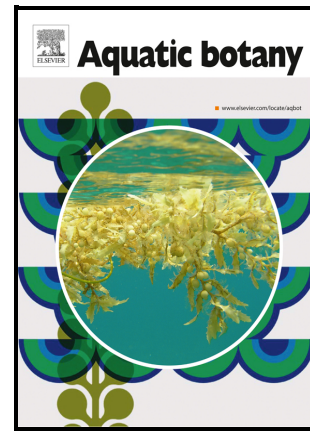


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Macroalgal assemblages associated to Mediterranean rhodolith beds

Piazzì L.*¹, Basso D.², Falace A.³, Kaleb S.³, Ria M.⁴, Cecchi E.⁴

¹Dipartimento di Scienze Chimiche, Fisiche, Matematiche e Naturali, Univ. di Sassari, Via Piandanna 4, 07100 Sassari, Italy

²Dipartimento di Scienze dell'Ambiente e della Terra, Univ. di Milano-Bicocca, P.zza della Scienza 4, 20126 Milano, Italy

³Dipartimento di Scienze della Vita, Univ. Di Trieste, Via L. Giorgieri, 10, 34127 Trieste, Italy

⁴ARPAT - Agenzia Regionale per la Protezione Ambientale della Toscana, Via Marradi 114, 57126 Livorno, Italy

***corresponding author: lpiazzì00@gmail.com**

Abstract

The present paper aims at contributing to the knowledge of rhodolith beds by describing the associated macroalgal assemblages of two beds in the western Mediterranean Sea: Gorgona Island in the Tuscan Archipelago National Park and Capo Carbonara Marine Protected Area in the southern Sardinia. Patterns of biodiversity and spatial variability were investigated through a multifactorial sampling design. A total of 84 macroalgal species was identified, 17 Heterokontophyta, 8 Chlorophyta and 59 Rhodophyta. Significant differences between beds were detected and the main species characterizing the two beds were highlighted. The mean number of species per sample was quite low and beta diversity high compared to most Mediterranean macroalgal assemblages.

Key words: Biodiversity; Italy; maërl; seaweeds

Introduction

Rhodolith beds are formed by the accumulation of various species of non-geniculate, unattached calcareous red algae (Rhodophyta); they consist of living and dead thalli and can be found from polar to tropical seas to depths of more than 150 m (Tuya et al., 2023). Rhodolith beds increase the structural complexity of soft bottoms creating a three-dimensional habitat characterized by high biodiversity; they are also important for climate regulation and as providers of ecosystem services (Tuya et al., 2023).

In the Mediterranean Sea, rhodolith beds are found in coarse coastal detritic areas under the influence of bottom currents mostly below 40 m depth (Basso et al., 2017; Ingrassia et al., 2023). Within the Marine Strategy Framework Directive (MSFD, 2008/56/EC) Mediterranean rhodolith beds are among the habitats to be assessed (Basso et al., 2016) and, consequently, their knowledge recently increased in term of distribution, extent, species composition and impacts (Sañé et al., 2016; Chimienti et al., 2020; Rendina et al., 2020; Farriols et al., 2022; Illa-Lopez et al., 2023). However, the overall biodiversity associated to the habitat remains poorly known and restricted to local descriptions (Longo et al., 2020; Bracchi et al., 2022; Deidum et al., 2022; Maggio et al., 2022).

The present paper aims at contributing to the knowledge of the habitat by describing the associated macroalgal assemblages of two rhodolith beds in the western Mediterranean Sea. Rhodolith associated macroalgal assemblages are worldwide described as characterized by high biodiversity (Nelson et al., 2014; Peña et al., 2014; Brasileiro et al., 2016; Helias and Burel, 2023). However, these assemblages are insufficiently known in the Mediterranean Sea (Joher et al., 2012, 2015). In the present study, patterns of biodiversity and spatial variability of macroalgae associated to rhodoliths were investigated through SCUBA diving sampling and a multifactorial sampling design.

