ($F_{1,3} = 11.6$, $P = 0.017$). The differences between infralittoral coralligenous reefs and circalittoral coralligenous reefs were mostly due to *Peyssonnelia* spp., *Meredithia microphylla*, *Osmundaea pelagosae* and *Halopteris filicina* that were more abundant in the latter habitat whereas *Padina pavonica*, *Dictyota* spp., *Sphacelaria cirrosa*, *Zanardinia typus*, *Flabellia petiolata*, *Laurencia chondrioides* and *Jania virgata* were more abundant in the

former (Table 3). The differences between infralittoral coralligenous reefs and infralittoral rocky bottoms were mostly due to *Ellisolandia elongata*, *Dictyopteris polypodioides* and *Halopteris scoparia*, which were more abundant in the latter habitat, whereas *Zanardinia typus*, *Tricleocarpa fragilis*, *Acrodiscus vidovichii*, *Sphaerococcus coronopifolius* and *Peyssonnelia* spp. were more abundant in the former (Table 3).

DISCUSSION

The results of the study showed that macroalgal assemblages developed on infralittoral coralligenous reefs are well structured, with high values of biodiversity. The dominant taxa included both photophilous species such as *Padina pavonica* and *Jania virgata* and sciaphilous species such as *Zanardinia typus*, *Flabellia petiolata*, *Tricleocarpa fragilis*, *Acrodiscus vidovichii*, *Sphaerococcus coronopifolius*, *Laurencia chondrioides* and *Peyssonnelia* spp. The species composition is intermediate from those described for sciaphilous

infralittoral assemblages and coralligenous assemblages (Boudouresque 1984, Giaccone et al. 1994). On the other hand, *Halimeda tuna* or Fucales, often characterizing assemblages of infralittoral coralligenous reefs (Ballesteros 1991, Ballesteros et al. 1998), showed low abundance everywhere.

This floristic feature makes the assemblage unique and different from the typical infralittoral and circalittoral macroalgal assemblages of the same geographic area (Balata and Piazzì 2008, Piazzì and Ceccherelli 2020). For example, *Meredithia microphylla*, *Osmundea pelagosae* and *Rodriguezella strafforrelloi*, which are dominant in coralligenous reefs were poorly present in the studied habitat, where they were replaced by photophilous species not found in the deeper reefs.

The presence of *Laurencia chondrioides* is also noteworthy. This alga had been wrongly considered an introduced and invasive species in the Mediterranean Sea (Boisset et al. 1998, Hoffmann et al. 2014), but only recently it has been eliminated from the list of Mediterranean non-indigenous species. This seaweed dominates the erect layer of the studied assemblages along with *F. petiolata* and *P. pavonica*, showing higher abundance values than those reported for the nearby circalittoral coralligenous reefs; this pattern suggests that this species prefers the deeper part of the infralittoral zone, though Hoffman et al. (2014) recorded it in a wider depth range. In addition, these findings highlight that, irrespective of its origin, the ecology of this species is still unclear and deserves further studies to understand its potential invasiveness (Hoffman et al. 2014) and its role in the coastal Mediterranean systems.

Our floristic list includes two alien invasive algae *Caulerpa cylindracea* and *Womersleyella setacea*, both showing a wide distribution and the latter showing high abundance values. These species are worth mentioning because they are described as particularly threatening for coralligenous reefs (Piazzì and Balata 2009, Piazzì et al. 2021a) and are supposed to have similar effects for infralittoral biogenic outcrops, although appropriate monitoring studies are necessary to accept or refute this hypothesis.

The assemblages showed high variability at a small and intermediate scale, while they were homogeneous at a large spatial scale. The high variability at a small scale suggests a patchy distribution of the organisms, which may generally reflect the heterogeneity of the substrate (Piazzì et al. 2016, 2021b). On the other hand, the observed variability between sites may be related to their spatial isolation: the seagrass bed surrounding the outcrops creates a sort of barrier that separates them from one another and influences the recruitment modalities, enhancing the beta diversity of the system. The low variability at a large spatial scale indicates that the assemblages have a particular structure that reoccurs across the study areas despite the variability at smaller scales, so a well-defined physiognomy of the assemblages can be recognized.

Irrespective of the floristic differences, the studied system showed a high level of biodiversity com-

parable to that reported for circalittoral coralligenous macroalgal assemblages (Piazzì et al. 2010, Piazzì and Ceccherelli 2020), suggesting a similar ability in guaranteeing conditions that can support highly diversified assemblages (Cocito 2004). In particular, the presence of biogenic structures similar to those of circalittoral coralligenous habitats helps create a substrate with a high heterogeneity which hosts highly diversified assemblages (Piazzì et al. 2022).

The characteristics of the studied assemblages, between the infralittoral photophilous communities and the deeper coralligenous biocoenosis, evocate those described for pre-coralligenous habitats or for coralligenous reefs (enclaves of the infralittoral zone). However, while the latter are characterized by a low level of bio-construction, the studied habitat consists of large structures with well-developed bio-construction, mainly occurring on horizontal substrata. These features suggest that infralittoral coralligenous reefs may be more complex than has been described until now and they should be considered a peculiar habitat that opens new perspectives and new approaches to obtaining further knowledge (SPA/RAC-UN ENVIRONMENT/MAP 2021). In addition, their high biodiversity, comparable to that of deeper coralligenous reefs, suggests that, like the latter, they could provide similar ecosystem services (Thierry de Ville d'Avray et al. 2019). In parallel, the main threats widely described for coralligenous reefs, such as sedimentation, pollution, mechanical destruction and invasion of alien species (Piazzì et al. 2012), can potentially affect infralittoral biogenic habitats in a similar way.

In conclusion, our results highlight that infralittoral coralligenous outcrops should be considered a peculiar system, and dedicated studies and appropriate monitoring programmes are desirable. The first step should be to obtain knowledge of the distribution and the extent of the habitat, which is of primary importance for planning further investigations and conservation programmes. Secondly, the structure and biodiversity of infralittoral coralligenous reefs should be investigated at a large spatial scale in order to evaluate their patterns of variability, their ecological values and the effects of human pressures. Finally, a standard, specific protocol should be developed, because the different characteristics prevent us from using the approaches adopted for circalittoral coralligenous reefs and infralittoral rocky bottoms.

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