UNIVERSIDADE FEDERAL DO ESPÍRITO SANTO
CENTRO DE CIÊNCIAS HUMANAS E NATURAIS
PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS

Diversidade taxonômica e funcional da macrofauna bentônica associada a bancos de rodolitos na plataforma continental Leste do Brasil

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Vitória - ES
Abril, 2021

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Orientador: Dr. Angelo Fraga Bernardino

Dissertação submetida ao Programa de Pós-Graduação em Ciências Biológicas (Biologia Animal) da Universidade Federal do Espírito Santo como requisito parcial para obtenção do grau de Mestre em Biologia Animal.

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“La mer, une fois qu'elle a jeté son sort, tient pour toujours dans son filet d'émerveillement.”

Jacques Yves Cousteau

SUMÁRIO

RESUMO

Rodolitos são algas calcárias marinhas de vida livre e morfologicamente diversificadas, comumente distribuídas no assoalho da plataforma continental. Eles aumentam a complexidade estrutural do fundo e são potencialmente importantes como fonte de alimentação e reprodução para diversos organismos da fauna marinha. A maior complexidade estrutural do fundo ocasionada por bancos de rodolitos (RBs) também pode aumentar a diversidade bentônica geral devido a criação de microhabitats distintos, mas esta relação tem sido raramente explorada dentro de RBs ao redor do mundo. Neste trabalho, comparamos a estrutura da assembléia da macrofauna bentônica (> 500µm) nos RBs (dentro dos nódulos) e nos sedimentos não consolidados subjacentes aos bancos (infauna), entre RBs de alta e baixa densidade de nódulos para testar se as assembléias bentônicas estavam associadas com a densidade dos RBs. Foi observado que a diversidade bentônica foi maior nos rodolitos, enquanto a densidade da macrofauna foi 16 vezes maior quando comparada aos sedimentos abaixo dos RBs, que também apresentaram baixo *nestedness* e alto *turnover* de táxa entre os habitats. A densidade dos RBs e a morfologia do nódulo explicaram a diversidade macrofaunal, taxonômica e funcional, nos rodolitos. RBs de alta densidade (204 ± 32.5 nódulos.m^{-2}) apresentaram maior diversidade macrofaunal (taxonômica e funcional) e exibiram nódulos tipicamente esferoidais com maior volume interno, sendo dominados por poliquetas do grupo Annelida. Em contraste, RBs de baixa densidade (61 ± 46.9 nódulos.m^{-2}) exibiram nódulos de forma discoidal com maior diâmetro médio e foram dominados por crustáceos peracarídeos. A diversidade taxonômica, densidade e diversidade funcional da macrofauna não apresentaram diferenças entre as densidades de RBs nos sedimentos, mas a estrutura da macrofauna foi influenciada pelos RBs, que aumentaram o teor de carbonatos e a qualidade orgânica do sedimento (proteínas e carboidratos) em estações de alta densidade. Esses resultados indicam que as comunidades bentônicas mudam visivelmente em resposta à densidade de RBs e morfologia dos nódulos, fornecendo habitat para espécies bentônicas únicas que não são encontradas em sedimentos não consolidados abaixo desses bancos em profundidades da plataforma continental. Este estudo destaca a importância de proteger a complexidade do habitat como um fator chave que influencia a diversidade da macrofauna em áreas de rodolitos.

Palavras-chave: Rodolitos, estrutura bentônica, grupos funcionais, APA marinha, Brasil.

ABSTRACT

Rhodoliths are free-living and morphologically diverse marine calcareous algae that are commonly distributed over the continental shelf seafloor. They increase seabed structural complexity and are of potential value as feeding and reproductive grounds for a myriad of marine fauna. The higher structural seabed complexity within rhodolith beds (RBs) may also increase overall benthic diversity by creating microhabitats, but this relationship has been rarely explored within RB worldwide. Here we compared benthic macrofaunal (> 500µm) structure RB (inside nodules) and within unconsolidated sediments under high and low-density beds to test whether benthic assemblages were associated with rhodolith bed density and nodule morphology. We observed that benthic diversity was higher in rhodoliths, whereas macrofaunal density was 16-fold higher when compared to sediments under RBs, which also displayed low nestedness and high taxa turnover between habitats. RB density and nodule morphology explained macrofaunal, taxonomic, and functional diversity in the rhodoliths. High-density RBs (204 ± 32.5 nodules.m^{-2}) had a higher macrofaunal diversity (taxonomic and functional) and exhibited typically spheroidal nodules with higher internal volume, being dominated by Annelid polychaetes. In contrast, low-density RBs (61 ± 46.9 nodules.m-2) exhibited discoid-shape nodules with a higher mean diameter and were dominated by peracarid crustaceans. Macrofaunal diversity, density, and functional diversity showed no differences between RBs densities, but macrofauna structure was influenced by the rhodolith beds, which increased carbonate content and sediment organic quality (protein and carbohydrates) in high-density stations. These findings indicate that benthic communities change markedly in response to RB density and nodule morphology, and provide critical habitat for several unique benthic species that are not encountered in unconsolidated sediment below these beds on continental shelf depths. This study highlights the importance of protecting habitat complexity as a key factor influencing macrofaunal diversity in rhodoliths areas.

Keywords: Rhodoliths, benthos structure, functional groups, MPA, Brazil.

1. Introduction

Rhodoliths are living nodules primarily composed of calcareous encrustations of non-geniculate, free-living red algae that are distributed globally on the continental shelf (Bosence, 1983; Foster, 2001; Amado-Filho et al., 2017; Teichert, 2014). They occur in areas with moderate hydrodynamics that prevents burial caused by particle sedimentation and protect them from physical impact, fragmentation, and removal by strong currents (Foster, 2001; Hinojosa-Arango et al., 2009; McConnico et al., 2017). The structure formed by the accumulation of these nodules are called rhodolith beds (RBs) and occurs in waters shallower than 150 m, with favorable temperature and irradiance for photosynthetic, respiratory and calcification processes (Schubert et al., 2019). These beds create a three-dimensional structure over the seafloor, modifying its physical characteristics and creating new microhabitats for many marine species (Steller et al., 2003; Berlandi et al., 2012; Qui-Minet et al., 2018). The RBs host a diverse and distinct fauna from typical unconsolidated seafloor habitats, suggesting their critical value for biodiversity conservation (Crain and Bertness, 2006; Figueiredo et al., 2007).

Supporting complex ecological interactions, RBs provide a large number of ecosystem services. They serve as refuge and nursery areas for many species (Kamenos et al., 2004; Steller and Cáceres-Martínez, 2009; Costa et al., 2020), some of them commercially important like scallops, crabs, and fish (Bosence, 1976; Kamenos et al., 2004; Riosmena-Rodriguez and Medina-López, 2010). They are one of the most important benthic habitats along the Brazilian continental shelf in terms of biodiversity and heterogeneity (Gherardi, 2004; Otero-Ferrer et al., 2019), harboring rare and endemic species of macroalgae, polychaetes, and ictiofauna (De Grave, 1999; Simon et al., 2016). Therefore, these living beds are key structures for the functionality and health of the ecosystem, contributing significantly to the increase of species richness and diversity (Steller et al., 2003).

There has been an expressive increase on anthropogenic pressures in marine coastal ecosystems and rhodolith beds are particularly vulnerable due to fishing, climate change and other direct impacts (Hall-Spencer and Moore, 2000; Horta et al., 2016; Sissini et al., 2020). Understanding the spatial drivers that

influences benthic biodiversity in RBs is thus critical for conservation planning (Cadotte et al., 2013). In addition to understanding the benthic taxonomic diversity associated to rhodoliths, determining the functional diversity of each taxa through variations of morphological, physiological, or behavioral characteristics of species may provide useful information on the functioning and uniqueness of communities or ecosystems (Violle et al., 2007; Mouchet et al., 2010). In this context, the different characteristics of species (Petchey and Gaston, 2006) complements the taxonomic richness to explain the structure and function of ecological communities (Mokany et al., 2008). RBs are habitats already known to exhibit high taxonomic diversity and are a priority for conservation on continental margins (Hall-Spencer, 1998; Grall and Hall-Spencer, 2003; Nelson, 2009). Thus, mapping its functionalities for conservation purposes must also focus on the different ecological characteristics that influence the processes and ecosystem dynamics (Diniz-Filho et al., 2013).

The benthic macrofauna has a crucial role in maintaining important ecosystem services in the ocean, such as energy-mass exchange and nutrient cycling between the water column and sediment (Van der Linden et al., 2017). Benthic organisms are also secondary producers in marine food webs and a source of food for higher trophic levels (Cusson and Bourget, 2005). In these interactions, the organism-sediment relationship of marine ecosystems is fundamental for the composition and diversity of benthic assemblages (Snelglove and Buttman, 1995; Cúrdia et al., 2015), where habitat complexity is considered the main driver of community structure and ecological functions (Yanovsky et al., 2017). RBs create habitats of high structural complexity over the seafloor increasing shelter and habitat resources available for the colonization of fauna (Sciberras et al., 2009; Buhl-Mortensen et al., 2012; Kovalenko et al., 2012). As a result, RBs are expected to host a higher diversity and abundance of benthic species compared to sand bottoms (Steller et al., 2003; Matias et al., 2010; Carvalho et al., 2017). These effects have been observed in a number of RBs globally, suggesting that the morphology and heterogeneity of beds are key factors to overall biodiversity in these ecosystems (Hily et al., 1992; Steller et al., 2003; Kamenos and Law, 2010; Burdett et al., 2014; Veras et al., 2020). The structural heterogeneity of RBs can vary spatially and temporally in a natural way,

but it also varies in response to anthropogenic impacts such as nodule extraction and bottom trawling (Hall-Spencer and Moore, 2000; Steller et al., 2003; Fredericq et al., 2014). As such, determining the spatial variability in RBs densities and macrofaunal taxonomic and functional diversity is crucial to understanding the effects of impacts and management responses on coastal marine ecosystems.

In Brazil, the biodiversity associated with RBs indicate a high diversity of species along extensive areas on the continental shelf (Villas-Boas et al., 2009; Figueiredo et al., 2015). Several studies have assessed the biodiversity associated to Brazilian RBs (Horta et al., 2016; Amado-Filho et al., 2017; Veras et al., 2020), but none have studied drivers of benthic infaunal diversity, composition, and functional dynamics in those ecosystems. Here we evaluated how the structural patterns of RBs influence benthic assemblies associated with RBs and within sediments below. Considering the important role of RBs as ecosystem engineers, this study examines how macrofauna assemblies change across habitats and beds with different nodule densities and morphology. We evaluate and quantified the diversity of the benthic macrofauna between RBs of varied structure, addressing two hypotheses: I) RBs will have a higher diversity than the unconsolidated sediment below it, and II) the density of rhodolith beds will be important to spatial patterns of benthic diversity in nodules and in the underlying sediments.

2. Materials and Methods

2.1. Study area and sampling design

The study area is located within the limits of the Costa das Algas Marine Protected Area (MPA) on the Eastern Marine Ecoregion of Brazil (Figure 1; Table 1; Spalding et al., 2007). This is a tropical region characterized by rainy summers, with predominantly NE and E winds, and dry winters, with energetic events from S and SE (Bernardino et al., 2015). The continental shelf on Eastern Brazil is influenced by the Tropical Water (TW) of the Brazil Current, with temperatures above 22 ºC and salinities above 36 (Palóczy et al., 2016; Mazzuco et al., 2019), with eventual seasonal summer upwelling of the South Atlantic Central Water (SACW) into the shelf with temperatures between 6 ºC and below 20 ºC, and

salinities between 34.6 and 36 (Quintana et al., 2015; Mazzuco et al., 2019). The continental shelf on the Espírito Santo basin includes a mixed system of terrestrial and carbonate sediments with RBs extending from middle to shelf break in the mesophotic zone (Figueiredo et al., 2015b).

Sampling was carried out by SCUBA diving in January 2019. The density of the RBs was a determining factor of the sampling design and based on preliminary images from the area, sampling stations were classified into two categories: “high-density” (H1, H2, and H3) and “low-density” (L1, L2, and L3; Figure 1). The differences in bed structure were further confirmed by measurements of rhodolith sphericity, internal volume and density of branches (detailed below). Abiotic data (temperature, salinity, depth, and visibility of the water column) were obtained at the time of sampling using a CTD and Secchi disk.