Material and Methods

The two investigated beds were located in two different geographic areas of the Mediterranean Sea: nearby the Island of Gorgona in the Tuscan Archipelago National Park, northwestern Italy

(43°25'20"N, 09°53'19"E, Falace et al., 2014), and at the Santa Caterina shoal, within the Marine Protected Area (MPA) of Capo Carbonara, southern Sardinia (39°04'40"N, 09°30'00"E, Bracchi et al., 2022). The Gorgona bed thrives between approximately 45 and 80 m deep, the Capo Carbonara one between 40 and 45 m deep. In each bed, two sites 10s m apart were randomly selected. At each site, three 2500 cm² samples were taken by SCUBA diving at a depth of 45-50 m at Gorgona Island and of 40-45 m in the Capo Carbonara MPA and stored at -40°C. Each sample consisted of all the rhodoliths occurring within the 2500 cm² surface. After defrosting the samples, rhodolith epiphytes were observed under the stereomicroscope for macroalgal identification. For detailed observation of the diacritic features and subsequent identification of rhodolith-forming red calcareous algae scanning electron microscopy (SEM) was employed at the facilities of the University of Milano-Bicocca and University of Trieste. Rhodoliths were identified based on morphoanatomy, pending further studies and full revision of the group based on integrated taxonomy. Morpho-anatomical characters and keys for species identification of Corallinophycidae Le Gall & G.W.Saunders follow Bressan and Babbini (2003) and more recent integrations and revisions by Basso et al. (2004; 2022), Basso and Rodondi (2006), Kato et al. (2006), Kaleb et al. (2011), Pezsolesi et al. (2019), Caragnano et al. (2020), Gabrielson et al. (2023). Among the fully calcified Peyssonneliales Kraysky, Fredericq & J.N.Norris, the identification of the genus *Polystrata* follows Denizot (1968) and Kato et al. (2006). Taxonomic nomenclature follows AlgaeBase (Guiry and Guiry, 2024). The coverage of each epiphytic species was expressed as percentage of rhodolith surface of each sample by splaying the algal thalli and measuring the surface occupied by each species. The frequency of each species was assessed as the percentage of samples in which the species was identified.

Spatial differences in the structure of macroalgal assemblages (presence and abundance of species) were analyzed by permutational analysis of variance in Primer6 + PERMANOVA (Anderson, 2001) based on Bray-Curtis similarity matrix of untransformed data. A 2-way model was used with Bed as fixed factor and Site (three levels) as random factor nested in Bed. A canonical principal co-ordinate analysis (CAP) was performed on untransformed Bray-Curtis similarity matrix to discriminate the

main species contributing to dissimilarities between beds. The beta-diversity was assessed for each bed as the distance of samples from centroids calculated by PERMDISP analysis on Jaccard similarity matrix (Anderson et al. 2006).

Results and discussion

Both study sites had a well-developed rhodolith bed, composed mainly of boxwork and praline morphostructures (Basso et al., 2016), with a bottom cover ranging between approximately 30% and 70%. The most abundant rhodolith-building species in the Gorgona rhodolith bed were: *Lithothamnion minervae*, *Roseolithon crispatum* and *Titanoderma pustulatum*; followed by *Lithophyllum racemus*, *Lithophyllum stictiforme*, *Mesophyllum macroblastum*, *Neogoniolithon brassica-florida*, *Neogoniolithon hauckii*, *Phymatolithon calcareum*, *Spongites fruticulosus* and *Sporolithon ptychoides*. In Capo Carbonara rhodolith bed, the most abundant species were: *Lithothamnion minervae* and *Spongites fruticulosus*, followed by *Lithophyllum racemus*, *Lithothamnion corallioides*, *Polystrata fosliei* and *Roseolithon crispatum*.

A total of 84 macroalgal species was identified in the assemblages associated to the two beds, including 17 Heterokontophyta, 8 Chlorophyta and 59 Rhodophyta (Table 1).

The PERMANOVA analysis detected significant differences between beds (Pseudo- $F_{1,8}=9.908$, $P(\text{MC})=0.002$), while variability among sites was not significant (Pseudo- $F_{2,8}=0.446$, $P(\text{MC})=0.921$). The CAP analysis showed a clear disjunction between beds (Fig. 1). At Gorgona the erect layer consisted mostly of *Gongolaria montagnei*, *Ericaria zosteroides*, *Sargassum hornschuchii*, *Sporochnus pedunculatus* and *Sebdenia dichotoma*, while *Rytiplaea tinctoria* and *Meredithia microphylla* were more abundant at Capo Carbonara (Fig. 1). *Osmundaria volubilis*, *Osmundea pelagosae* and *Phyllophora crispa* were common in erect layer of both beds. The encrusting layer was mainly characterized by *Zanardinia typus* and *Peyssonnelia* spp. Other frequent species were *Botryocladia botryoides*, *Acrodiscus vidovichii* and *Eupogodon planus* (Table 1). Differences between beds may be related to biogeographic patterns, as the northern Gorgona assemblage was

dominated by brown erect macroalgae, which are considered of boreal origin and associated to colder areas (Piazzi et al. 2021). However, the occurrence of local-acting physical and chemical factors, such as currents or nutrient availability, cannot be excluded as drivers of the observed differences.

Although the species composition of rhodolith epiphytes was quite similar to that described for the coralligenous assemblages (Piazzi et al., 2010; Piazzi and Ceccherelli, 2020), the beds were nevertheless characterised by a greater abundance of rheophilous species typical of detrital bottoms, such as *Arthrocladia villosa* and *Sporochnus pedunculatus*, confirming a pattern already described in the Mediterranean Sea (Lanfranco et al., 1999; Joher et al., 2015).

Three introduced species were found: *Caulerpa cylindracea*, *Acrothamnion preissii* and *Womersleyella setacea*. The three species have been already observed on rhodolith beds and the impact of *C. cylindracea* on the habitat has also been described (Klein and Verlaque, 2009; Caronni et al., 2022), but their abundance was low at the investigated sites.

The average number of epiphyte species per sample was 23.8 ± 1.9 (mean \pm SE, $n=6$) at Gorgona and 21.0 ± 1.6 at Capo Carbonara, while the total epiphyte percentage cover was 21.5 ± 2.9 and 17.5 ± 1.2 , respectively.

The beta diversity did not vary significantly between rhodolith beds ($F_{1,10}=1.21$, $P(\text{Perm})=0.369$). The values of the mean distance between centroids were high (47.6 ± 3.6) compared to most Mediterranean macroalgal assemblages and comparable to the highest values found in coralligenous assemblages (Piazzi and Ceccherelli, 2020). In contrast, the alpha diversity (the mean number of species per sample) and the percent cover generally showed lower values than in macroalgal assemblages of other Mediterranean habitats (Piazzi and Ceccherelli, 2020). Probably, the characteristics of the unstable substrate consisting of unattached nodules and the environmental conditions influencing the beds interact to determine the peculiar patterns of the assemblages. Moreover, the species richness was lower than that described for rhodolith beds of oceanic regions (Nelson et al., 2014; Brasileiro et al., 2016). The restricted depth range characterizing Mediterranean rhodoliths may influence the

biodiversity and the structure of associated assemblages (Veras et al. 2020), contributing to the peculiarity of Mediterranean rhodolith beds.

The results confirm previous observations on this habitat performed in different geographic areas (Joher et al., 2012, 2015) and suggest that the rhodolith-associated epiphyte assemblages show peculiar characteristics related to dominant and rare species, biodiversity and pattern of spatial variability. It is therefore important to improve specific studies aimed at increasing knowledge about the biodiversity and functioning of this habitat, also in order to better implement the conservation objectives included in the MSFD, the regulatory instrument on which the conservation of our sea today essentially depends.