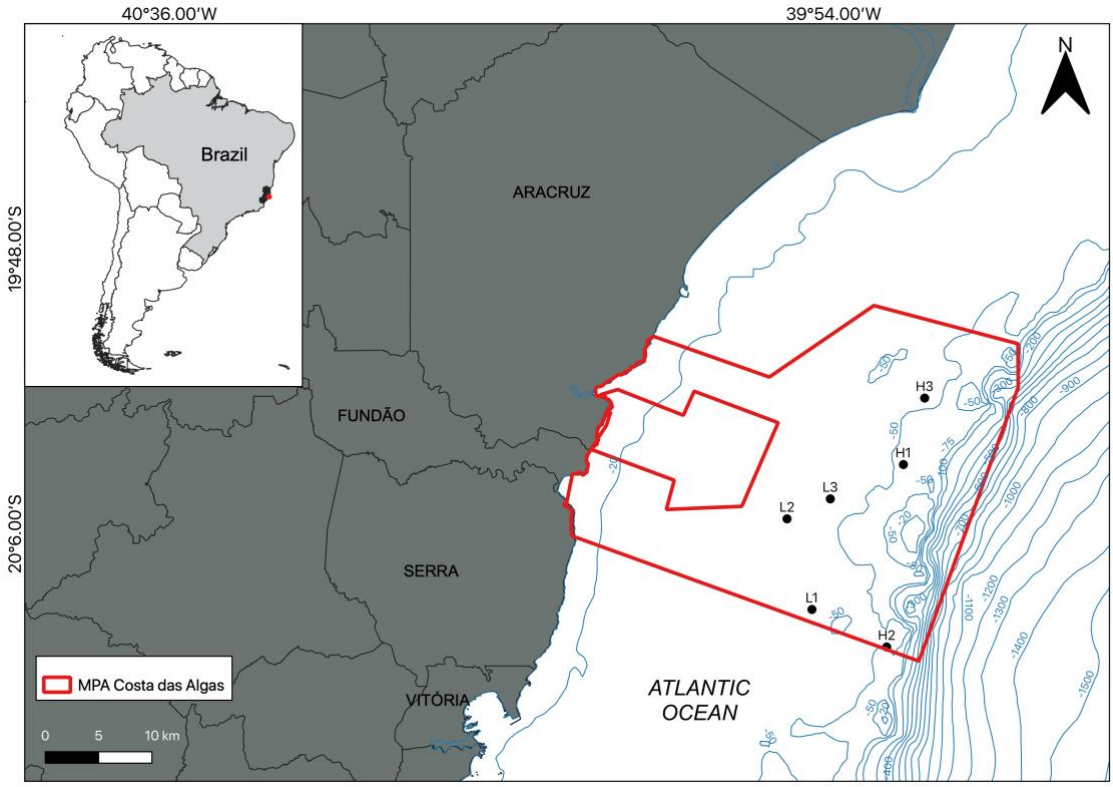

Figure 1. Location of the study area (MPA Costa das Algas, larger polygon) and the six sampled stations on the Eastern Continental shelf of Brazil. Bathymetric isobaths are shown in blue.

In each station, scuba divers sampled manually all rhodoliths within a 0.5 m^2 quadrat, in three replicates randomly distributed along a 20m-long random transect (Figure 2-D). After manual sampling of rhodoliths inside the quadrat, the

underlying unconsolidated sediment was manually sampled using PVC corers of 10 cm in diameter, and sealed with lids. The rhodolith nodules were packed in cloth bags with <0.5 mm mesh and sealed to prevent loss of macrofauna during recovery on board, where they were immediately fixed with formaldehyde (10%) and borax to avoid carbonate degradation. In addition to macrofaunal invertebrates, sediment underlying the rhodolith beds was sampled for grain size, organic matter and biopolymers analysis using corers (10 cm diameter), preserved in ice on board, and frozen until processing. Due to sample loss, sedimentary analysis was not done in station L3.

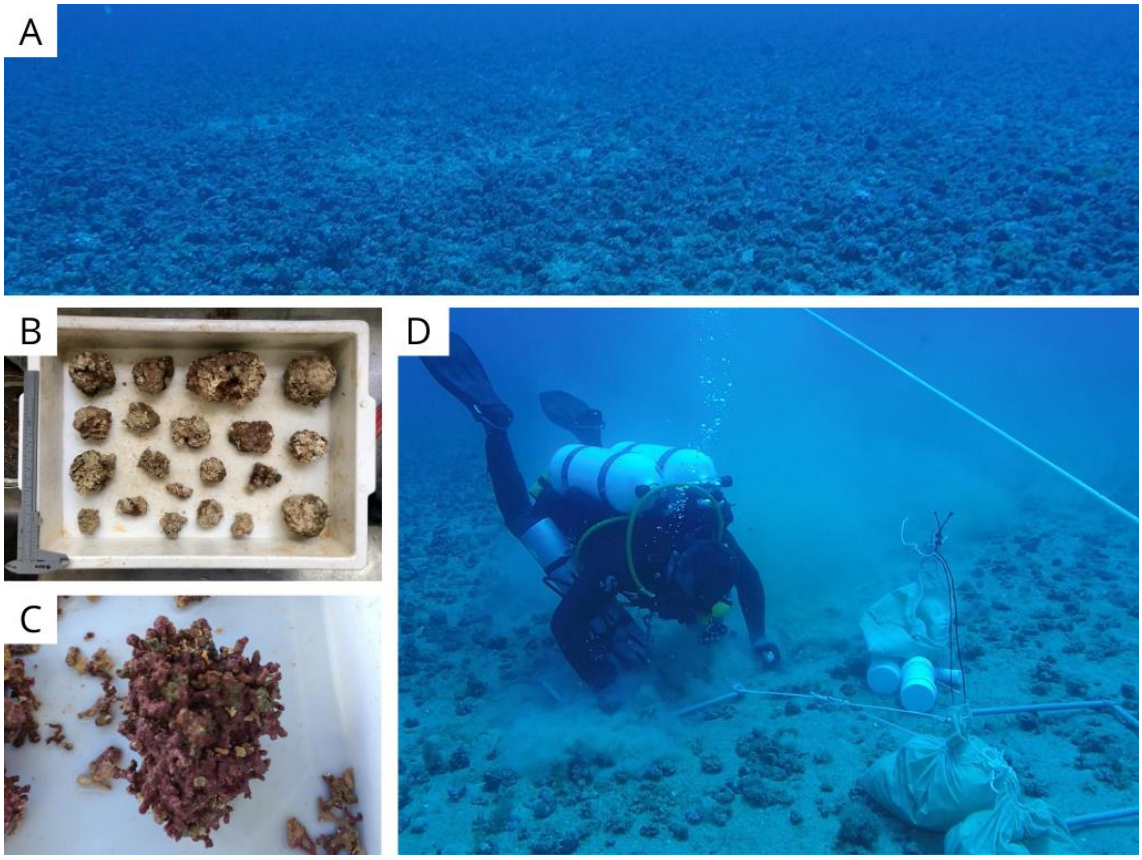

Figure 2. A) High-density RBs within the study area, B-C) a range of rhodoliths sampled in this study, and D) SCUBA sampling from this study.

2.2. Laboratory analysis

In the laboratory, the nodules were broken and macrofaunal samples were sieved (500 µm) and preserved in 70% ethanol until sorting. All organisms were identified to family or the lowest possible taxonomic level under a

stereomicroscope. Macrofaunal trophic group analysis followed the main feeding types (deposit feeders, detritivore feeders, filter feeders, OCO - omnivores, carnivores and others – feeders, and suspension feeders) according to Jumars et al., (2015).

The classification of rhodolith morphology was determined by measuring the largest, intermediate, and minor axis of each nodule, which resulted in a mean nodule diameter and sphericity for each station (Figure 2; Bosence and Pedley, 1982). The morphological rhodolith dataset was plotted on a TRIPLOT spreadsheet developed by Graham and Midgley (2000), and drawn on the pebble shape diagram of Sneed and Folk (1958) that discriminates rhodoliths in spheroidal, discoidal, or ellipsoidal shape. The RB density was estimated from the number of nodules sampled within each quadrat (nodules.m^{-2}). The mean diameter of the nodules of each station was averaged from the three replicated samples.

There is a relationship between the degree of protuberance and biodiversity in rhodoliths (Steller et al., 2003) and to estimate this complexity, the nodules were qualitatively classified by the relative branching density (Bosence et al., 1983). Nodules were classified into four groups: I = a single branch; II = few branches; III = frequent branching; IV = dense and solid branching. The average internal volume of the rhodoliths in each site was determined by water volumetric displacement (Basso and Tomaselli, 1994; Steller et al, 2003). Rhodoliths were covered with a plastic film and then submerged in a graduated container of a known volume (V_i). The difference between the initial volume Vi and the displacement of the liquid (V_{F1}) is called V_1.

$$V_1 = V_{F1} – V_i \qquad \text{(Eq. 1)}$$

Secondly, the rhodoliths were again submerged but without the plastic film (V_{F2}). The same measurement method was used to estimate the V_2 volume.

$$V_2 = V_{F2} – V_i \qquad \text{(Eq. 2)}$$

Finally, the difference between V_1 and V_2 was calculated to estimate the internal volume of the nodules (V_R) within the quadrat area (m^{-2}).

$$V_R = V_1 – V_2 \qquad \text{(Eq. 3)}$$

For sediment granulometric and carbonate content, the samples were thawed and placed in an oven at 60 ºC for 48 hours. The dry sediment was macerated and taken to a stirrer, where the grain size was determined by sieving it between -1.5 phi (Φ) sieves and 4 Φ, with 1 Φ intervals. Subsequently, the values of Φ were added to the SysGran 3.0 software (Camargo, 2006) to analyze the granulometric properties (i.e., average grain size and the total percentage of gravel, sand, silt and carbonate). The carbonate contents of the sediment were determined by combustion in a muffle (550 ºC for 4 hours) with an additional hour at 800 ºC.

All sedimentary organic biopolymers (carbohydrates, lipids, and proteins) analysis were made in triplicates, following the methods in Danovaro (2010). Total protein analysis (PRT) was carried after its extraction with NaOH (0.5 M, 4 hours) and was determined according to Hartree (1972), modified by Rice (1982), to compensate for phenol interference. Total carbohydrate (CHO) was analysed according to Gerchacov and Hatcher (1972). Total lipids (LPD) were analysed according to the protocol described in Marsh and Weinstein (1966), being extracted from 1 g of homogenized sediment lyophilized by 11 ultrasonication (20 min) in 10 ml of chloroform:methanol (2:0 1 v/v). Blanks for each analysis were taken with pre-combusted sediments at 450 and 480 °C for 4 hours. The concentrations of PRT, CHO, and LPD were displayed as bovine serum albumin (BSA), glucose, and tripalmitin equivalents, respectively. The concentrations of PRT, CHO, and LPD were converted into carbon equivalents assuming a conversion factor of 0.49, 0.40, and 0.75, respectively (Fabiano and Danovaro, 1994). Also, protein to carbohydrate (PRT:CHO) and carbohydrate to lipid (CHO:LPD) ratios were applied to assess the state of biochemical degradation processes (Galois et al., 2000). The sum of biopolymer concentrations were added to the analysis as a measure of biopolymeric carbon (BPC; Fabiano et al., 1995; Hadlich et al., 2018).

2.3. Statistical analysis

Benthic assemblages were compared across rhodolith beds with high and low densities (bed), and between nodule and underlying sediments (habitats). Macrofaunal richness (S), diversity (Shannon H') and evenness (J') were

determined for each bed and habitat. In addition, macrofaunal functional diversity was determined from the functional richness (FRic), functional dispersion (FDis), functional evenness (FEve), and entropy (FRaoQ; Mason et al., 2005). FRic indicates the amount of niche space filled by species in the community; FEve describes the evenness of abundance distribution in a functional trait space (Mason et al., 2005); and FDis and RaoQ are indices quantifying how functionally similar are the individuals spatially (Botta-Dukát, 2005).

Spatial differences in rhodolith bed structure (nodule density, internal volume, morphology and branching density), in sediments (total organic matter, carbonate, biopolymers, and granulometry), and in macrofaunal assemblages (density, richness, evenness, diversity, and functional diversity) were tested between rhodolith beds through analysis of variance (ANOVA) for univariate parameters (Underwood, 1997) or permutational multivariate analysis of variance (PERMANOVA; Anderson, 2017) for multiple and dependent variables. All analyses were hierarchically designed with one fixed factor (beds, two levels: high and low); and station (nested in bed) or habitat (fixed) with two levels (RB and sediment). ANOVA premises were assessed by Kolmogorov-Smirnov test (normality; Conover, 1971) and Bartlett test (homogeneity of variances; Bartlett, 1937). PERMANOVAs were based on a Bray-Curtis resemblance matrix under a reduced residuals model and data was square-root transformed to give more weight to rare taxa in the analyses (Clarke and Gorley, 2006). Post-hoc pairwise tests (Tukey or PERMANOVA) were performed to identify significant differences within factor levels (Underwood, 1997; Anderson, 2008).

A non-metric Multidimensional Scaling Analysis (nMDS) was applied to visualize the similarities of macrofauna assemblies between densities and habitats, using the square-root abundance of all taxa from the Bray-Curtis similarity matrix. To assess assemblage compositional changes across samples and habitats (rhodolith and sediment), we applied a multi-site analysis to discriminate total dissimilarity (i.e., beta diversity) into turnover (i.e., total replacement of species) and nestedness (i.e., species-poor sites are subsets of speciose ones), based on presence-absence data and Sørensen index and its respective components of turnover (βSIM) and nestedness (βSN; Baselga, 2010). A canonical analysis of principal coordinate (CAP; Anderson and Willis,

2003) was performed to determine the association between environmental variables and benthic assemblages between beds and habitats. Graphic design and analysis were performed using R Project (R Development Core Team, 2005) with packages: ‘ggplot2’ (Wickham, 2016), ‘oce’ (Kelley and Richards, 2017), ‘stats’, ‘vegan’ (Oksanen et al., 2018), MASS (Ripley et al., 2019), mgcv (Wood, 2012), MuMIn (Barton and Barton, 2013), and FD (Laliberté et al., 2014).

3. Results

3.1. Pelagic conditions

During sampling, surface and bottom (38.4-54.8 m) temperature ranged from 26-28 ºC and 19-23 ºC, respectively, while salinity ranged from 37.7-38.3 (Table 1, Figure 3). Stations H1 and H2 had water column profiles with a marked halocline in the first 10 meters, whereas at stations H3, L2, and L3 the halocline occurred at 15 to 35m depth. Temperature showed a similar bathymetric profile between stations. The maximum depth of stations varied between 38-55 m (Table 1). Secchi's depth varied between 20-34 m deep and the incidence of light in the water column reached greater depths in station L2 (Table 1).