Author contributions

Conceptualization: L. Piazzzi, E. Cecchi

Formal analysis: L. Piazzzi

Investigation: L. Piazzzi, D. Basso, A. Falace, S. Kaleb, Ria M., E. Cecchi

Roles/Writing - original draft: L. Piazzzi, D. Basso, A. Falace

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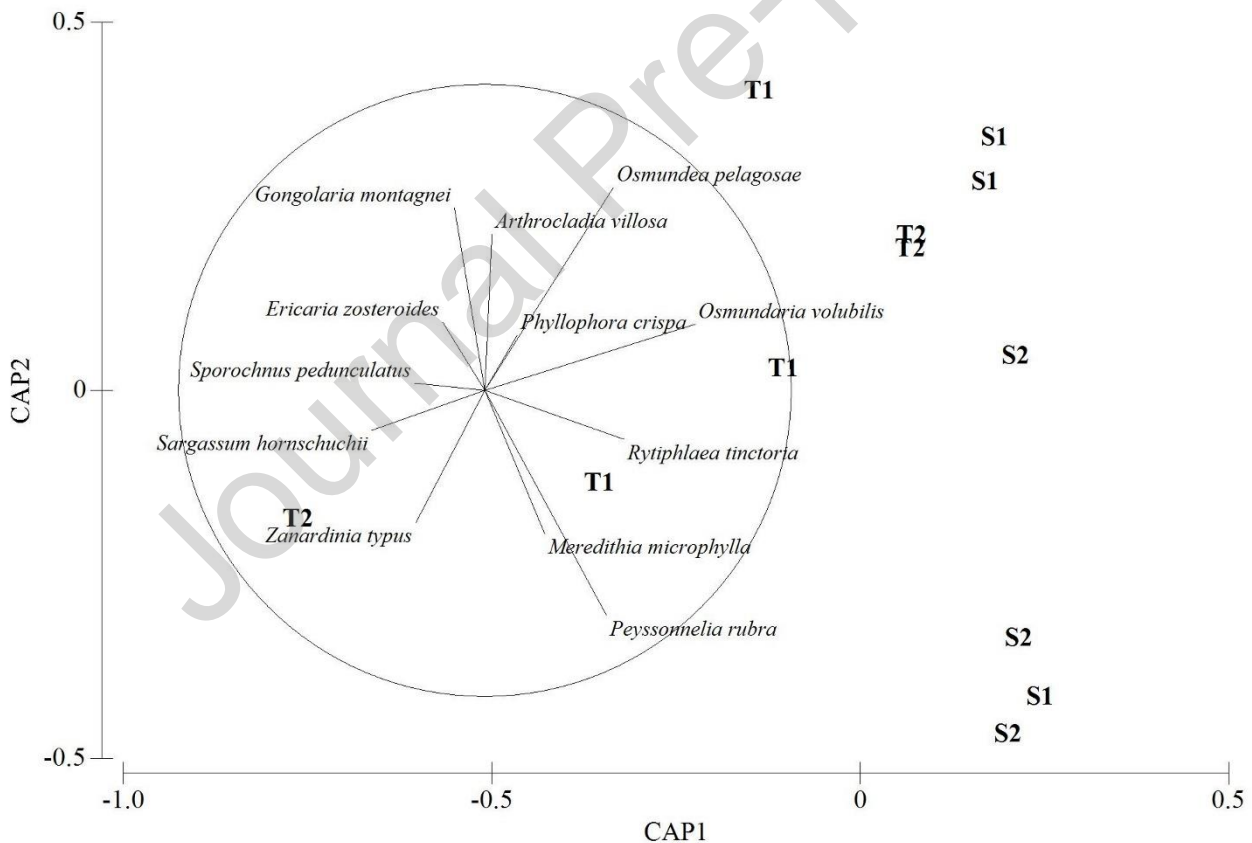


Figure 1. CAP analysis on macroalgal assemblages associated to rhodolith beds. T=Tuscany (Island of Gorgona), S=Sardinia (Capo Carbonara). Numbers refer to study sites

Table 1. List of taxa of rhodolith associated assemblages. The mean percentage cover (R%) and the Standard Error (SE, n=6) per site and the total frequency were also reported for each taxon. T=Tuscany (Gorgona), S=Sardinia (Capo Carbonara).