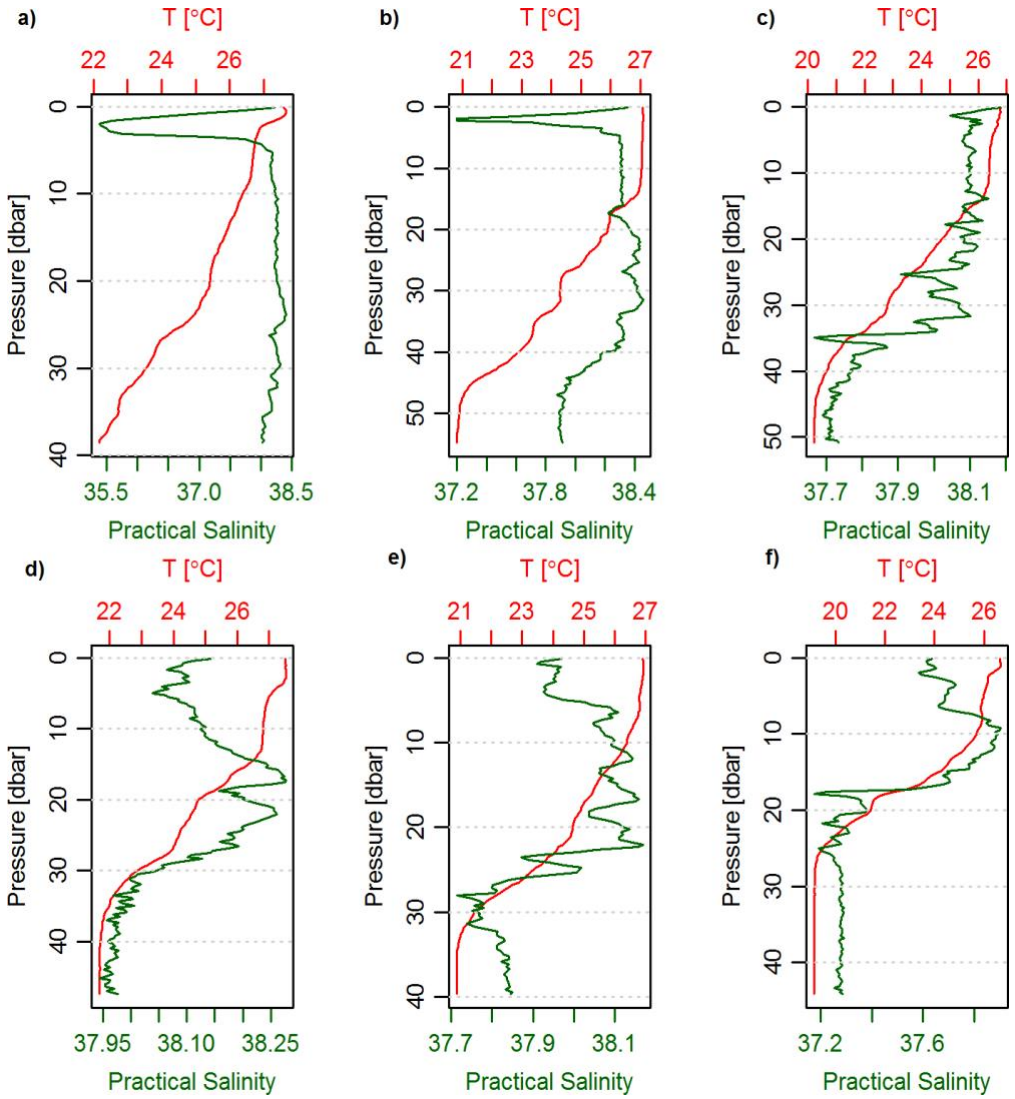

Figure 3. Vertical profiles of temperature (ºC, red) and salinity (green) along a bathymetric gradient in the sampled stations during January 2019. a) H1, b) H2, c) H3, d) L1, e) L2 and f) L3.

Table 1. Location and characterization of maximum depth (Max Depth), Secchi's depth (D_{SC}), bottom temperature (B_T) and salinity (B_S), nodule density (ND), mean internal volume (V_I), mean diameter (D_M) of the nodules, biopolymeric carbon (BPC), and mean percentage of gravel, sand, silt and carbonate in the sampling stations. Note: standard deviation is shown within the parentheses.

Station (Lat/Long)	Max Depth (m)	D_{SC} (m)	B_T (ºC)	B_S	ND ($N.m^{-2}$)	V_I ($cm^3.m^{-2}$)	D_M (cm)	BPC ($mg.g^{-1}$)	Gravel (%)	Sand (%)	Silt (%)	Carbonate (%)
H1 (20°01'36.5"S/39°49'35.1"W)	38.4	34	22.2	38	171	153.3 (±120.1)	2.8 (±0.9)	4.4	28.4 (±15.8)	70.1 (±15.4)	1.5 (±0.5)	5.4 (±0.5)
H2 (20°13'8.4"S/39°50'38.4"W)	54.8	30	20.8	37.9	206	346.6 (±59.2)	3.9 (±0.8)	4.5	19.5 (±11.0)	78.1 (±11.2)	2.4 (±0.7)	5.0 (±0.2)
H3 (19°57'24.6"S/39°48'14.4"W)	50.6	33	20.2	37.7	236	436.6 (±178.5)	3.7 (±0.9)	4.8	19.8 (±8.5)	78.6 (±8.3)	1.6 (±0.3)	7.2 (±0.6)
L1 (20°10'46.2"S/39°55'21.96"W)	47.2	20	21.7	38	104	246.6 (±52.04)	3.8 (±1.2)	3.6	7.0 (±1.9)	91.4 (±2.0)	1.6 (±0.4)	4.0 (±0.5)
L2 (20°05'02.4"S/39°56'56.4"W)	39.5	25	20.9	37.8	68	368.3 (±230.2)	5.3 (±1.7)	4.7	18.6 (±1.8)	79.6 (±1.3)	1.8 (±0.5)	5.3 (±0.4)
L3 (20°03'46.8"S/39°54'12.3"W)	45.6	-	19.1	37.3	11	4.0 (±0.39)	3.8 (±1.7)	-	-	-	-	-

3.2. Sediment characteristics

The sediments under the RBs had similar sedimentary characteristic, composed predominantly of coarse and medium sand, followed by gravel (Table 1). Sediment carbonate content ranged from 3% and 8%, with higher carbonate content at the high-density beds (F = 5.74, *p* = 0.0323; Appendix A1, Table 1).

Two sediment biopolymers (protein and lipids) had higher concentrations in high-density RBs (F = 27.3, *p* = 0.0002; Appendix A1, Figure 4-a). Protein and lipid concentrations in sediments of high-density beds ranged from 0.43 to 0.85 mg.g-1 and 0.02 to 0.30 mg.g-1, respectively (Figure 4-a). Biopolymers ratios (PRT:CHO, CHO:LPD) did not differ between high and low-density RBs, but showed spatial variation among samples (0.23 to 2.81 PRT:CHO, 2.4 to 111.3 CHO:LPD; Appendix A1, Figure 4-b-c). BPC concentration did not vary between RBs densities (*p* > 0.05; Appendix A1, Table 1).

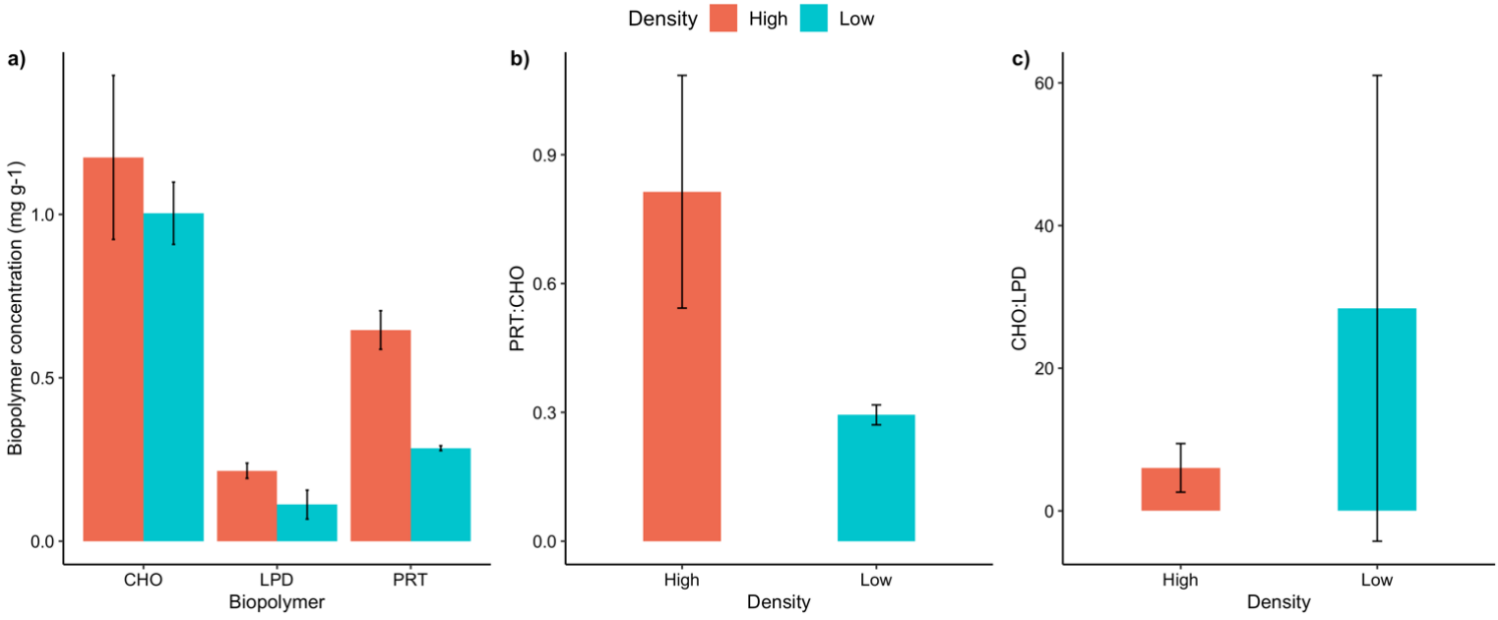

Figure 4. Average values (±SE) of a) carbohydrate, lipid, and protein concentration, b) the PRT:CHO, and c) CHO:LPD ratios in sediments with high and low densities of rhodoliths.

3.3. Rhodoliths characteristics

The number of rhodolith nodules and their morphology varied markedly between high and low-density RBs. The density of rhodoliths nodules in high-density beds (204 ± 32.5) was over 3 times higher when compared to the low-density beds (61 ± 46.9; F = 47.9, $p < 0.0001$; Appendix A2). High-density beds were dominated by rounded nodules (36%) leaning to elongated (15%), whereas in low-density beds the nodules were predominantly discoidal (22%) leaning to spherical (14%; F = 3.12, $p = 0.05$; Appendix A2, Figure 5). Internal nodule volume was higher in high-density beds (Table 1) with a significant difference between sampling stations (F = 5.68, p = 0.0183; Appendix A2). The average diameter of nodules varied between 3.5 ± 0.5 in high-density RBs and 4.4 ± 0.7 in low-density beds (F = 7.69, $p = 0.0071$; Appendix A2, Table 1). Overall, the majority of the nodule's branching types were classified as IV with solid branching (88%) with no difference between high and low-density beds (F = 1.32, $p = 0.33$; Appendix A2). The branching type I nodules were typical at high-density beds (F = 5.17, $p = 0.04$; Appendix A2).

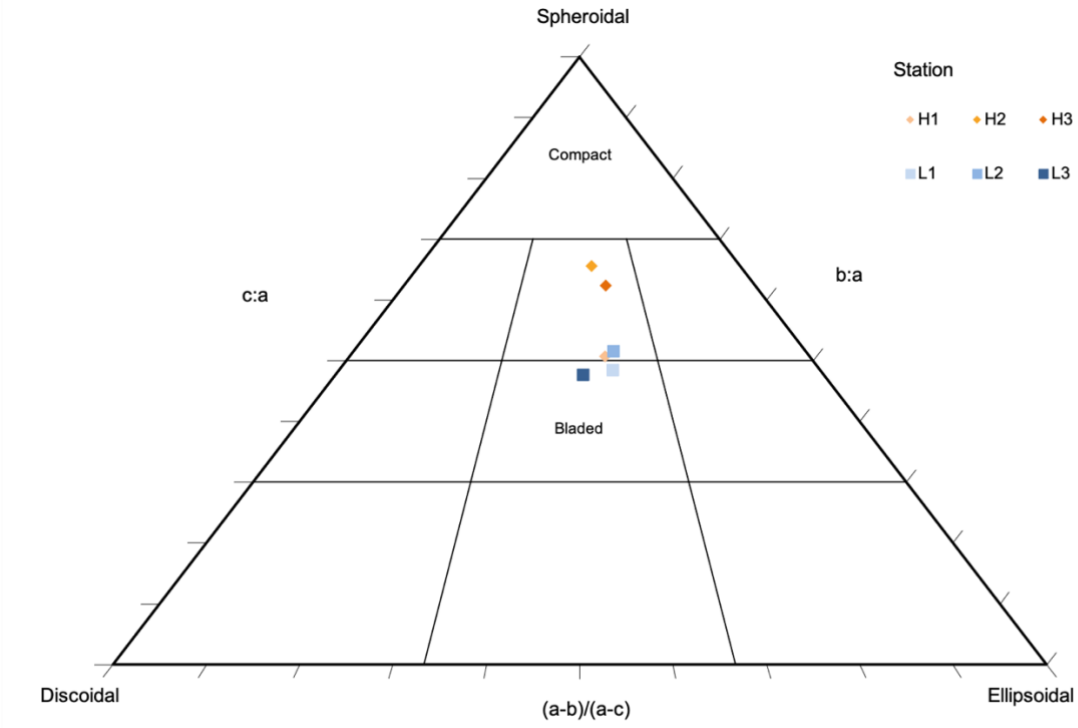

Figure 5. Morphological distribution of rhodoliths sampled on Eastern Brazil in a TRIPLOT diagram (Graham and Midgley, 2000; Sneed and Folk, 1958).