TAXA	T		S		Tot. Freq.
	R%	SE	R%	SE	
HETEROKONTOPHYTA					
<i>Arthrocladia villosa</i> (Hudson) Duby	0.30	0.13	0.00	0.00	25.0
<i>Asperococcus bullosus</i> Lamouroux	0.28	0.20	0.08	0.08	25.0
<i>Cutleria chilosa</i> (Falkenberg) P.C.Silva (sporophyte “ <i>Aglaozonia</i> ”)	0.08	0.05	0.02	0.02	25.0
<i>Dictyopteris polypodioides</i> (A.P. De Candolle) J.V. Lamouroux	0.07	0.07	0.05	0.05	16.7
<i>Dictyota implexa</i> (Desfontaines) J.V.Lamouroux (C. Agardh)	0.05	0.03	0.20	0.10	41.7
<i>Ericaria zosteroides</i> (C.Agardh) Molinari & Guiry	5.17	1.69	0.00	0.00	33.3
<i>Gongolaria montagnei</i> (J.Agardh) Kuntze	1.33	0.75	0.17	0.16	41.7
<i>Halopteris filicina</i> (Grateloup) Kützing	0.25	0.09	0.02	0.02	41.7
<i>Nereia filiformis</i> (J. Agardh) Zanardini	0.07	0.05	0.03	0.03	25.0
<i>Phyllariopsis brevipes</i> (C. Agardh) Henry & South	0.67	0.65	0.00	0.00	8.3
<i>Sargassum hornschurchii</i> C. Agardh	0.75	0.73	0.00	0.00	8.3
<i>Spermatochnus paradoxus</i> (P.H. Roth) Kützing	0.23	0.23	0.00	0.00	8.3
<i>Sphacelaria cirrosa</i> (P.H. Roth) C. Agardh	0.02	0.02	0.05	0.02	33.3
<i>Sphacelaria plumula</i> Zanardini	0.07	0.02	0.03	0.02	50.0
<i>Sporochnus pedunculatus</i> (Hudson) C. Agardh	1.67	0.74	0.08	0.08	33.3
<i>Stilophora tenella</i> (Esper) P.C. Silva	0.08	0.05	0.02	0.02	25.0
<i>Zanardinia typus</i> (Nardo) G. Furnari	0.18	0.06	0.15	0.09	50.0
CHLOROPHYTA					
<i>Caulerpa cylindracea</i> Sonder	0.08	0.05	1.33	0.70	41.7
<i>Cladophora prolifera</i> (Roth) Kützing	0.00	0.00	0.57	0.32	25.0
<i>Codium bursa</i> (Linnaeus) C.Agardh	0.00	0.00	0.65	0.56	16.7
<i>Lychaete echinus</i> (Biasoletto) M.J.Wynne	0.00	0.00	0.13	0.06	33.3
<i>Microdictyon umbilicatum</i> (Velle) Zanardini	0.00	0.00	0.02	0.02	8.3
<i>Pseudochlorodesmis furcellata</i> (Zanardini) Børgesen	0.00	0.00	0.00	0.00	8.3
<i>Valonia macrophysa</i> Kützing	0.05	0.02	0.07	0.02	58.3
PRASINODERMATOPHYTA					
<i>Palmophyllum crassum</i> (Naccari) Rabenhorst	0.05	0.05	0.00	0.00	8.3
RHODOPHYTA					
<i>Acrodiscus vidovichii</i> (Meneghini) Zanardini	0.27	0.12	0.00	0.00	0.27
<i>Acrothamnion preissii</i> (Sonder) Wollaston	0.07	0.02	0.11	0.03	0.07
<i>Agissea stoechas</i> (Boudouresque & Denizot) Pestana, Lyra, Cassano & J.M.C.Nunes	0.00	0.00	1.58	0.50	0.00
<i>Antithamnion cruciatum</i> (C. Agardh) Nägeli	0.00	0.00	0.07	0.03	0.00
<i>Antithamnion tenuissimum</i> (Hauck) Schiffner	0.00	0.00	0.03	0.02	0.00
<i>Apoglossum ruscifolium</i> (Turner) J. Agardh	0.05	0.02	0.02	0.02	0.05
<i>Balliella cladoderma</i> (Zanardini) Athanasiadis	0.02	0.02	0.00	0.00	0.02
<i>Botryocladia botryoides</i> (Wulfen) Feldmann	0.15	0.07	0.03	0.03	0.15
<i>Carradoriella elongata</i> (Hudson) Savoie & G.W.Saunders	0.02	0.02	0.02	0.02	0.02

<i>Ceramium bertholdii</i> Funk	0.02	0.02	0.00	0.00	0.02
<i>Ceramium diaphanum</i> (Lightfoot) P.H. Roth	0.02	0.02	0.02	0.02	0.02
<i>Champia parvula</i> (C.Agardh) Harvey	0.02	0.02	0.05	0.02	0.02
<i>Chondria capillaris</i> (Hudson) M.J.Wynne	0.00	0.00	0.03	0.02	0.00
<i>Chrysmenia ventricosa</i> (J.V. Lamouroux) J. Agardh	0.20	0.20	0.00	0.00	0.20
<i>Contarinia squamariae</i> (Meneghini) Denizot	0.02	0.02	0.02	0.02	0.02
<i>Crouania attenuata</i> (C.Agardh) J.Agardh	0.00	0.00	0.02	0.02	0.00
<i>Cryptonemia palmetta</i> (S.G.Gmelin) Woelkerling, G.Furnari, Cormaci & McNeill	0.33	0.33	0.00	0.00	0.33
<i>Dasya baillouviana</i> (S.G. Gmelin) Montagne	0.02	0.02	0.05	0.03	0.02
<i>Dasya corymbifera</i> J. Agardh	0.02	0.02	0.00	0.00	0.02
<i>Dasya ocellata</i> (Grateloup) Harvey	0.02	0.02	0.02	0.02	0.02
<i>Dasya rigidula</i> (Kützing) Ardissonne	0.07	0.02	0.02	0.02	0.07
<i>Dudresnaya verticillata</i> (Withering) Le Jolis	0.83	0.53	0.07	0.03	0.83
<i>Eupogodon planus</i> (C. Agardh) Kützing	0.25	0.15	0.13	0.04	0.25
<i>Feldmannophycus rayssiae</i> (Feldmann & G.Feldmann) H.Augier & Boudouresque	0.00	0.00	0.02	0.02	0.00
<i>Gelidium pectinatum</i> (Montagne) Montagne	0.00	0.00	0.05	0.05	0.00
<i>Gloiocladia furcata</i> (C. Agardh) J. Agardh	0.05	0.05	0.00	0.00	0.05
<i>Gracilaria bursa-pastoris</i> (S.G. Gmelin) P.C. Silva	0.33	0.33	0.00	0.00	0.33
<i>Gracilaria dura</i> (C. Agardh) J. Agardh	0.33	0.33	0.00	0.00	0.33
<i>Griffithsia schousboei</i> Montagne	0.02	0.02	0.02	0.02	0.02
<i>Halydictyon mirabile</i> Zanardini	0.00	0.00	0.02	0.02	0.00
<i>Haraldia lenormandii</i> (Derbès et Solier) J. Feldmann	0.02	0.02	0.00	0.00	0.02
<i>Hypoglossum hypoglossoides</i> (Stackhouse) Collins & Harvey	0.02	0.02	0.02	0.02	0.02
<i>Jania pedunculata</i> var. <i>adhaerens</i> (J.V.Lamouroux) A.S.Harvey, Woelkerling & Reviere	0.08	0.05	0.03	0.02	0.08
<i>Kallymenia feldmannii</i> Codomier	0.33	0.33	0.00	0.00	0.33
<i>Lomentaria chylocladiella</i> Funk	0.02	0.02	0.02	0.02	0.02
<i>Lomentaria clavaeformis</i> Ercegovic	0.08	0.02	0.00	0.00	0.08