3.4. Macrofaunal assemblages

We sampled a total of 11,421 macrofaunal organisms associated to the RBs, with marked differences between RBs densities and habitats ($p < 0.05$; Appendix A3). High-density beds had a similar macrofaunal density (average 1,429 ind.m^{-2}) when compared to low-density beds (average 1,275 ind.m^{-2}; F = 0.27, $p = 0.601$; Appendix A3, Figure 6-a). However, macrofaunal density was significantly higher inside nodules (2,538 ind.m^{-2}) when compared to the underlying sediments (166 ind.m^{-2}; F = 66.18, $p < 0.0001$). In sediments, macrofaunal density was higher under low-density RBs (average 211 ind.m^{-2}) but with no differences between densities ($p > 0.05$; Appendix A3).

We identified 151 macrofaunal taxa within nodules and sediments, with pronounced contrasts between habitats (Appendix A3, Figure 7). Rhodoliths were colonized by 137 macrofaunal taxa, with a higher taxonomic diversity and evenness in high-density RBs (H' = 3.20, J' = 0.74; $p < 0.001$; Appendix A3, Figure 6-b-c), where low-density RBs showed close values when compared to the unconsolidated sediments at low-density beds (Figure 6-b). The sediment macrofauna under RBs were colonized by 64 taxa, with similar diversity under high and low-density RBs ($p > 0.001$; Appendix A3, Figure 6-b-c).

Macrofaunal composition changed markedly between habitats and beds ($p < 0.05$; Appendix A4, Figure 7). Rhodolith nodules were mostly dominated by Annelida (47%) and Crustacea (44%; Figure 7-a) with a marked difference between high and low-density RBs. Annelida (Syllidae, Nereididae, and *Lysidice* sp) dominated high-density RBs (51%), whereas Crustacea (Gammaridae, Melitidae, and *Elasmopus* sp) dominated (64%) low-density beds (Figure 7-a). In contrast, sediment macrofaunal assemblages were relatively similar under high and low-density RBs being dominated by Crustacea (63%; Ostracoda, Melitidae, and *Leptochelia* sp) and Mollusca (22%; *Meioceras* sp and Cardiidae; Figure 7-b).

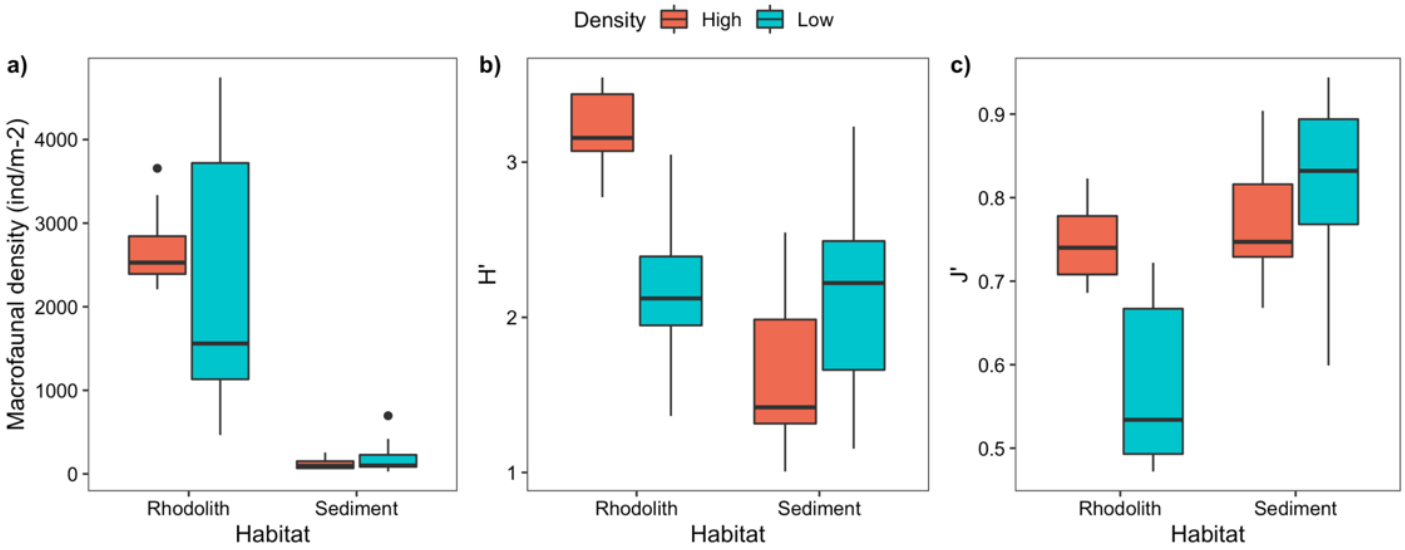

Figure 6. Changes (±SE) in a) macrofaunal density (ind.m^{-2}), b) H', and c) J' through habitats and high (red) and low-density (blue) RBs.

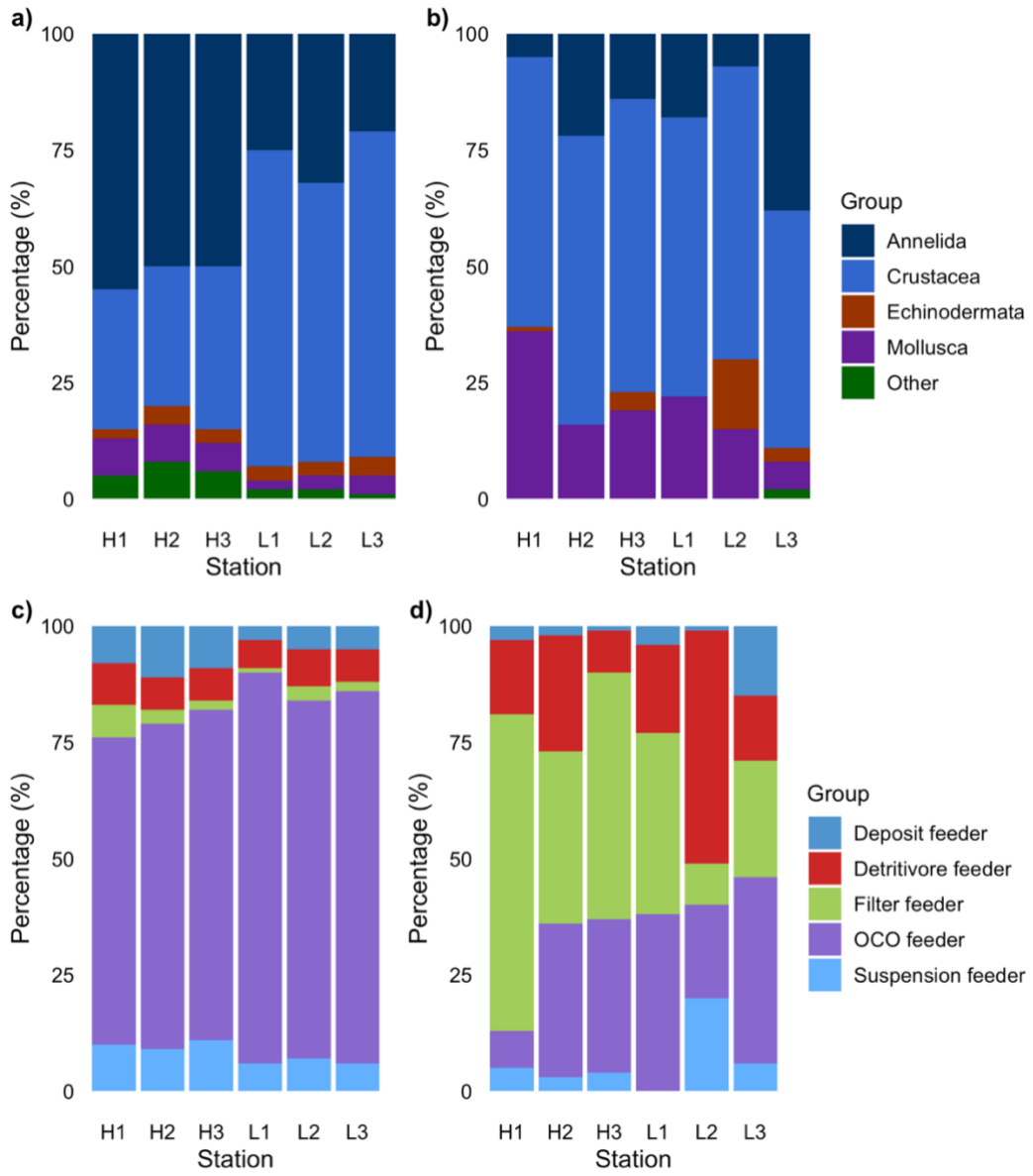

Figure 7. Relative abundance of macrofauna assemblages among RBs (a, c) and unconsolidated sediment stations (b, d). a) Taxonomic composition of macrofauna in rhodolith beds; b) Taxonomic composition of macrofauna in unconsolidated sediment under rhodoliths. c) relative abundance of macrofaunal trophic groups in RBs; d) relative abundance of macrofaunal trophic groups in unconsolidated sediment under rhodoliths.

Macrofaunal trophic group richness exhibited distinct dominance between habitats (Figure 7-c-d). The dominant trophic group in RBs were OCO feeders (74.6%), while sediments were dominated by filter feeders (38.5%) and OCO feeders (28.5%). Macrofaunal functional richness (FRic) was higher in RBs (7 ± 0.8) when compared to the sediment underneath (5 ± 1.3; F = 27.00, $p < 0.0001$; Appendix A4, Figure 8-a). In contrast to FRic, macrofaunal functional evenness

(FEve) showed an opposite pattern, being higher in sediments (0.32 ± 0.1) than in the rhodolith nodules (0.09 ± 0.04), with significant differences across beds and habitats (F = 75.39, $p < 0.0001$; Appendix A4, Figure 8-b). In high-density RBs, macrofaunal functional dispersion (FDis) and entropy (FRaoQ) were higher (0.24 ± 0.02 and 0.07 ± 0.009, respectively) when compared to low-density beds (0.1 ± 0.02, 0.05 ± 0.09, respectively; $p < 0.05$; Appendix A4, Figure 8-c-d). In the sediments, FDis and FRaoQ values were higher under low-density beds (0.27 ± 0.04, 0.08 ± 0.01, respectively) when compared to high-density beds (0.24 ± 0.04, 0.07 ± 0.01, respectively; $p < 0.005$; Appendix A4, Figure 8-c-d).

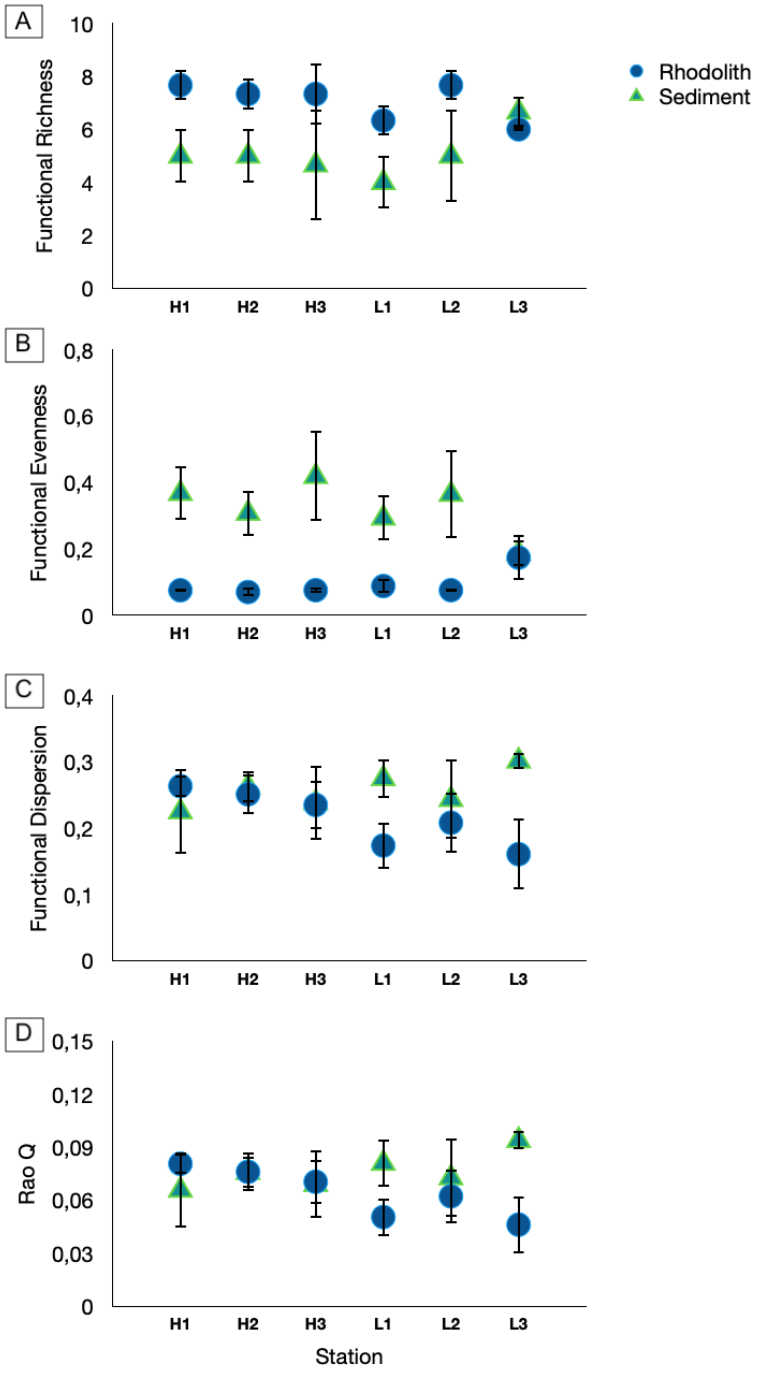

Figure 8. Mean (±SE) macrofaunal functional diversity indices. A) Functional richness (FRic), B) functional evenness (FEve), C) functional dispersion (FDis) and D) entropy (Rao Q) from rhodolith nodule (blue spheres) and underlying sediment assemblages (green triangles).

3.5. Multivariate analysis

There was a high degree of patchiness within the benthic assemblage among the RBs (Sørensen Index = 0.92). Analysis showed low nestedness and high taxa turnover between sediments and rhodoliths (Table 2, Figure 9). We also

observed a strong spatial variability in macrofaunal assemblages in underlying sediments (F = 20.0, *p* = 0.01; Appendix A3), which contrasted to the lower spatial dissimilarity in the rhodolith nodule fauna (Figure 9).

Table 2. Results of the multiple-site analysis to test for dissimilarity (Sørensen index), turnover (βSIM), and nestedness (βSNE) in the benthic assemblage across the RBs (Baselga, 2010). Note: significant results are in bold.

	Dissimilarity indices				
	Sørensen	βSIM	βSNE	C-score (species mean)	Pr(sim)
Rhodolith + Sediment	0.92	0.77	0.14	12.58	**0.01**
Rhodolith	0.88	0.80	0.08	5.49	**0.01**
Sediment	0.89	0.80	0.09	0.84	0.99

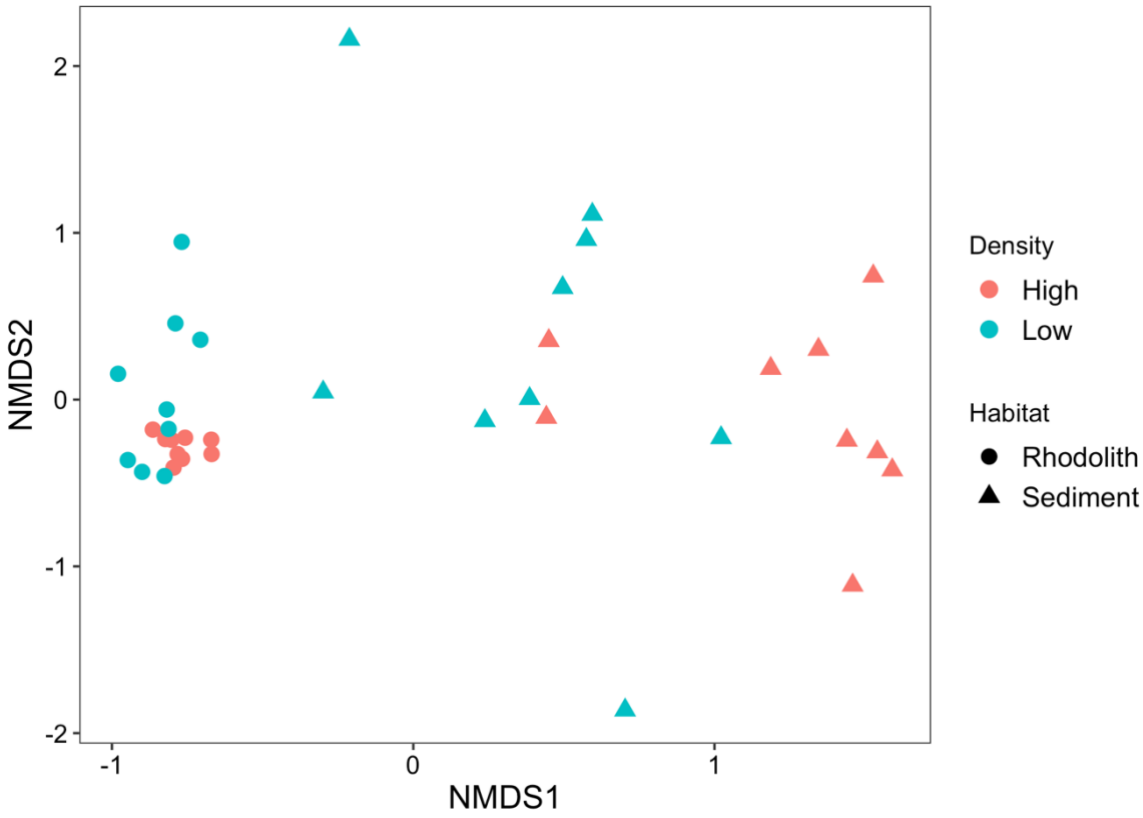

Figure 9. Plot of nMDS analysis for the similarities (Bray-Curtis) of the total abundance of the benthic macrofauna between the RBs and unconsolidated sediment below the beds. Red spheres represent high-density stations of RBs; Blue spheres represent low-density stations of RBs; Red

triangles represent high-density stations in unconsolidated sediment; Blue triangles represent low-density stations in unconsolidated sediment. Test stress: 0.1333.

The CAP analysis supported the spatial dissimilarity in macrofaunal assemblages between RBs and sediments, suggesting a strong effect of density of beds on macrofaunal structure (Figure 10, Appendix A5). The CAP ordination showed that benthic assemblages of high-density beds were more similar than low-density RBs, with greater contribution of Syllidae and Sipuncula, which were associated to nodule shape and density of beds. Low-density RBs had a higher contribution of gammarid amphipods, being positively associated with nodule diameter and shape of rhodoliths (Figure 10). The unconsolidated sediment had a higher contribution of Ostracoda, Melitidae and Amphiuridae, and were also mostly distributed along axis 1 (>29%). Only the sediment carbonate was associated with benthic assemblage composition (F = 1.71, p < 0.01, Appendix A6, Figure 10), especially in high-density stations.

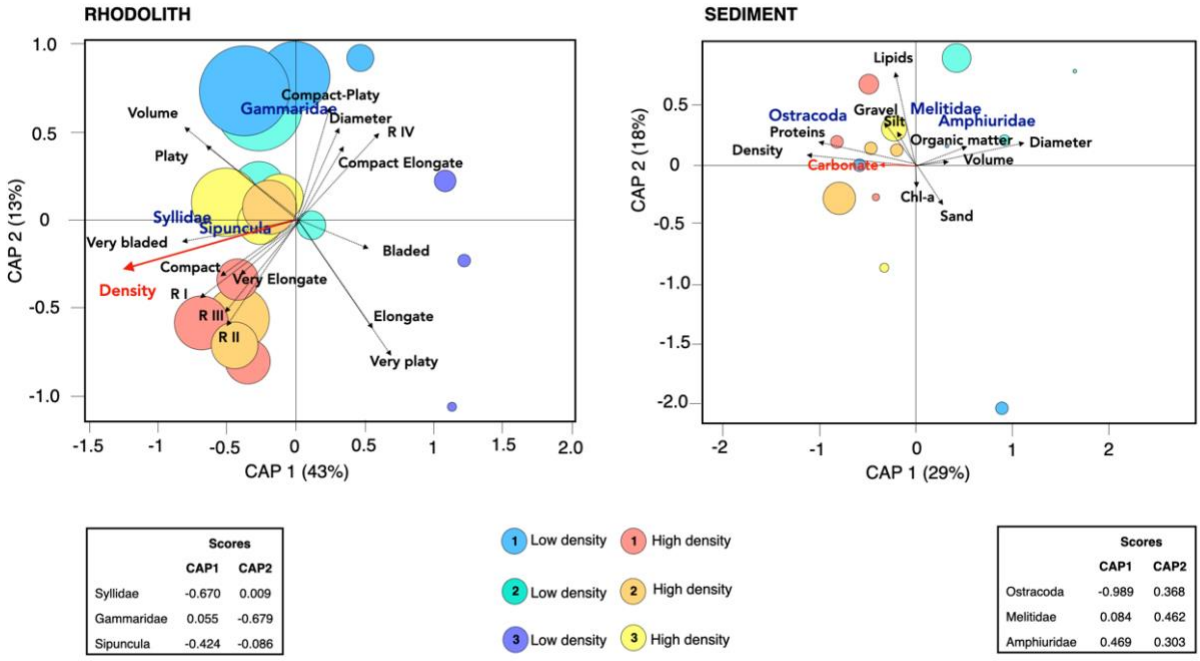

Figure 10. Canonical analyses of principal coordinates (CAP) indicating differences in the macrofaunal assemblages in RBs and the underlying unconsolidated sediments at the sampled stations (H1, H2, H3, L1, L2 and L3). Vectors are based on Spearman correlation values > 0.5 (p < 0.5) for environmental variables and scores for taxa. The proportion of data explained by axis 1 and 2 are in parenthesis. Size of circles represents macrofaunal total abundance in each station.

4. Discussion

This study showed that habitat complexity within RBs, represented by the presence, density, and morphology of rhodolith nodules, is important to macrofaunal abundance, composition, and functional diversity in RBs on the continental shelf of SE Brazil. Thus, our results support previous assessments of the interacting role of rhodolith nodule density and shape with benthic assemblages (Carvalho et al., 2017; Gabara et al., 2018), and reveal similar ecological processes of substrate complexity governing benthic ecosystems observed in other coastal marine habitats (Archambault and Bourget, 1996; Mazzuco et al., 2020). It was observed that environmental heterogeneity contributes to maintaining greater species diversity or variation in species composition between habitats through species substitution (high taxa turnover), meaning that the macrofauna of the sediment is not a subset of the macrofauna of rhodoliths (and vice versa). Our findings also revealed that rhodolith nodules are important to the macrofaunal assemblages in underlying unconsolidated sediments, by the abundance and taxonomic richness of benthic macrofauna (Steller et al., 2003; Hinojosa-Arango et al., 2014).

The hypothesis of the close link between RBs density and macrofaunal assemblages was supported by the distinct abundance, dominance, and composition of organisms between high and low-density RBs. These effects have been largely observed within rhodolith beds in the Mediterranean and on the coast of California (Steller et al., 2003; Hinojosa-Arango and Riosmena-Rodríguez, 2004). Despite high-density RBs on eastern Brazil being typically characterized by a smaller mean diameter of nodules due to the lower light penetration and high sedimentation rates (Amado-Filho et al., 2007; Amado-Filho et al., 2017; Riul et al., 2009) the density factor can also be important to bed stability, whereas high density beds may be more resistant to wave disturbance and consequently may provide a more stable environment (Marrack, 1999; Hinojosa-Arango and Riosmena-Rodríguez, 2004). Therefore, nodules are mostly characterized by rounded spheric nodules and have also greater internal volume (Gagnon et al., 2012). This sphericity provides more internal space for the colonization of macrofauna, potentially resulting in higher faunal density and diversity. Such morphological changes in rhodolith nodules may also be related

to depth over larger spatial scales (Veras et al., 2020; Otero-Ferrer et al., 2020), but these effects were not tested in this study. In addition, although we have not determined the effects of algae diversity and rhodolith forming species over the benthic macrofauna in our study, it may also be related to variations in rhodolith morphology and consequently influence benthic assemblages in RBs (Foster, 2001; Hinojosa-Arango and Riosmena-Rodríguez, 2004; Figueiredo et al., 2007).

Polychaeta and Crustacea dominated RBs in Eastern Brazil in a similar pattern observed in other continental margins at similar depths (Bordehore et al., 2003; Hinojosa-Arango and Riosmena-Rodríguez, 2004; Grall et al., 2006; Harvey and Bird, 2008). The greater abundance and dominance of these two groups in the RBs has been attributed to their wide feeding strategies, making it possible for them to occupy different microhabitats (Fauchald and Jumars, 1979; Harvey and Bird, 2008; Sciberras et al., 2009). Macrofaunal structure within RBs is likely locally related to nodule morphology, size and density of beds, and different levels of disturbance (Steller et al., 2003; Sciberras et al., 2009; Tompkins and Steller, 2016). Our data support those effects locally, with macrofaunal assemblages being strongly associated to both nodule density and morphology. High-density RBs were dominated by polychaeta, especially Syllidae; while low-density RBs are dominated by Crustacea (mostly Gammaridae). The changes in the dominance of polychaetas or crustaceans in RBs may be associated to food-web, habitat and disturbance dynamics among areas (Grall et al., 2006; Figueiredo et al., 2007), since habitat was significantly associated to faunal dominance. It is also likely that temporal changes in macrofaunal structure occurs within these dynamic ecosystems as a result of bottom transport and disturbance (Navarro-Mayoral et al., 2020), which will need to be assessed for our study area.

Our study revealed that underlying sediments in RBs support a distinct set of macrofaunal organisms when compared to the nodules. Mollusks and crustaceans were the most dominant groups in the unconsolidated sediment, which are groups with a predominant burrowing behavior (Snelglove and Buttman, 1995). Carbonate also played an important role structuring macrofaunal assemblies in the unconsolidated sediment, specifically at high-density stations, probably due to the greater aggregation and contribution of the carbonate

nodules to the sediment below the beds. This supports that rhodoliths have a strong influence on sediment macrofaunal structure by changing its sedimentary and organic content. The organic supply from rhodoliths to underlying sediments is supported by higher concentration of proteins in high-density stations. The higher organic matter liability may come from both higher pelagic detrital inputs being deposited and an increased organic algal input from rhodoliths in high density nodules (Grall et al., 2006). These results suggest that the physical structure of rhodoliths may be greatly important for the organic input to the benthos in the nodules and in the underlying sediments, supporting the pervasive effects of physical disturbance to their biodiversity and functioning (Hall-Spencer and Moore, 2000; Grall and Hall-Spencer, 2003).