<i>Meredithia microphylla</i> (J. Agardh) J. Agardh	0.18	0.12	0.68	0.18	0.18
<i>Monosporus pedicellatus</i> (Smith) Solier	0.00	0.00	0.03	0.02	0.00
<i>Neurocaulon foliosum</i> (Meneghini) Zanardini	0.33	0.33	0.00	0.00	0.33
<i>Osmundaria volubilis</i> (Linnaeus) R.E. Norris	1.23	0.39	2.95	0.62	1.23
<i>Osmundea pelagosae</i> (Schiffner) F.W. Nam	0.80	0.30	0.78	0.27	0.80
<i>Peyssonnelia rubra</i> (Greville) J. Agardh	0.15	0.07	2.47	1.28	0.15
<i>Peyssonnelia squamaria</i> (S.G. Gmelin) Decaisne	0.18	0.08	0.00	0.00	0.18
<i>Phyllophora crispa</i> (Hudson) P.S. Dixon	1.13	0.52	0.17	0.16	1.13
<i>Plocamium cartilagineum</i> (Linnaeus) P.S. Dixon	0.03	0.02	0.02	0.02	0.03
<i>Pterothamnion plumula</i> (J. Ellis) Nägeli	0.03	0.02	0.00	0.00	0.03
<i>Ptilocladopsis horrida</i> Berthold	0.02	0.02	0.00	0.00	0.02
<i>Ptilothamnion pluma</i> (Dillwyn) Thuret	0.02	0.02	0.02	0.02	0.02
<i>Radicilingua reptans</i> (Kylin) Papenfuss	0.02	0.02	0.00	0.00	0.02
<i>Rhodymenia ardissonnei</i> J. Feldmann	0.03	0.03	0.00	0.00	0.03
<i>Rytiphlaea tinctoria</i> (Clemente) C. Agardh	0.30	0.19	2.83	0.50	0.30
<i>Scinaia furcellata</i> (Turner) J. Agardh	0.33	0.33	0.00	0.00	0.33
<i>Sebdenia dichotoma</i> Berthold	1.13	0.50	0.00	0.00	1.13

<i>Sphaerococcus coronopifolius</i> Stackhouse	0.03	0.03	0.00	0.00	0.03
<i>Stirkia codii</i> (H.Richards) Barros-Barreto & Maggs	0.02	0.02	0.07	0.02	0.02
<i>Tricleocarpa fragilis</i> (Linnaeus) Huisman & R.A.Townsend	0.00	0.00	0.32	0.24	0.00
<i>Vertebrata subulifera</i> (C. Agardh) Kuntze	0.07	0.02	0.73	0.32	0.07
<i>Womersleyella setacea</i> (Hollenberg) R.E. Norris	0.32	0.08	0.13	0.07	0.32
<i>Wrangelia penicillata</i> (C. Agardh) C. Agardh	0.02	0.02	0.02	0.02	0.02

Declaration of Interest: None

Highlights

The associated macroalgae of two Mediterranean rhodolith beds were described

Patterns of biodiversity and spatial variability were investigated

Eight Chlorophyta, 17 Heterokontophyta, and 59 Rhodophyta were identified

Significant differences between beds were detected

The beta diversity was higher than in most Mediterranean macroalgal assemblages