The dominance of trophic groups within RBs were mainly structured by OCO feeders in a similar pattern observed in other nodule communities (Grall et al., 2006). In contrast, sediment macrofaunal assemblages were dominated by filter feeders, likely favored by an increased quality of pelagic organic matter (Snelglove and Buttman, 1995; De Grave and Whitaker, 1999). Trophic group richness was similar between RBs and the underlying sediments, suggesting a wide niche availability in both habitats (Paganelli et al., 2012; Bolam et al., 2017). In addition, functional richness (FRic) was correlated RBs supporting that RBs host a diverse range of macrofaunal organisms that are not typically observed over sedimentary habitats. Higher functional evenness (FEve) agrees with lower FRic in sediments, supporting a more uniform range of organisms in the sediments (Schumm et al., 2019).The higher FDis and RaoQ in RBs at high-density suggests that niche availability increases with nodule density providing a lower competition for resources (Mason et al., 2005). The greater organic matter quality within high-density RBs may also have an effect on supporting a large number of organisms within similar functional groups.

This study suggests that physical impacts that may remove rhodolith nodules can lead to a marked change in the structure of benthic assemblages and their taxonomic and functional diversity. We showed that RBs provide a unique habitat for a diverse and distinct macrofaunal assemblage, including organisms in the underlying sediments. Additionally, the nodule morphology, internal volume, and density are key parameters influencing RBs benthic

macrofauna. Rhodoliths may provide an increased food quality to local benthic assemblages, which partially support a higher macrofaunal functional diversity. Moreover, since RBs are vulnerable to global changes and the exploratory pressure grows upon these habitats through fishing and the oil and mining industries, our results support the importance of these ecosystems to overall marine biodiversity on the Brazilian continental margin. As Brazil holds extensive areas of rhodolith beds, our study suggests that determining priority areas for conservation in areas of higher nodules density would protect assemblages with higher functional diversity.

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APPENDICES

Appendix A1. ANOVAs and PERMANOVAs results evaluating differences in sediment granulometry (sand, gravel, silt), carbonate content, biopolymeric carbon, and biopolymers concentration (protein PRT, carbohydrate CHO, lipids LPD) contribution in organic matter between RB density D (high and low) in the unconsolidated sediment underneath the rhodolith beds. Note: significant results ($p \leq 0.05$) are in bold.

		Biopolymeric Carbon				Carbonate				Granulometry			
	df	SS	MS	F	*p*	SS	MS	F	*p*	SS	MS	Pseudo-F	*p*
D	1	1.38	1.38	4.15	0.0643	5.76	5.76	5.74	**0.032 (H>L)**	0.01	0.01	3.51	0.07
Residuals	13	4.01	0.33			13.05	1.00			0.05	0.004		
Total	14									0.06			

		Protein				Carbohydrate				Lipids				PRT/CHO				CHO/LPD			
	df	SS	MS	F	*p*	SS	MS	F	*p*	SS	MS	F	*p*	SS	MS	F	*p*	SS	MS	F	*p*
D	1	0.44	0.44	27.3	**0.0002**	0.10	0.10	0.31	0.584	0.03	0.03	4.95	**0.045**	1.14	1.14	2.71	0.126	2781	2781.4	3.84	0.0735
Residuals	12	0.19	0.01			3.79	0.31			0.09	0.01			5.06	0.42			8682	723.5		

Appendix A2. ANOVA and PERMANOVA (and significant post-hoc) results evaluating differences in rhodoliths densities, internal volume, mean diameter and branching density between RB density D (high and low) and stations S in the studied RBs. Note: significant results ($p \leq 0.05$) are in bold, ns not significant.

		Density					Volume					Diameter					
	df	SS	MS	F	*p*	*Tukey p*	SS	MS	F	*p*	*Tukey p*	SS	MS	F	*p*	*Tukey p*	
D	1	10272.2	10272.2	47.9	**< 0.001**	H1-L3 0.007	36630	36630	2.07	0.175	H3:L3 0.0357	3.91	3.91	48.57	**< 0.001**	H1-L1 0.0038	L3:H1 0.0028
S(D)	2	84.1	42.1	0.2	0.8242	H2-L2 0.0218	79295	39648	2.24	0.1480		4.98	2.49	30.93	**< 0.001**	H1:H2 0.0042	L2:L1 0.0005
D*S	2	2087.4	1043.7	4.8	**0.0282**	H2-L3 0.016	2000249	100124	5.68	**0.0183**		1.24	0.62	7.69	**0.0071**	H1:L2 <0.0001	L2:H2 0.0004
Residuals	12	2569.3	214.1			H3-L1 0.028	211521	17627				0.96	0.08			H1:H3 0.0132	H3:L2 0.0001
						H3-L2 0.0053											L3-L2 0.0006
						H3-L3 0.004											

		Morphology				Branching			
	df	SS	MS	Pseudo-F	*p*	SS	MS	Pseudo-F	*p*
D	1	0.24	0.24	3.12	**0.05**	0.02	0.02	1.32	0.33
S(D)	1	0.13	0.13	1.76	0.10	0.06	0.06	5.11	**0.05**
D*S	1	0.15	0.15	1.89	0.15	0.07	0.07	5.17	**0.04**
Residuals	14	1.11	0.08			0.18	0.01		
Total	17	1.64				0.32			

Appendix A3. ANOVA results (and significant post-hoc) evaluating variability within taxonomic differences in macrofaunal assemblages (density, H', J') between RB density D (high and low) and habitats H (rhodolith and unconsolidated sediments). Note: significant results ($p \leq 0.05$) are in bold.

		Density					H'				
	df	SS	MS	F	*p*	*Tukey p*	SS	MS	F	*p*	*Tukey p*
D	1	$21x10^4$	$21x10^4$	0.27	0.601	Rhodolith Low-Sediment Low < 0.0001	0.81	0.81	2.98	0.0937	Rhodolith Low-Rhodolith High 0.0017
H	1	$51x10^6$	$51x10^6$	66.18	**< 0.0001**	Rhodolith High-Sediment High < 0.0001	6.18	6.18	22.81	**< 0.0001**	Rhodolith High-Sediment High < 0.0001
D*H	1	$53x10^4$	$53x10^4$	0.69	0.410	Rhodolith High-Sediment Low < 0.0001	4.25	4.25	15.71	**0.0003**	Rhodolith High-Sediment Low 0.0003
Residuals	32	$24x10^6$	$76x10^4$			Rhodolith Low-Sediment High < 0.0001	8.67	0.27			

		J'					Assemblage composition				
	df	SS	MS	Pseudo-F	*p*	*Tukey p*	df	SS	MS	Pseudo-F	*p*
D	1	0.03	0.03	4.98	**0.0326**	Rhodolith Low-Rhodolith High 0.0009	1	0.59	0.59	3.41	**0.02**
H	1	0.16	0.16	22.82	**< 0.0001**	Rhodolith Low-Sediment High 0.0001	1	3.51	3.51	20.01	**0.01**
D*H	1	0.10	0.10	14.10	**0.0007**	Rhodolith Low-Sediment Low < 0.0001	1	0.46	0.46	2.63	0.06
Residuals	32	0.23	0.01				32	5.61	0.17		
Total							35	10.18			

Appendix A4. ANOVA results (and significant post-hoc) evaluating variability within functional differences in macrofaunal assemblages (richness FRic, dispersion FDis, evenness FEve, and entropy FRaoQ) between RB density (high and low) and habitats (rhodolith and unconsolidated sediments). Note: significant results ($p \leq 0.05$) are in bold.

		FRic					FEve				
	df	SS	MS	F	*p*	*Tukey p*	SS	MS	F	*p*	*Tukey p*
D	1	0.44	0.44	0.33	0.568	Rhodolith High-Sediment High 0.0002	0.004	0.004	0.69	0.4114	Rhodolith High-Sediment High < 0.0001
H	1	36.00	36.00	27.00	**< 0.0001**	Rhodolith High-Sediment Low 0.0015	0.47	0.47	75.39	**< 0.0001**	Rhodolith High-Sediment Low < 0.0001
D*H	1	2.78	2.78	2.08	0.159	Rhodolith Low-Sediment High 0.0012	0.03	0.03	5.26	**0.0284**	Rhodolith Low-Sediment High < 0.0001
Residuals	32	42.67	1.33				0.20	0.006			Rhodolith Low-Sediment Low 0.0004
		FDis					FRaoQ				
	df	SS	MS	F	*p*	*Tukey p*	SS	MS	F	*p*	*Tukey p*
D	1	0.003	0.003	1.88	0.1789	Rhodolith Low-Rhodolith High 0.0061	0.0002	0.0002	1.21	0.2793	Rhodolith Low-Rhodolith High 0.0091
H	1	0.01	0.01	9.61	**0.004**	Rhodolith Low-Sediment High 0.0170	0.001	0.001	6.56	**0.0152**	Rhodolith Low-Sediment Low 0.0005
D*H	1	0.02	0.02	13.40	**0.0008**	Rhodolith Low-Sediment Low 0.0002	0.002	0.002	13.85	**0.0007**	
Residuals	32	0.05	0.001				0.006	0.0002			

Appendix A5. Results of canonical analyses of principal coordinates (CAP) to evaluate the contribution of rhodolith morphological parameters (density, volume, diameter) and morphology (Compact, Compact-Platy, Compact-Elongate, Platy, Bladed, Elongate, Very platy, Very bladed, and Very elongate), and branching (number of spikes 1 to 4) to variations in the benthic assemblage composition (abundance per taxa) in the study area (H1, H2, H3, L1, L2 and L3). Spearman correlation values for each environmental variable are described for in CAP axis 1-2. Note: proportion of variability explained by CAP axes are between parentesis '()', F for statistic, significant results ($p \leq 0.05$) are in bold.

	F = 1.85, p = 0.143			
	CAP 1 (43%)	CAP 2 (13%)	F	p
Density	-0.76	-0.15	7.97	**0.002**
Volume	-0.55	0.36	2.22	0.127
Diameter	0.20	0.36	1.53	0.264
Compact	-0.34	-0.18	1.84	0.188
Compact-Platy	0.15	0.45	1.45	0.273
Compact-Elongate	0.22	0.29	0.89	0.577
Platy	-0.42	0.28	2.21	0.136
Bladed	0.32	-0.08	1.34	0.338
Elongate	0.35	-0.38	1.73	0.221
Very platy	0.43	-0.47	1.50	0.273
Very bladed	-0.54	-0.06	1.37	0.293
Very elongate	-0.30	-0.17	0.61	0.787
Number of spikes				
1	-0.47	-0.26	1.44	0.312
2	-0.32	-0.34	1.41	0.299
3	-0.29	-0.28	0.85	0.592

4	0.39	0.33	1.30	0.331

Appendix A6. Results of canonical analyses of principal coordinates (CAP) to evaluate the contribution of sediment composition (organic matter, carbonate, gravel, sand, silt, proteins, lipids, chlorophyll-a) and rhodolith morphological parameters (density, volume, diameter) to variations in the benthic assemblage composition (abundance per taxa) in the study area (H1, H2, H3, L1, L2 and L3). Spearman correlation values for each environmental variable are described for in CAP axis 1-2. Note: proportion of variability explained by CAP axes are between parenthesis '()', F for statistic, significant results ($p \leq 0.05$) are in bold.

	F = 1.33, p = 0.206			
	CAP 1 (29%)	CAP 2 (18%)	F	p
Organic matter	0.36	0.10	1.13	0.355
Carbonate	-0.09	-0.002	2.00	**0.051**
Gravel	-0.19	0.22	0.93	0.512
Sand	0.19	-0.23	0.99	0.445
Silt	-0.13	0.19	1.25	0.276
Proteins	-0.68	0.12	1.61	0.124
Lipids	-0.002	-0.13	1.51	0.185
Chlorophyll-a	-0.15	0.53	1.49	0.151
Density	-0.78	0.06	1.38	0.226
Volume	0.22	0.01	1.19	0.326
Diameter	0.77	0.13	1.20	0.339

APPENDIX A7. List of taxa and mean benthic macrofauna total abundance in RBs and unconsolidated sediment (±SE) through the sampled stations.

Taxonomic group and Taxa	Rhodolith beds						Unconsolidated sediment					
	H1	H2	H3	L1	L2	L3	H1	H2	H3	L1	L2	L3
Annelida												
N id sp1	10.0 (± 2.0)	8.3 (± 5.1)	30.0 (± 9.5)	4.7 (± 4.2)	4.0 (± 2.0)	1.7 (± 0.6)	–	–	–	–	–	–
N id sp2	0.7 (± 1.1)	–	–	–	–	–	–	–	–	–	–	–
N id sp3	3.3 (± 0.6)	4.3 (± 1.5)	2.0 (± 1.0)	2.0 (± 2.6)	0.3 (± 0.6)	–	–	–	–	–	–	–
N id sp4	1.3 (± 1.2)	1.0 ± (1.0)	–	–	–	–	–	–	–	–	–	–
N id sp6	0.3 (± 0.6)	–	–	–	1.3 (± 2.3)	0.7 (± 0.6)	–	–	–	–	–	–
N id sp7	10.0 (± 9.2)	0.3 (± 0.6)	0.3 (± 0.6)	1.7 (± 2.1)	1.3 (± 2.3)	–	–	–	–	–	–	–
Syllidae	130.7 (± 21.0)	148.3 (± 97.4)	160.0 (± 31.6)	80.7 (± 42.1)	104.0 (± 88.0)	24.3 (± 9.7)	0.3 (± 0.6)	4.7 (± 4.7)	1.7 (± 1.5)	1.3 (± 0.6)	–	12.0 (± 8.5)
Nereididae	21.7 (± 15.0)	33.0 (± 9.5)	16.7 (± 10.3)	11.3 (± 12.9)	18.3 (± 7.1)	0.3 (± 0.6)	–	1.0 (± 1.7)	–	0.3 (± 0.6)	0.3 (± 0.6)	3.7 (± 1.5)
Oweniidae	–	0.3 (± 0.6)	–	–	0.3 (± 0.6)	1.0 (± 1.0)	–	–	–	0.3 (± 0.6)	–	2.3 (± 3.2)

Cirratulidae	–	1.3 (± 0.6)	1.0 (± 1.0)	1.3 (± 1.5)	2.3 (± 1.5)	0.3 (± 0.6)	0.3 (± 0.6)	–	–	–	–	2.3 (± 2.5)
Orbinidae	–	0.7 (± 0.6)	–	–	2.3 (± 2.1)	–	0.3 (± 0.6)	–	0.3 (± 0.6)	–	–	0.7 (± 1.2)
Flabelligeridae	0.3 (± 0.6)	0.7 (± 0.6)	0.3 (± 0.6)	–	1.3 (± 2.3)	–	–	0.3 (± 0.6)	–	–	–	–
Nephytidae	–	0.7 (± 0.6)	–	0.3 (± 0.6)	0.3 (± 0.6)	–	–	–	–	–	–	–
Mangelonidae	0.3 (± 0.6)	0.3 (± 0.6)	–	–	0.7 (± 1.2)	–	–	–	–	–	–	–
Capitellidae	1.7 (± 2.9)	2.3 (± 0.6)	1.7 (± 1.2)	0.3 (± 0.6)	1.7 (± 1.5)	0.7 (± 0.6)	–	–	–	0.3 (± 0.6)	0.3 (± 0.6)	3.0 (± 4.4)
Paraonidae	1.7 (± 2.1)	6.0 (± 1.0)	4.0 (± 2.0)	0.7 (± 1.2)	9.3 (± 6.5)	3.7 (± 1.2)	–	–	–	–	–	–
Onuphidae	0.3 (± 0.6)	3.0 (± 3.6)	4.7 (± 4.5)	13.0 (± 3.6)	0.7 (± 1.2)	–	–	–	–	–	–	–
Iospilidae	0.3 (± 0.6)	–	–	–	–	0.3 (± 0.6)	–	–	0.3 (± 0.6)	–	–	–
Dorvilleidae	4.7 (± 3.2)	3.0 (± 2.0)	1.3 (± 0.6)	–	2.0 (± 1.0)	0.7 (± 0.6)	–	–	0.3 (± 0.6)	–	–	0.3 (± 0.6)
Ampharetidae	0.3 (± 0.6)	–	0.3 (± 0.6)	–	0.3 (± 0.6)	–	–	–	–	–	–	–
Sternaspidae	0.7 (± 0.6)	0.7 (± 1.2)	–	–	0.3 (± 0.6)	–	–	–	–	–	–	–

Aphroditidae	0.7 (± 0.6)	0.7 (± 0.6)	0.3 (± 0.6)	1.3 (± 1.2)	0.7 (± 0.6)	–	–	–	–	–	–	–
Hesionidae	2.3 (± 1.2)	1.3 (± 2.3)	0.3 (± 0.6)	0.3 (± 0.6)	1.0 (± 1.7)	–	–	–	–	–	–	–
Maldane sp	0.7 (± 0.6)	0.7 (± 0.6)	0.7 (± 1.2)	0.7 (± 1.2)	–	–	–	–	–	–	–	–
Lysidice sp	18.3 (± 6.4)	19.0 (± 6.2)	15.3 (± 2.1)	28.0 (± 6.1)	13.3 (± 9.7)	1.3 (± 1.5)	–	–	–	–	–	–
Eunice sp	3.3 (± 3.1)	3.7 (± 1.2)	5.0 (± 4.6)	4.0 (± 3.0)	4.0 (± 1.0)	0.7 (± 0.6)	–	0.3 (± 0.6)	–	–	–	0.7 (± 0.6)
Palolo sp	0.7 (± 0.6)	0.3 (± 0.6)	0.3 (± 0.6)	2.0 (± 1.0)	5.3 (± 6.7)	0.3 (± 0.6)	–	–	–	–	–	–
Marphysa sp	0.3 (± 0.6)	0.7 (± 1.2)	0.7 (± 1.2)	–	–	–	–	–	–	–	–	–
Megalomma sp	13.3 (± 5.7)	7.0 (± 3.0)	26.3 (± 17.4)	12.0 (± 12.2)	8.3 (± 6.7)	0.7 (± 0.6)	–	–	–	–	–	–
Hydroides sp	0.7 (± 1.2)	1.3 (± 1.2)	1.0 (± 1.7)	1.0 (± 1.0)	–	–	–	–	–	–	–	–
Pseudovermilia sp	21.3 (± 9.3)	12.3 (± 2.1)	13.0 (± 13.5)	5.7 (± 3.1)	3.0 (± 1.7)	1.7 (± 1.2)	–	–	0.3 (± 0.6)	–	–	1.0 (± 1.0)
Vermiliopsis sp	3.0 (± 2.6)	3.0 (± 1.0)	3.0 (± 3.0)	0.7 (± 0.6)	0.3 (± 0.6)	0.3 (± 0.6)	–	–	–	–	–	–
Anaitides sp	5,3 (± 1.5)	4.0 (± 2.0)	6.0 (± 2.0)	3.3 (± 4.9)	1.7 (± 0.6)	–	–	–	–	–	–	–

Phyllodoce sp1	9.3 (± 6.4)	4.3 (± 4.0)	5.3 (± 2.9)	1.7 (± 1.5)	3.3 (± 0.6)	–	–	–	–	–	–	1.7 (± 1.2)
Phyllodoce sp2	1.7 (± 1.2)	1.7 (± 1.5)	–	0.7 (± 1.2)	1.0 (± 1.0)	–	–	–	–	–	–	–
Pectinaria sp	–	–	0.3 (± 0.6)	–	0.3 (± 0.6)	0.3 (± 0.6)	–	–	–	–	–	–
Arabella sp	1.3 (± 1.2)	3.7 (± 4.7)	–	–	1.0 (± 1.0)	1.3 (± 1.2)	–	–	–	–	–	0.3 (± 0.6)
Oenone sp	0.3 (± 0.6)	0.7 (± 1.2)	–	–	0.7 (± 1.2)	–	–	–	–	–	–	–
Lumbrineris sp	2.0 (± 2.6)	4.0 (± 1.0)	4.3 (±2.9)	2.0 (± 2.6)	1.0 (± 1.0)	–	–	0,0	0.3 (± 0.6)	–	–	0.3 (± 0.6)
Notopygos sp	5.3 (± 3.2)	16.0 (± 10.0)	3.0 (± 2.0)	2.0 (± 1.0)	1.3 (± 2.3)	0.3 (± 0.6)	–	0.3 (± 0.6)	–	–	–	0.3 (± 0.6)
Glycinde multidens	–	–	0.3 (± 0.6)	–	–	–	–	–	–	–	–	–
Glycera lapidum	0.3 (± 0.6)	2.7 (± 3.8)	–	–	–	–	–	–	–	–	–	–
Goniadides sp	2.0 (± 2.6)	2.0 (± 1.0)	1.7 (± 2.1)	0.6 (± 0.6)	1.0 (± 1.0)	–	–	–	–	–	–	4.7 (± 4.5)
Hemipodia californiensis	–	0.3 (± 0.6)	–	0.7 (± 1.2)	–	–	–	–	–	–	–	–
Glycera sp	–	2.7 (± 1.5)	0.7 (± 1.2)	–	0.3 (± 0.6)	–	–	0.3 (± 0.6)	0.3 (± 0.6)	0.7 (± 0.6)	0.3 (± 0.6)	0.3 (± 0.6)

Hemipodia sp	0.3 (± 0.6)	0.7 (± 1.2)	–	–	–	–	–	–	–	–	–	–
Harmothoe sp	7.7 (± 5.0)	14.0 (± 1.0)	11.0 (± 6.2)	11.0 (± 7.9)	16.3 (± 6.5)	–	–	–	0.3 (± 0.6)	–	0.3 (± 0.6)	0.7 (± 1.2)
Lepidonotus sp	2.0 (± 1.0)	3.0 (± 2.6)	2.0 (± 2.6)	1.0 (± 1.7)	1.7 (± 0.6)	–	–	–	–	–	–	–
Polynoidae sp4	10.7 (± 12.4)	26.0 (± 7.2)	8.3 (± 4.5)	1.0 (± 1.0)	1.0 (± 1.7)	–	–	1.3 (± 1.5)	–	–	–	1.3 (± 1.2)
Polynoidae sp5	24.0 (± 4.0)	11.3 (± 4.7)	15.3 (± 8.1)	7.3 (± 10.1)	9.7 (± 8.4)	0.3 (± 0.6)	–	–	–	0.3 (± 0.6)	0.3 (± 0.6)	2.3 (± 2.1)
Polynoidae sp7	0.3 (± 0.6)	–	–	0.7 (± 1.2)	1.7 (± 1.5)	–	–	–	–	–	–	–
Minuspio sp	0.7 (± 0.6)	1.0 (± 0.0)	–	–	2.0 (± 2.6)	0.3 (± 0.6)	–	–	–	–	–	4.0 (± 5.3)
Terebellides sp	4.3 (± 3.1)	1.0 (± 1.0)	2.3 (± 0.6)	0.7 (± 1.2)	3.7 (± 2.3)	–	–	–	–	–	–	–
Pholoe sp	1.3 (± 1.5)	2.3 (± 3.2)	1.0 (± 0.0)	2.7 (± 2.9)	2.3 (± 0.6)	–	–	–	–	–	–	–
Polydora sp	1.0 (± 1.0)	0.7 (± 1.2)	0.3 (± 0.6)	2.7 (± 4.6)	0.3 (± 0.6)	–	–	–	–	–	–	–
Prionospio sp	1.3 (± 2.3)	–	0.3 (± 0.6)	–	1.3 (± 1.5)	–	–	–	–	–	–	–

Longosomatidae sp	–	–	0.7 (± 1.2)	–	–	–	–	–	–	–	–	–
Eurythoe sp	–	0.3 (± 0.6)	–	–	–	–	–	–	–	–	–	–
Oligochaeta	1.3 (± 2.3)	–	0.7 (± 1.2)	–	2.0 (± 3.5)	–	–	–	–	–	–	–
Crustacea Mithracidae	1.0 (± 1.0)	–	0.3 (± 0.6)	0.3 (± 0.6)	1.3 (± 0.6)	–	–	–	–	–	–	–
Xanthidae sp1	–	0.3 (± 0.6)	1.0 (± 0.0)	0.3 (± 0.6)	1.0 (± 0.0)	–	–	–	–	–	–	–
Teleophrys sp	0.7 (± 0.6)	–	0.7 (± 1.2)	0.3 (± 0.6)	2.3 (± 2.1)	–	–	–	–	–	–	–
Brachiura n id	0.3 (± 0.6)	–	–	–	0.7 (± 0.6)	–	–	–	–	–	–	0.3 (± 0.6)
Pilumnidae	1.3 (±1.5)	0.3 (± 0.6)	0.7 (± 0.6)	0.3 (± 0.6)	2.0 (± 1.7)	–	–	–	–	–	–	–
Stenorhynchus sp	–	0.3 (± 0.6)	–	–	1.0 (± 1.7)	–	–	–	–	–	–	–
Xanthidae sp2	0.3 (± 0.6)	0.3 (± 0.6)	0.3 (± 0.6)	0.7 (± 0.6)	1.3 (± 0.6)	–	–	–	–	–	–	–
Ocypodidae	–	–	–	–	–	–	–	0.3 (± 0.6)	–	–	–	–
Epialtus sp	–	–	–	–	0.3 (± 0.6)	–	–	–	–	–	0.3 (± 0.6)	0.3 (± 0.6)

Ebalia sp	–	–	–	0.3 (± 0.6)	–	–	–	–	–	–	–	–
Porcellanidae	–	–	0.7 (± 0.6)	–	–	–	–	–	–	–	–	–
Paractaea sp	–	–	0,0	0.3 (± 0.6)	–	–	–	–	–	–	–	–
Paguropsina sp	–	–	1.3 (± 2.3)	–	0.7 (± 1.2)	–	–	–	–	–	–	–
Coenobitidae sp	–	–	0.3 (± 0.6)	–	–	–	–	–	–	–	0.3 (± 0.6)	–
Aniculus sp	0.3 (± 0.6)	3.0 (± 2.0)	3.7 (± 2.5)	2.3 (± 1.5)	9.7 (± 7.5)	–	–	–	–	0.3 (± 0.6)	–	–
Caridea	2.7 (± 1.5)	5.0 (± 6.9)	7.0 (± 4.6)	3.7 (± 0.6)	14.7 (± 2.9)	–	–	0.3 (± 0.6)	–	–	–	4.7 (± 6.4)
Mysidae sp1	2.0 (± 1.7)	–	1.3 (± 1.2)	2.0 (± 3.5)	3.3 (± 5.8)	–	–	–	–	–	–	–
Mysidae sp2	2.0 (± 1.7)	0.3 (± 0.6)	1.7 (± 1.2)	0.3 (± 0.6)	2.0 (± 1.7)	–	–	–	–	–	–	–
Decapoda n id	0.3 (± 0.6)	–	–	–	–	–	–	–	–	–	–	–
Aristiidae	4.0 (± 3.6)	4.7 (± 4.0)	3.0 (± 3.0)	1.3 (± 1.5)	8.3 (± 4.7)	–	–	–	–	–	0.3 (± 0.6)	1.7 (± 2.1)

Caprellidae	0.7 (± 1.2)	0.3 (± 0.6)	2.3 (± 2.1)	0.7 (± 0.6)	3.7 (± 4.0)	–	–	–	–	–	0.7 (± 1.2)	–
Dexamine spinosa	2.0 (± 2.6)	0.7 (± 1.2)	1.0 (± 1.0)	–	0.3 (± 0.6)	–	–	–	–	–	–	–
Gammaridae	65.7 (± 13.7)	102.6 (± 95.1)	141.3 (± 34.1)	452.7 (± 273.1)	310.3 (± 214.3)	111.3 (± 54.7)	–	1.7 (± 2.9)	2.3 (± 3.2)	0.3 (± 0.6)	1.0 (± 1.7)	3.0 (± 3.6)
Melitidae	7.0 (± 5.6)	8.7 (± 8.1)	9.7 (± 3.2)	24.7 (± 8.4)	22.7 (± 19.6)	12.7 (± 18.5)	–	1.7 (± 1.5)	–	–	11.3 (± 19.6)	–
Amphilochidae	8.3 (± 3.1)	5.7 (± 3.2)	3.0 (± 5.2)	4.0 (± 6.1)	5.7 (± 8.1)	0.3 (± 0.6)	–	–	–	–	–	–
Elasmopus sp	1.7 (± 2.1)	6.0 (± 2.0)	11.3 (± 6.4)	21.3 (± 16.4)	4.3 (± 4.9)	4.0 (± 4.6)	0.7 (± 1.2)	1.0 (± 1.7)	0.3 (± 0.6)	0.3 (± 0.6)	–	1.7 (± 2.1)
Leptochelia sp	16.7 (± 2.5)	10.0 (± 5.0)	15.3 (± 12.1)	11.0 (± 6.6)	8.0 (± 5.6)	0.3 (± 0.6)	–	0.3 (± 0.6)	1.3 (± 2.3)	1.7 (± 2.1)	0.7 (± 1.2)	4.7 (± 1.2)
Tanaidæ	8.0 (± 5.6)	10.7 (± 3.5)	11.7 (± 8.6)	9.0 (± 13.0)	3.7 (± 2.1)	0.3 (± 0.6)	0.3 (± 0.6)	3.3 (± 5.8)	0.3 (± 0.6)	0.3 (± 0.6)	–	4.3 (± 2.1)
Anthuridae	9.7 (± 7.4)	19.3 (± 8.1)	12.7 (± 3.2)	9.0 (± 3.6)	–	2.0 (± 1.0)	–	–	–	–	0.3 (± 0.6)	3.3 (± 4.9)
Janiridae	11.7 (± 10.8)	17.0 (±7.0)	11.3 (± 4.5)	6.3 (± 2.1)	11.7 (± 10.7)	0.3 (± 0.6)	–	0.7 (± 1.2)	0.3 (± 0.6)	0.7 (± 1.2)	–	2.3 (± 1.2)
Cirolanidae	2.3 (± 2.3)	3.7 (± 3.8)	1.0 (± 1.0)	–	3.0 (± 1.7)	0.3 (± 0.6)	–	0.3 (± 0.6)	–	0.3 (± 0.6)	–	1.0 (± 1.0)
Gnathiidae sp1	3.3 (± 0.6)	0.7 (± 0.6)	0.7 (± 0.6)	–	2.3 (± 2.3)	–	0.3 (± 0.6)	–	–	–	0.3 (± 0.6)	0.3 (± 0.6)

Gnathiidae sp2	1.3 (± 0.6)	–	–	–	–	–	–	–	–	–	–	–
Apseudidae	15.7 (± 8.1)	9.0 (± 8.5)	4.7 (± 6.4)	0.7 (± 1.2)	5.0 (± 4.4)	–	–	–	–	–	–	–
Oniscus sp	–	–	0.3 (± 0.6)	–	–	–	–	–	–	–	–	–
Ostracoda	11.7 (± 7.0)	2.7 (± 1.2)	1.7 (± 1.2)	0.3 (± 0.6)	–	–	13.3 (± 8.5)	12.0 (± 1.0)	13.0 (± 4.4)	6.3 (± 6.5)	1.7 (± 2.1)	26.3 (± 4.9)
Cumacea	2.3 (± 1.5)	3.0 (± 1.0)	2.0 (± 1.7)	3.7 (± 4.7)	5.0 (± 4.4)	0.7 (± 0.6)	0.3 (± 0.6)	1.7 (± 1.5)	–	0.3 (± 0.6)	0.7 (± 0.6)	2.3 (± 1.5)
Valvifera	–	0.3 (0.6)	–	–	1.7 (± 1.2)	0.7 (± 0.6)	–	–	–	0.3 (± 0.6)	–	1.0 (± 1.7)
Isochnochiton sp	7.0 (± 1.7)	14.3 (± 4.5)	15.7 (± 7.6)	2.7 (± 3.8)	2.3 (± 1.5)	0.3 (± 0.6)	–	–	0.3 (± 0.6)	–	–	0.3 (± 0.6)
Mollusca - Gastropoda Nudibranchia	1.3 (± 1.5)	–	1.0 (± 1.7)	0.3 (± 0.6)	1.0 (± 1.0)	–	–	–	–	–	–	–
Mollusca n id	9.0 (± 10.4)	13.0 (± 4.0)	9.0 (± 13.9)	5.3 (± 0.6)	1.0 (± 1.0)	2.7 (± 4.6)	–	–	–	–	–	–
Rissoidae	–	–	–	0.3 (± 0.6)	–	–	1.3 (± 1.5)	1.3 (± 1.5)	–	–	–	–
Pyramidellidae	–	0.3 (± 0.6)	–	–	–	–	–	–	–	–	–	–

Turridae	–	–	–	–	1.0 (± 1.0)	–	–	–	–	–	–	–
Hydrobiidae	–	0,7 (± 0.6)	–	–	0.3 (± 0.6)	–	–	0.3 (± 0.6)	0.3 (± 0.6)	–	0.3 (± 0.6)	–
Marginellidae	–	–	–	–	–	–	–	–	0.3 (± 0.6)	–	–	–
Lepetidae	–	–	–	0.3 (± 0.6)	–	–	–	–	–	–	–	–
Lottiidae	–	–	0.3 (± 0.6)	–	0.3 (± 0.6)	–	–	–	–	–	–	–
Phasianellidae	–	–	–	–	0.3 (± 0.6)	–	–	–	–	–	–	–
Eulimidae	0.3 (± 0.6)	–	–	0.3 (± 0.6)	0.3 (± 0.6)	–	0.3 (± 0.6)	–	–	0.3 (± 0.6)	0.7 (± 0.6)	–
Costellariidae	0.3 (± 0.6)	0.3 (± 0.6)	0.3 (± 0.6)	–	0.7 (± 1.2)	–	–	–	–	–	–	–
Architectonicidae	–	–	–	–	0.3 (± 0.6)	–	–	–	–	–	–	–
Trochidae	0.3 (± 0.6)	0.3 (± 0.6)	0.3 (± 0.6)	–	0.3 (± 0.6)	–	–	–	–	–	–	–
Meioceras sp	1.0 (± 0.0)	1.0 (± 1.7)	–	–	1.0 (± 1.7)	–	2.3 (± 1.5)	1.7 (± 1.5)	0.3 (± 0.6)	1.0 (± 1.7)	0.3 (± 0.6)	1.7 (± 2.9)
Gastropoda n id	–	–	0.7 (± 0.6)	–	–	–	–	–	0.3 (± 0.6)	0.3 (± 0.6)	0.3 (± 0.6)	–

Capulidae	1.7 (± 0.6)	0.7 (± 1.2)	0.7 (± 0.6)	0.3 (± 0.6)	0.3 (± 0.6)	–	–	0.3 (± 0.6)	–	–	–	–
Coralliophilidae	0.3 (± 0.6)	–	–	–	–	–	–	–	–	–	–	–
Naticidae	1.7 (± 2.9)	0.3 (± 0.6)	0.3 (± 0.6)	–	–	–	–	–	–	–	0.3 (± 0.6)	0.3 (± 0.6)
Nassariidae	–	–	–	–	–	–	–	–	1.0 (± 1.7)	1.0 (± 1.7)	–	–
Planaxidae	1.0 (± 1.7)	0.7 (± 0.6)	0.3 (± 0.6)	–	0.7 (± 1.2)	–	0.3 (± 0.6)	–	0.3 (± 0.6)	1.0 (± 1.7)	–	–
Cerithiopsidae	2.3 (± 3.2)	1.0 (± 1.7)	0.3 (± 0.6)	0.3 (± 0.6)	1.3 (± 2.3)	–	0.3 (± 0.6)	–	0.3 (± 0.6)	–	0.7 (± 0.6)	–
Gastropoda	–	–	0.3 (± 0.6)	–	–	–	–	–	–	–	–	–
Mollusca - Bivalvia												
Pectinidae	1.3 (± 1.2)	2.0 (± 1.0)	–	–	2.0 (± 1.0)	–	–	–	–	–	–	–
Veneridae	9.7 (± 3.1)	5.7 (± 4.2)	2.7 (± 3.1)	0.7 (± 1.2)	2.0 (± 1.7)	0.3 (± 0.6)	1.0 (± 1.7)	1.0 (± 1.0)	0.7 (± 1.2)	0.3 (± 0.6)	0.7 (± 1.2)	1.0 (± 0.0)
Crassatellidae	1.7 (± 2.9)	1.3 (± 1.5)	1.0 (± 1.0)	0.3 (± 0.6)	0.3 (± 0.6)	–	0.7 (± 0.6)	0.7 (± 1.2)	–	–	0.7 (± 0.6)	0.3 (± 0.6)
Tellinidae	3.3 (± 2.9)	6.3 (± 1.5)	7.3 (± 1.2)	2.7 (± 3.8)	2.7 (± 1.5)	1.7 (± 0.6)	–	0.3 (± 0.6)	–	–	–	–
Mesodesma	1.0 (± 1.0)	1.7 (± 0.6)	0.3 (± 0.6)	0.3 (± 0.6)	1.0 (± 1.0)	–	–	–	–	–	–	–

Cardiidae	5.7 (± 7.2)	2.7 (± 2.1)	0.3 (± 0.6)	0.3 (± 0.6)	3.3 (± 2.1)	0.3 (± 0.6)	2.7 (± 2.3)	0.3 (± 0.6)	1.3 (± 1.2)	–	–	1.3 (± 2.3)
Mytilidae	–	0.7 (± 0.6)	0.3 (± 0.6)	–	0.3 (± 0.6)	0.3 (± 0.6)	–	–	–	–	–	–
Bivalva n id	0.7 (± 0.6)	1.3 (± 2.3)	0.3 (± 0.6)	–	–	–	–	–	–	–	–	–
Isognomon	–	0.7 (± 0.6)	–	1.7 (± 1.5)	–	–	–	–	–	–	–	–
Thraciidae	–	0.7 (± 0.6)	–	–	–	0.3 (± 0.6)	–	–	–	–	–	–
Lucinidae	–	0.3 (± 0.6)	0.7 (± 1.2)	0.3 (± 0.6)	1.0 (± 1.0)	0.7 (± 1.2)	–	–	–	–	0.3 (± 0.6)	1.3 (± 2.3)
Chamidae	–	–	0.3 (± 0.6)	0.3 (± 0.6)	0.3 (± 0.6)	–	–	–	–	–	–	–
Arcidae	0.3 (± 0.6)	–	1.0 (± 0.0)	1.3 (± 1.5)	1.0 (± 0.0)	–	0.3 (± 0.6)	–	–	–	–	–
Echinodermata Holothuroidea	1.3 (± 2.3)	0.3 (± 0.6)	0.3 (± 0.6)	–	1.0 (± 1.0)	0.7 (± 0.6)	–	–	–	–	0.3 (± 0.6)	1.0 (± 1.0)
Psolidae	7.7 (± 6.5)	7.0 (± 6.9)	3.0 (± 2.0)	–	1.3 (± 1.5)	0.3 (± 0.6)	–	–	–	–	–	–
Dendrochirotida	–	0.7 (± 1.2)	0.3 (± 0.6)	0.3 (± 0.6)	1.0 (± 0.0)	–	–	–	–	–	–	–
Amphiuridae	3.0 (± 1.0)	14.0 (± 8.7)	12.0 (± 7.9)	22.0 (± 10.4)	15.3 (± 1.5)	5.7 (± 2.9)	–	–	0.7 (± 1.2)	–	4.0 (± 0.0)	2.7 (± 4.6)

Amphipolis sp	0.3 (± 0.6)	1.0 (± 1.7)	–	1.7 (± 2.9)	0.7 (± 1.2)	–	–	–	–	–	–	–
Ophioderma sp	–	0.3 (± 0.6)	–	–	–	–	–	–	–	–	–	–
Ophiothrix sp	1.0 (± 1.0)	3.0 (± 2.6)	4.7 (± 3.8)	1.7 (± 1.5)	3.3 (± 4.2)	–	0.3 (± 0.6)	–	–	–	–	–
Ophionereididae	0.7 (± 1.2)	1.0 (± 1.0)	0.3 (± 0.6)	1.0 (± 1.0)	0.7 (± 1.2)	–	–	–	–	–	–	–
Asteroidae	–	0.3 (± 0.6)	–	–	0.3 (± 0.6)	–	–	–	–	–	–	–
Crinoidae	–	–	–	–	1.0 (± 0.0)	–	–	–	–	–	–	–
Echinoidea sp1	0.3 (± 0.6)	0.7 (± 1.2)	0.3 (± 0.6)	0.7 (± 0.6)	–	–	–	–	–	–	–	–
Echinoidea sp2	–	–	–	–	–	–	–	–	0.3 (± 0.6)	–	–	–
Other												
Nemertea	1.0 (± 0.0)	1.7 (± 0.6)	1.0 (± 1.7)	–	2.3 (± 1.2)	0.3 (± 0.6)	–	–	–	–	–	–
Sipuncula	27.3 (± 14.0)	58.3 (± 14.2)	38.3 (± 7.0)	13.3 (± 6.5)	5.7 (± 3.1)	1.7 (± 2.1)	–	–	–	–	–	2.7 (± 0.6)
Echiura	0.3 (± 0.6)	–	1.7 (± 2.9)	–	1.3 (± 1.2)	–	–	–	–	–	–	–
Nematoda	2.7 (± 2.5)	–	2.7 (± 4.6)	–	5.0 (± 8.7)	–	–	–	–	–	–	–

Platyhelminthes	–	–	–	–	0.3 (± 0.6)	–	–	–	–	–	–	–